Effects of winter storms and oceanographic conditions on survival to weaning: a 37 year study of northern elephant seals on the Farallon Islands

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ABSTRACT: Northern elephant seals *Mirounga angustirostris* were extirpated from California in the 19th century, and only in recent decades have they recolonized. A key demographic parameter underlying population viability is the survival of pups, from birth to weaning. We evaluated local factors acting directly on pup survival prior to weaning and basin-wide factors reflecting oceanic conditions which may impact maternal condition and behavior, using a 37 yr time series from 2 adjacent islands off central California: Southeast Farallon Island (SEFI) and West End Island (WEI). Mixed-effects logistic regression indicated that annual pup survival decreased with increasing frequency of extreme waves during January and February, which may inundate haulout locations when pups are present, and increased with the North Pacific Gyre Oscillation (NPGO) index, reflecting increased primary productivity. Moreover, the impact of extreme waves was manifest only for WEI, which may reflect a greater risk of inundation compared to SEFI. Annual pup survival was most highly correlated with NPGO values during the 6 mo period preceding and including arrival and the pupping period (fall and winter). Our findings suggest that favorable foraging conditions for females during the 4 mo prior to hauling out led to better maternal condition, which improved pup survival. Impacts of storm surges on pup survival is of concern since the frequency and severity of storms is expected to increase in the future. To support population recovery, we recommend studies consider demographic parameters such as recruitment of females to the Farallon breeding population and to adjacent coastal California colonies.

KEY WORDS: Pup survival · Northern elephant seal · Winter storms · Climate change · NPGO · Maternal condition · Tide height · *Mirounga angustirostris* · Mixed-effects logistic regression

1. INTRODUCTION

Northern elephant seals *Mirounga angustirostris* were hunted to near-extinction in the late 1800s, but with the end of commercial sealing and the provision of legal protection, numbers have rebounded strongly (Stewart et al. 1994, Hoelzel et al. 2002). The Farallon Islands were subsequently recolonized, with the first pup being born in 1972 (Le Boeuf et al. 1974). To maintain robust populations in an unpredictable future with many threats to viability, including climate change, it is of high conservation concern to understand what factors influence the demographic parameters that determine population viability (Morris & Doak 2002). This is especially important for the Farallon population because, over the last 30 yr, the number of pups surviving to weaning has declined from a mean of 190 yr⁻¹ in the 1990s to a mean of

64 yr^{-1} in the 2010s (Duncan 2021). Here we focus on factors that influence one important demographic parameter underlying population viability: the probability a pup survives from birth to weaning age (henceforth, 'pup survival' probability).

Oceanographic conditions, at both local and much larger spatial scales, have been shown to affect the foraging behavior and demography of northern elephant seals and other pinniped species (Sydeman & Allen 1999, Le Boeuf et al. 2000, Bradshaw et al. 2004, Crocker et al. 2006, Hadley et al. 2007, Simmons et al. 2007, Lee 2011, Robinson et al 2012). Climate change, current and future, can act to exacerbate such impacts (McMahon & Burton 2005, Perry et al. 2005, Hoegh-Guldberg & Bruno 2010). Reproduction in species such as the northern elephant seal and the southern elephant seal *M. leonina* is especially vulnerable to the impacts of oceanic conditions because these species are consummate examples of capital breeders: females fast during the entire nursing period (i.e. from birth until weaning), ca. 24 d, drawing on energy reserves built up during the months of the pre-breeding (gestational) foraging trip (Arnbom et al. 1997, Le Boeuf 2021). At the same time, pups are very vulnerable during the weeks immediately following parturition, as they are completely dependent on their mother for nutrition and are incapable of swimming (Le Boeuf 2021). Multiple factors can contribute to failure of a pup to survive to weaning age, relating either to indirect impacts, such as the condition and maternal behavior of the mother (Bowen et al. 2001), or direct impacts, such as the local conditions at the pup-rearing locations (Sepúlveda et al. 2020).

The northern elephant seal, like its congener the southern elephant seal, has been the subject of many long-term studies focused on its breeding biology, which have documented substantial annual variability in pup survival. In particular, low pup survival rates were noted in 2 especially strong El Niño years, 1983 and 1998 (Huber et al. 1991, Le Boeuf & Reiter 1991, Le Boeuf & Crocker 2005). Reduced pup survival was attributed to both direct and indirect effects of oceanographic conditions. Direct effects, as noted by Le Boeuf & Reiter (1991), were due to high waves, high surface water levels, and high coastal winds, which either led to pups drowning or affected female behavior (such as abandonment of the pup), and thus, ultimately, impacted pup survival. Inundation of haulout beaches caused pups to be separated from their mothers as well as be swept out to sea. Le Boeuf & Reiter (1991) hypothesized that indirect effects associated with changes in water currents and up-welling, as well as other perturbations, may have affected the composition, distribution, abundance, and/or availability of food for females. Evidence for such indirect effects was provided by Crocker et al. (2006), who documented reduction in foraging success of female elephant seals during the strong El Niño event of 1997–1998, in the months following breeding. Similarly, the Antarctic fur seal *Arctocephalus gazella* also exhibited reduced catch rates of its primary prey (myctophids, i.e. lanternfish), which was associated with poor body condition of mothers and pups during the same strong El Niño of 1997–1998 (Lea et al. 2006).

Sepúlveda et al. (2020) highlighted the significance of extreme waves during coastal storms for survival of South American sea lion pups *Otaria byronia*. Both wave height and wave power were identified as critical determinants of pup stranding rates. Similarly, in the brown fur seal *A. pusillus*, large storm surge events have resulted in high pup mortality rates (Pemberton & Gales 2004).

Here we investigate both direct and indirect pathways affecting pup survival using a long-term (37 yr) time series monitoring northern elephant seals breeding on the South Farallon Islands (see Huber 1987, Sydeman et al. 1991, Lee & Sydeman 2009, Lee 2011). We evaluate the overarching hypothesis that annual pup survival reflects the influences of both local factors (acting directly on pup survival) and basin-wide factors (acting indirectly, by affecting breeding females). At the local scale, we consider whether storm surges and high waves associated with major storm events could be resulting in pup mortality during the pup nursing period, which falls almost entirely in the months of January and February at the South Farallon Islands and elsewhere on the California coast (Sydeman et al. 1991).

While the primary objective of this study was to better understand direct and indirect impacts on pup survival, we recognize that a female's annual reproductive success also reflects natality (i.e. whether a female present at a breeding colony gave birth to a pup). To put results of pup survival in a broader context, we therefore present supplementary analysis on an individual female's annual reproductive success, also termed weaning success, which is the product of natality (whether or not the female gave birth) and pup survival (survival of a pup from birth to weaning age).

Regarding the indirect pathway acting on pup survival, we consider 3 climate indices that span a large portion of the Pacific basin: the Southern Oscillation Index (SOI), the Pacific Decadal Oscillation (PDO;

Mantua & Hare 2002), and the North Pacific Gyre Oscillation (NPGO); see summaries in Di Lorenzo et al. (2013). We consider this large spatial scale because in the 10 mo between post-breeding departure in one year and subsequent return to the breeding grounds, females range widely throughout the Northeast Pacific Ocean, often beyond the California Current and well into the Gulf of Alaska and the central Pacific (Le Boeuf et al. 2000, Robinson et al. 2012, Abrahms et al. 2018).

While El Niño–Southern Oscillation (ENSO) events (reflected in the SOI), and, to a lesser extent, the PDO, have received attention in previous studies of northern elephant seals, no previously published study of this species has considered the NPGO. As the originators of the NPGO index state, the NPGO reflects 'interannual and decadal variations of salinity, nutrient upwelling, and surface chlorophyll *a* (chl *a*) in the Northeast Pacific' and thus tracks well long-term patterns in primary productivity (Di Lorenzo et al. 2008). In particular, the NPGO tracks decadal variability associated with changes in the strength of the subtropical and subpolar gyres. Recent studies have demonstrated that the NPGO index predicts the state of higher trophic levels as well, e.g. zooplankton abundance (Sydeman et al. 2013) and salmon survival (Kilduff et al. 2015).

Regarding the impact of storms (especially high waves), we hypothesized that a higher frequency of extreme waves during January and February will be associated with reduced annual pup survival due to inundation of pupping locations. Risk of inundation depends on several factors (e.g. elevation, topography, and aspect of beach habitat) but would be expected to be greater with increasing frequency of extreme waves or, more generally, due to high water levels.

At the South Farallon Islands, northern elephant seals breed on 2 adjacent islands, Southeast Farallon Island (SEFI) and West End Island (WEI), which differ in topography of beach habitat and thus potentially differ in inundation risk. In particular, the slope of elephant seal pupping beach habitat differs between the 2 islands, with the mean slope (±SE) on SEFI nearly twice that of WEI (14.19° ± 3.29° vs. 7.60° ± 3.48°; N. Nur & J. Howar unpubl.). This difference provides an initial basis for examining whether the impact of extreme waves and/or high water levels differs between the 2 islands.

In contrast, we hypothesized that the effect of basin-scale climate indices will be similar for both islands, since the climate indices reflect conditions at large spatial scales prior to breeding and would presum-ably be similar for all cows, regardless of where they pup on the Farallon Islands.

We therefore pose the following specific hypotheses, which we test here: (1) Variation in pup survival is associated with oceanographic/climate conditions, as reflected in basin-scale climate indices, which have indirect impacts on breeding females. (2) Higher frequency of extreme waves during the pupping season reduces pup survival. (3) The effect of major storms on pup survival differs between WEI (greater risk of inundation) and SEFI (lower risk). (4) The effect of basin-scale climate variables on pup survival does not differ between the 2 islands.

2. MATERIALS AND METHODS

2.1. Study species and study area

Northern elephant seals are large marine mammals (adult females generally weighing 400–800 kg) that give birth during January and February each year at rookeries along the Pacific coasts of Mexico and California (Le Boeuf et al. 2000, Le Boeuf 2021). Principal prey are mesopelagic squid and mesopelagic fish, especially lanternfish (Myctophidae) and deep-sea smelt (Bathylagidae) (Saijo et al. 2017, Goetsch et al. 2018, Yoshino et al. 2020).

Recolonization of the Farallon Islands began in 1959, with the first pup born in 1972. Since that year, Point Blue Conservation Science ('Point Blue'; formerly Point Reyes Bird Observatory) has studied the population biology of this species on the South Farallon Islands, part of the Farallon Islands National Wildlife Refuge, 45 km west of San Francisco, California (37° 42′ N, 123° 00′ W; Fig. 1). Principal haulout locations for SEFI and WEI are indicated in Fig. 1.

On the South Farallon Islands, the first births are generally at the beginning of January. By 4 wk of age, the pup has tripled its birth weight and is weaned when the mother returns to sea in February or early March. The female forages for 2 mo postpartum to recover the one-third of her body mass lost during nursing (Robinson et al. 2012). Following their postpartum foraging bout, females return to land to molt, and then return to sea to forage for 7–8 mo during gestation. During these 2 foraging bouts (postpartum and during gestation), females disperse widely throughout the Northeastern Pacific, thousands of km to the north and west of their breeding colony (Robinson et al. 2012). After continuous foraging during the gestational foraging bout (June–December), females return to rookeries to give birth (Le Boeuf et al. 2000).
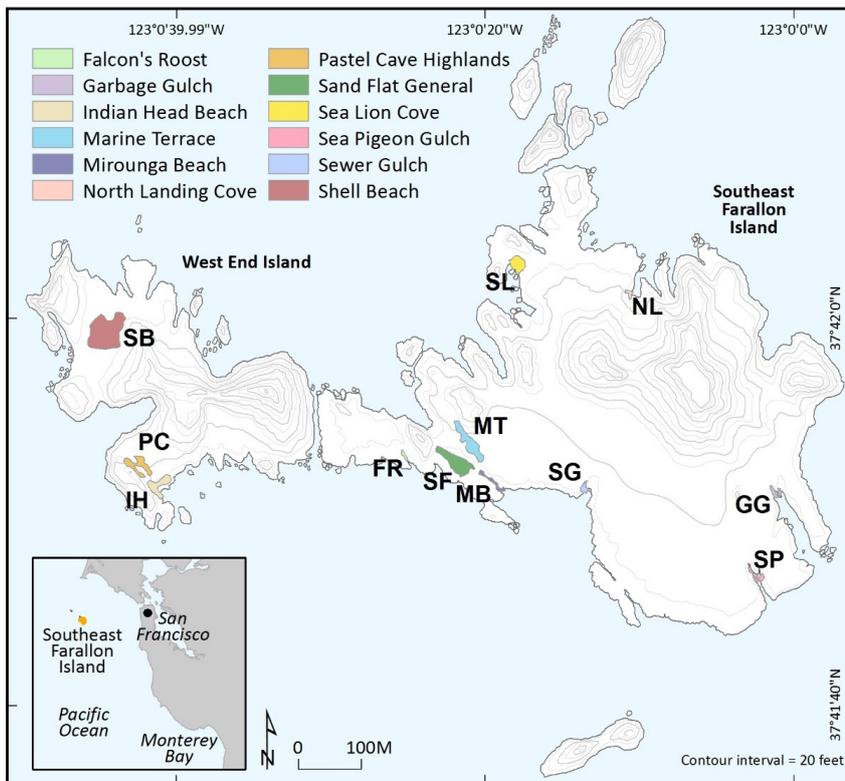
Fig. 1. South Farallon Islands (west of California; inset), indicating the major northern elephant seal haulout locations on Southeast Farallon Island and West End Island. Main breeding colonies: Mirounga Beach (MB), Sand Flat (SF), Marine Terrace (MT), Indian Head Beach (IH), Pastel Cave Highlands (PC), and Shell Beach (SB); additional breeding at: Falcon's Roost (FR), Garbage (GG), North Landing Cove (NL), Sea Lion Cove (SL), Sea Pigeon Gulch (SP), and Sewer Gulch (SG)

2.2. Data collection on elephant seals

Biologists from Point Blue determined attendance patterns of adult males and females, birth dates, and weaning date of pups, and recorded pup mortality, as well as resighted previously tagged elephant seals and tagged new pups, juveniles, and adults for demographic analyses over the 37 yr time period of this study (1983–2019).

In every year, nearly all weaned pups and several immature animals were flipper-tagged (Dalton Supplies). Point Blue biologists identified returning females by flipper tags or distinguishing marks such as scars. After recording tag numbers, the biologists used hair dye (Clairol) to temporarily and uniquely mark females so they could be easily identified and observed from a distance throughout the breeding season. Pups were also marked with dye to ensure they could be tracked even if they became separated from the cow. On SEFI, the biologists conducted daily surveys throughout the season (December–March) to determine the number and identity of all cows and pups present at the colony. From these surveys, biologists determine when each cow gives birth, the status of each individual pup (present,

absent, weaned, or dead), and whether they survived to weaning. Access to WEI is limited and logistically challenging; the island is designated wilderness, limiting the frequency of visits. Therefore, tag resighting, parturition, and pup survival are determined by visiting the WEI colonies approximately once every 2 wk through the end of the season (i.e. December–March). While the reduced frequency of surveys on WEI results in reduced precision, and the possibility of missing a birth, the overall number of females attending, pups born, and pups surviving to weaning age per year per island can still be reasonably estimated. We acknowledge potential error in estimating pup survival for any given year, but because the protocol for WEI has remained the same over the entire time series (i.e. since 1983), we consider that results from analyses of variation in pup survival among years can provide valuable insights. All work was carried out according to guidelines of the American Society of Mammalogists (Gannon et al. 2007), under Marine Mammal Permit 373-1868-00.

Data were missing for some environmental variables prior to 1983; hence our analysis is of pup survival from 1983 through the 2019 breeding season.

2.3. Environmental variables

2.3.1. Basin-scale variables

We considered 3 climate indices that have been widely used in studies of marine systems (Di Lorenzo et al. 2013): SOI, PDO, and NPGO. A fourth candidate climate index was the Multivariate El Niño Index (MEI), but it was highly correlated with the SOI (e.g. $r = +0.949$ for correlation of winter MEI and SOI), hence we did not analyze it further.

While these indices have been shown to reveal pervasive effects of changes in oceanographic conditions which may consequently affect northern elephant seals, we had no specific mechanisms identified *a priori* at the basin scale, and therefore considered 5 relevant time periods for each climate index: (1) winter (i.e. December–February), which encompasses the 2 mo during which pups are born and nursed (January and February) as well as the month prior to that when females arrive at the rookeries in preparation for birth (December), (2) fall: the 3 mo prior to female arrival in December (i.e. September–November), (3) previous summer: about 6 mo prior to the onset of the pupping season (i.e. June–August), (4) previous spring: about 9 mo prior to the onset of the pupping season (i.e. March–May), which are the 3 mo following the previous year's pup nursing period, during which females forage for ca. 2–2.5 mo and regain body mass lost during nursing, and (5) previous winter: the 3 winter months in the previous year.

The latter 4 time periods allowed for lagged effects of approximately 3, 6, 9, and 12 mo, respectively. While analysis of effects of climate indices season by season can provide important insights, it was also important to examine cumulative effects over longer intervals. For each of the 3 indices, we also analyzed values averaged over 6 mo (fall–winter, summer–fall, spring–summer, and previous-winter–spring), 9 mo (summer–fall–winter, spring–summer–fall, and previous-winter–spring–summer), and 12 mo (spring to current winter [March–February], and previous winter to the fall immediately preceding breeding [December–November]). Thus, for each index, there was a total of 12 candidate metrics, ranging from 3 to 12 mo.

2.3.2. Local variables

We investigated the effects of extreme waves associated with major storms and, more generally, risk of inundation using a focused approach based on previous observational studies (including our own). First, we restricted the analysis to wave and inundation metrics from the months of January and February, the 2 mo that represent the principal period pups are at risk from extreme waves and inundation. Only a few pups are present before (i.e. born in late December) or after (i.e. still being nursed in early March) that period. We did not consider any lagged local effects since we were evaluating the hypothesis of a direct effect of waves/storms on pup survival. Second, we used hourly data on wave height from NOAA's San Francisco buoy (Stn 46026 (LLNR 357), 18 nautical miles [nmi; 33 km] west of San Francisco, CA), the closest buoy to the Farallon Islands (8.5 nmi [16 km] away), to extract 3 specific candidate metrics. The first 2 metrics were the mean wave height and the maximum wave height calculated by month and then averaged for the January–February period. The third metric ('extreme wave index') was an index that we devised *a priori*: the number of days per month that wave height exceeded 4 m, calculated for January and February of each year. We chose a threshold of 4 m based on previous observations of large wave events that potentially impacted pup survival at the Farallon Islands. Our preliminary analysis indicated that using a threshold of 4 m wave height provided a better predictor of pup survival than using a threshold of 3 m wave height, but we did not investigate the question of the critical threshold any further than that. A similar critical wave height threshold of 3.8 m was shown by Sepúlveda et al. (2020) to affect survival of sea lion pups.

We calculated all wave metrics in 2 ways. Initially, we restricted the wave metrics to only enumerate days in which winds were from the south sector (defined as between 120° and 240°), because major storms in the winter in coastal California are predominantly atmospheric river (AR) events, which come from the south (Gershunov et al. 2017). Our rationale was that the criterion of winds from the south would better capture the incidence of major storms associated with inundation, which was our prime concern. We did not have information on the direction of waves, only wind direction.

We theorized that repeated high waves during a pupping season would be more detrimental to pup survival than 1 or 2 extreme waves, since the latter might not occur during the time of peak vulnerability of pups, a time window which is quite narrow, as demonstrated by Le Boeuf & Reiter (1991). The extreme wave index displayed substantial inter-annual variation (range: 0–11.5, mean: 2.41, SD: 2.80), and hence had high potential as a predictor.

Our primary index of extreme waves was the average number of days in January and February for which (1) winds were from the south, southeast, or southwest, and (2) maximum wave height that day exceeded 4 m. However, to confirm our assumption that storms from the south had the greatest impact, we also evaluated the comparable wave index, irrespective of wind direction. In any case, the 2 extreme wave indices (whether restricted to the south sector or not) were highly correlated (r = + 0.961, p < 0.0001). Likewise, we also considered mean wave height and maximum monthly wave height, calculated without any restrictions on wind direction.

We analyzed 2 additional environmental variables that may influence the impact of extreme waves due to storms. The first was recorded tide height (actual mean higher high water, MHHW) as determined at the closest NOAA station, Point Reyes, CA. We analyzed monthly mean values of MHHW and monthly maximum water levels for January and February. MHHW values reflected both astronomical tide and storm events. The second metric was monthly rainfall recorded on SEFI by Point Blue biologists, on the assumption that major storms would produce extreme rainfall (Gershunov et al. 2017). To provide additional insights into the relationship between the wave, tide, and rainfall metrics analyzed and winter storms, we analyzed indices of AR events in winter (December, January, and/or February), with respect to their frequency and magnitude at the location closest to the South Farallon Islands (37.5° N, 122.5° W; Gershunov et al. 2017; data available at http://cw3e.ucsd.edu/Publications/SIO-R1-Catalog).

For all local variables, we analyzed mean values across January and February, combined. We also analyzed all 'winter months' (i.e. including December), but in no case did inclusion of December improve the statistical associations presented below (Sections 3.3.1 and 3.3.2) for local metrics.

To summarize, our statistical analysis considered 36 basin-scale candidate variables affecting pup survival, i.e. 3 seasonal climate indices, each lagged 0, 3, 6, 9, or 12 mo, and for intervals of 3 to 12 mo, as detailed in Section 2.3.1. None of the NPGO and PDO indices were correlated with the extreme wave index; however, SOI for summer, fall, and current winter were significantly negatively correlated with the extreme wave index (p < 0.001, p < 0.001, p = 0.016, respectively). Complementary to the basin-scale analysis, we analyzed 3 wave-related metrics, monthly mean and maximum wave height (averaged over January and February), along with the extreme wave index, i.e. the number of days per month that wave height exceeded 4 m. Each metric was calculated for days in which winds were from the southern sector as well as calculated for all days. Finally, mean and maximum MHHW, rainfall, and frequency and magnitude of AR events were calculated for January and February.

2.4. Trends in year and effect of environmental variables

For analysis of pup survival, we fit generalized linear models, specifically mixed-effects logistic regression, in which the random effect was year, using the xtlogit command in Stata 16.1 (StataCorp 2019). We assumed that in addition to any fixed effects (basin-scale and/or local variables, as identified in Section 2.3), there was variation in pup survival among years due to unspecified factors. While pup survival was treated as a Bernoulli-distributed variable (0 or 1), the survival of each pup within a year-cohort exhibited a correlated response. We analyzed pup survival in relation to trends with year, for each island separately. We considered linear as well as polynomial trends up to fourth order.

Regarding the effects of environmental variables (drivers), we hypothesized that the basin-scale variable or variables would affect both islands similarly, as stated in Hypothesis 4, but that local variables could potentially have different effects on the 2 islands, due to differences in topography (Hypothesis 3). To evaluate such hypotheses, we took an iterative approach in statistical modeling: We began by considering the suite of 36 basin-scale candidate variables and first identified the single basin-scale variable which best explained pup survival, allowing for a main effect of 'island'. Once the climate variable was identified, and its interaction included if significant, we analyzed the suite of candidate local variables, with the identified basin-scale variable included. For each local variable, we fit models with and without an interaction between 'island' and the local variable (see Hypothesis 3 in Section 1). This allowed us to test for the interaction, as well as estimate the island-specific coefficients for predictor variables.

We then considered whether any other candidate variable (local or basin-scale) was significant given the inclusion of basin-scale and local variables as identified above. We used the Akaike information criterion (AIC) (sample size was sufficiently large such that corrected AIC [AICc] did not differ from AIC) to initially identify the best predictive model, and also report Wald tests and likelihood ratio tests (LRTs), as appropriate (Hosmer et al. 2013), to evalu-

ate statistical significance of predictor variables and their interactions with island. We also use AIC to compare among alternative models (both nested and non-nested). We also examined whether pup survival in a given year was correlated with the number of adult females present on each island during the pupping period to determine if there was evidence of density dependence.

Though the focus of this study was to better understand direct and indirect impacts on pup survival, we conducted supplemental analysis on a metric which we term 'weaning success' (Sydeman et al. 1991). Weaning success combines natality (= 1 if a female present at a pupping location gave birth; 0, if she did not) and pup survival (= 1 if a pup survived from birth to weaning age, 0 if it did not). Thus, weaning success = 1 for a female that produced a surviving pup, and 0 if the female did not give birth or if the pup died prior to weaning. Our objective in analyzing weaning success was to confirm whether the patterns and drivers that we identified regarding pup survival were found to have comparable effects with respect to the more inclusive metric, weaning success. By analyzing both variation in pup survival and weaning success, we could determine the extent to which differences in pup survival translated into differences in weaning success.

3. RESULTS

3.1. Pup survival and weaning success

A total of 6651 pups were born on WEI and SEFI over the 37 yr (Table 1). Natality rates were similar between the 2 islands (difference: <2%, Table 1), but rates of pup survival to weaning were greater on WEI than SEFI (0.803 ± 0.019 [mean ± SE] vs. 0.711 ± 0.015, LRT, p < 0.0001, Table 1). As a result, weaning success was also greater on WEI than SEFI (LRT, p < 0.0001, Table 1).

Pup survival and weaning success differed substantially among years. While neither island showed a significant linear trend in pup survival (p > 0.05 for each island), SEFI demonstrated a significant cubic trend (Fig. 2A; logistic regression coefficient for cubic term, β = −0.000215 ± 0.000063, p < 0.001, mixed-effects logistic regression). Pup survival showed an initial decrease in the first 10–12 yr, followed by an increase between ca. 1993 and ca. 2013, with a drop-off in the most recent 5 yr. WEI demonstrated a much less marked cubic trend than SEFI (Fig. 2B), and was generally trending positive during the entire time

Table 1. Northern elephant seal population and reproductive success summary statistics for Southeast Farallon Island (SEFI) and West End Island (WEI), 1983−2019: (A) counts; (B) annual rates of natality, survival probability and weaning success (mean and SD: among-year mean and SD)

(A) Counts of females, pups born, pups weaned						
Island	Females		Pups born		Pups weaned	
	Total	Mean	Total	Mean	Total	Mean
WEI	3674	99.29	3153	85.22	2446	66.11
SEFI	3873	104.67	3496	94.49	2477	66.95

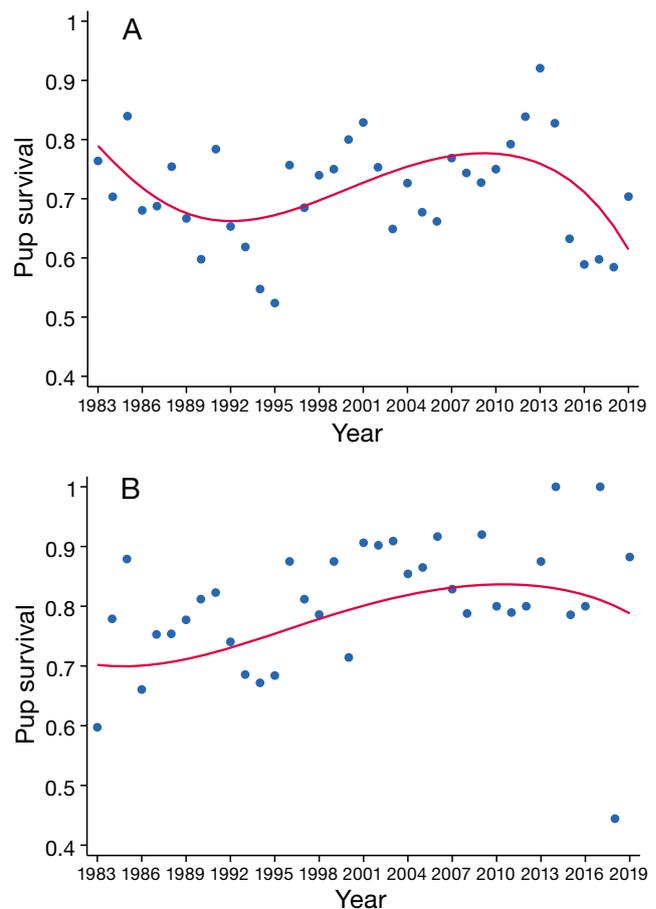| (B) Annual rates						
Island	Natality rate		Pup survival		Weaning success	
	Mean	SD	Mean	SD	Mean	SD
WEI	0.881	0.103	0.803	0.109	0.712	0.139
SEFI	0.900	0.053	0.711	0.090	0.640	0.084

Fig. 2. Variation in northern elephant seal pup survival probability among years, by island. Cubic trends shown, back-transformed from mixed-effects logistic regression model. (A) Southeast Farallon Island (for the cubic term, $z = −3.42$, p < 0.001); (B) West End Island (for the cubic term, $z = −1.80$, p = 0.072)

period. The cubic term for WEI was not quite significant (β = −0.000171 ± 0.000095, p = 0.072), but on the basis of AIC, a cubic trend for WEI was preferred over alternatives (no trend, linear trend, or quadratic).

3.2. Frequency of extreme waves

The number of days per month with extreme waves during January and February, and in which winds were from the south sector (i.e. southwest, south, or southeast), averaged 2.41 yr^{-1}, ranging from 0 to 11.5. Including all days per month, irrespective of wind direction, there were on average 3.93 d mo^{-1} (SD: 3.30, range: 0–15) where wave height was 4 m or greater; as previously noted (Section 2.3.2), the 2 wave metrics were highly correlated among years. The highest recorded wave for January was 8.60 m in 2008, and for February was 7.34 m in 1998.

3.3. Analysis of pup survival

3.3.1. Preferred statistical model for pup survival

The strongest predictor of pup survival among all environmental variables, basin-wide and local, was the NPGO index of the fall and current winter (September–February), as determined through analysis of each of the candidate variables in turn. Pup survival increased with increasing positive values of NPGO (p < 0.0001, controlling for island main effect; mixed-effects logistic regression). Furthermore, there was no significant quadratic curvature in the response (p > 0.4), nor did the effect of fall–winter NPGO differ between the 2 islands (p > 0.7). Considering both islands combined, the fall–winter NPGO index accounted for 36.8% of the variance among years in pup survival. This index had the greatest predictive ability among all 6 mo indices and was a stronger predictor than indices of shorter (3 mo) or longer (9 and 12 mo) durations. Fig. 3 illustrates the relationship, with reference to both islands combined.

We then identified the best predictive model with respect to both basin-scale and local variables, while evaluating whether variables differed in their effect between the 2 islands, as per our specific hypotheses (3 and 4). Through evalua-
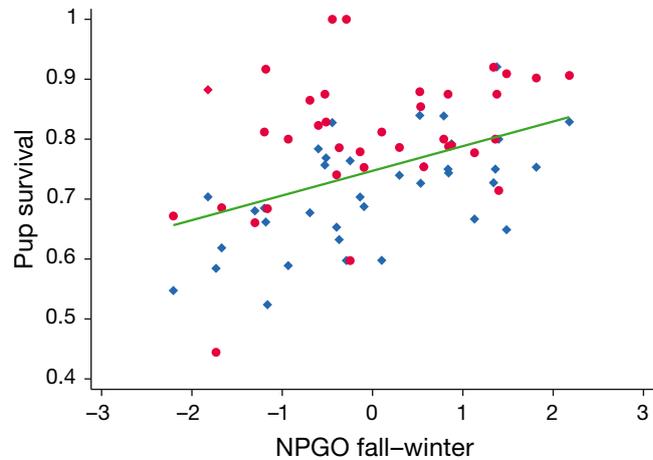

Fig. 3. Northern elephant seal pup survival probabilities on West End Island (red filled circles) and Southeast Farallon Island (blue diamonds) in relation to North Pacific Gyre Oscillation (NPGO) index for fall and winter. The estimated effect of NPGO was very similar for the 2 islands (p > 0.7 for the difference in slope between islands) and therefore a single line of best fit is shown (p < 0.0001 for the common slope, mixed-effects logistic regression)

tion of all candidate variables, we determined that the best predictive model, as determined by AIC, included the effect of NPGO (positive) and the effect of the extreme wave index (for days in which winds were from the south), with pup survival decreasing as the frequency of extreme waves increased (Table 2).

The model included a significant negative effect of extreme waves on pup survival on WEI (p = 0.041,

Table 2. Determinants of northern elephant seal pup survival probability on Southeast Farallon Island (SEFI) and West End Island (WEI). Results of the preferred model of pup survival in relation to environmental variables, including main effect of island (SEFI vs. WEI, base level), fitting mixed-effects logistic regression on pup survival. Effect of extreme wave index differed between the 2 islands (z = 2.22, p = 0.026); model output shows estimated slope coefficients for each island. Effect of fall–winter North Pacific Gyre Oscillation (NPGO) did not differ between the 2 islands (z = −0.39, p > 0.6), hence only a single slope was fit. Model assumes outcomes are clustered by year (random intercept for year). Estimate of variance due to random effect (year) = 0.244 ± 0.047; likelihood ratio test that this differs from 0: $\chi^2(1)$ = 30.48, p < 0.0001

Model statistics: no. of observations = 6651; no. of groups = 37
Log likelihood = −3735.38; Wald $\chi^2(4)$ = 79.64; p < 0.0001

	Coeff.	SE	z	p > |z|	95% CI
NPGO fall–winter	0.237	0.046	5.10	0.000	0.146 to 0.327
Effect of island					
SEFI	−0.563	0.081	−6.98	0.000	−0.721 to −0.405
Effect of wave index by island					
SEFI	0.0024	0.0206	0.12	0.907	−0.038 to 0.043
WEI	−0.0431	0.0211	−2.04	0.041	−0.085 to −0.002
Intercept	1.482	0.0851	17.42	0.000	1.315 to 1.649

Table 2), but a weak, nonsignificant effect on SEFI (p > 0.9, Table 2). Moreover, the 2 island-specific slopes differed significantly (difference in slopes: −0.0455 ± 0.0205, p = 0.026, comparing WEI to SEFI).

The NPGO index for fall–winter was not correlated with the extreme wave index (r = −0.107, p > 0.5), thus there was little confounding between the 2 predictors. Furthermore, there was no statistical interaction between the 2 predictors in terms of their effect on pup survival (p > 0.6); in short, the effects of the 2 variables appear to be independent of each other.

Annual pup survival values, adjusted for the effect of NPGO (as shown in Table 2), are shown in relation to the extreme wave index for WEI (Fig. 4), since only for WEI was there a significant effect. There was no significant quadratic curvature to the relationship (p > 0.3, LRT). In addition, the extreme wave index for January and February was superior to that calculated for January or February only; thus, both months contributed to the ability of the index to predict annual pup survival. Furthermore, the estimated effects for the extreme wave indices calculated for January only and February only were statistically similar (p > 0.7, Wald test).

Predicted survival probabilities (±95% CI) in relation to the extreme wave index, as determined from the preferred model (Table 2), are shown for the 2 islands in Fig. 5A. The difference between the 2 islands in the effect of extreme waves, while controlling for the effect of NPGO, is illustrated.
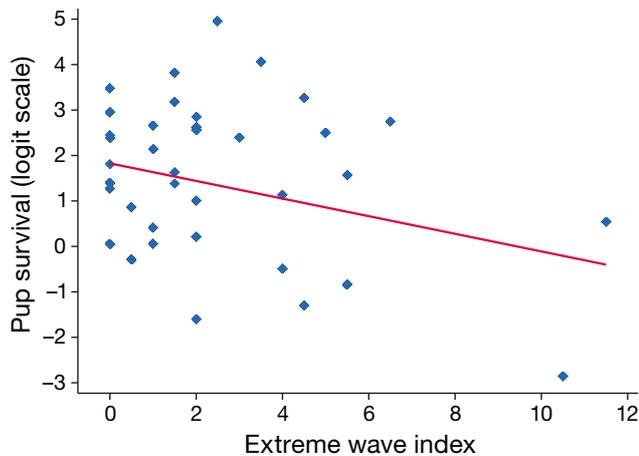

Fig. 4. Annual northern elephant seal pup survival probability in relation to extreme wave index (days per month with wave height ≥4 m and winds from the south) for West End Island. Annual values of the logit of pup survival (= ln($p/(1 − p)$), where p = pup survival probability), adjusted for the effect of the fall–winter North Pacific Gyre Oscillation index, are shown, as well as the slope of the relationship. See Table 2 for statistical details
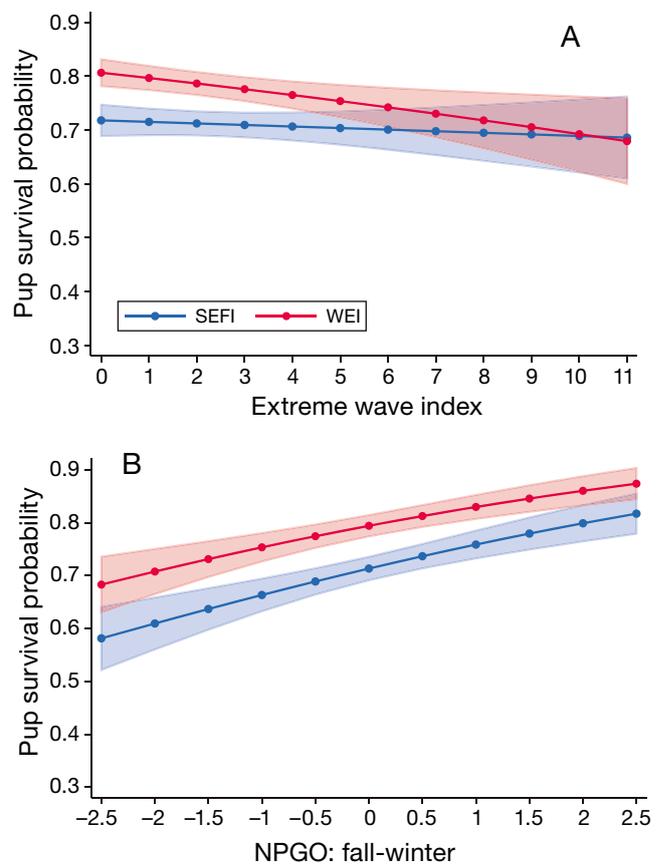

Fig. 5. Model-predicted northern elephant seal pup survival probabilities for Southeast Farallon Island (SEFI) and West End Island (WEI), illustrating results of Table 2. (A) 95% CIs around the predicted effect of the extreme wave index, adjusting for the effect of the North Pacific Gyre Oscillation (NPGO) index; (B) 95% CIs around the predicted effect of NPGO index, adjusting for effect of the extreme wave index

While the effect of extreme waves differed by island, as noted above, the effect of NPGO was similar on both islands, as illustrated in Fig. 5B (logistic regression coefficients for slope, adjusting for effect of extreme wave index, β = +0.228 ± 0.051 and β = +0.250 ± 0.057, for SEFI and WEI, respectively; p > 0.6 for difference in slopes).

We also note that the extreme wave index based on winds from the south sector was superior to the comparable model in which extreme wave index was based on winds from all directions (for the latter, ΔAIC = +1.16, Table 3). Qualitatively, results for the latter were similar to that of the preferred model. Notably, there was no significant effect of the number of days with extreme waves when the wind direction was not from the south (for each island, p > 0.1 for the effect of such an index).

Table 3. Analysis of northern elephant seal pup survival probability on West End Island and Southeast Farallon Island, with mixed-effects logistic regression: comparison of models incorporating extreme wave and other local metrics as well as climate indices. Preferred model (Model 1; AIC = 7482.76) detailed in Table 2. Four competing models (2–5) regarding local wave metrics (each with the selected basin-scale climate index, North Pacific Gyre Oscillation [NPGO] for fall–winter) are compared to Model 1, either with winds from the south only or all directions and with or without interaction. Four other competing models (6–9) are shown with alternative local metrics, including a model with no local metric (Model 9). For local metrics in Models 6–8, the no-interaction by island model had superior AIC in each case and is shown. Five competing models regarding climate indices (10–14), each with the selected local wave metric, extreme wave index (south), are compared to Model 1. These include the 3 most competitive NPGO-based alternatives (10–11), the best Pacific Decadal Oscillation (PDO)-based model, and the best Southern Oscillation Index (SOI)-based predictive model. Winter: current winter; prevwint: previous winter; AR: atmospheric river; MHHW: mean higher high water

	Model	df	ΔAIC
1	NPGO fall–winter, island, extreme wave index by island (south)	6	0
	Comparison with other wave metric models		
2	NPGO fall–winter, island, extreme wave index by island (all)	6	1.16
3	NPGO fall–winter, island, extreme wave index (south), no interaction	5	2.94
4	NPGO fall–winter, island, maximum wave height by island (south)	6	3.11
5	NPGO fall–winter, island, maximum wave height (south), no interaction	6	3.60
	Comparison with other local metric models		
6	NPGO fall–winter, island, MHHW, no interaction	5	1.73
7	NPGO fall–winter, island, rainfall, no interaction	5	2.64
8	NPGO fall–winter, island, frequency AR events, no interaction	5	3.97
9	NPGO fall–winter, island only (no local metric)	4	2.04
	Comparison with other basin metrics		
10	NPGO summer–fall–winter; island, extreme wave index by island (south)	6	1.84
11	NPGO fall, island, extreme wave index by island (south)	6	1.85
12	NPGO winter, extreme wave index by island (south)	6	2.39
13	PDO prevwint–spring–summer–fall; island, extreme wave index by island (south)	6	10.50
14	SOI spring–summer–fall–winter; island, extreme wave index by island (south)	6	14.16

3.3.2. Alternative basin-scale variables

Among all seasonal climate indices, fall–winter NPGO (i.e. the 2 mo of the pupping season and the 4 mo preceding it) was most strongly associated with pup survival, whether or not local drivers of pup survival were also included in the analysis. There were a number of other NPGO indices that were competitive (Table 3), in particular, the 9 mo index, summer–fall–winter, and the 3 mo index for fall only (ΔAIC = +1.84, +1.85, respectively). The fourth best climate predictor among all analyzed was the NPGO index for the current winter (December–February), for which ΔAIC = +2.39, compared to preferred model with fall–winter NPGO. Thus, the top 4 predictors all included fall NPGO and/or winter NPGO.

No model with PDO, with respect to any of the 3, 6, 9, or 12 mo intervals analyzed, was within 10 AIC units of the preferred model (Table 3); the same was true for SOI metrics. Furthermore, with fall–winter NPGO included in the model, there was no signifi-

cant effect of any other climate variable (NPGO, PDO, or SOI).

3.3.3. Alternative local variables

We evaluated several alternative local metrics; the following models all included the effect of fall–winter NPGO and a main effect of island, for which there was strong support for both (as detailed in Table 2). We note that, in no case did inclusion of an additional local variable (listed in Section 2.3.2) improve the AIC value of a model that contained fall–winter NPGO and the extreme wave metric. Regarding the 2 alternative wave metrics, monthly maximum and mean wave height, these models were not as competitive, i.e. not as supported, ΔAIC being greater than 3.0 units in all cases compared to the preferred model with the extreme wave index (Table 3).

To better understand the risk of inundation, we also examined models in which the local metric was either mean or maximum MHHW (by month),

averaged over January and February. Models with mean MHHW, either with no interaction with island or with an interaction, were clearly competitive (ΔAIC = +1.73, +1.84, respectively, Table 3). These 2 models also had superior AIC compared to a model with fall–winter NPGO and island main effect only (Model 9, Table 3). Notably, the model with an interaction by island evidenced a significant effect of mean MHHW for WEI, but not for SEFI (p = 0.045, p > 0.4, respectively).

With regard to rainfall in January and February, a model with no interaction with island was preferred to the model with an interaction, but neither model was within 2 AIC units (ΔAIC = +2.64, +2.92, respectively) and had a worse AIC than the model with fall–winter NPGO and island main effect only (Table 3).

With regard to the frequency of AR events, the most competitive AR model had no interaction with island and was not competitive with the preferred model (ΔAIC = +3.97). While not correlated directly with pup survival, the frequency of AR events in January and February, however, was well correlated with the extreme wave index, especially for the preferred index enumerating days for which wind direction was from the south (r = +0.530, p < 0.001). Conversely, there was no significant correlation between the frequency of AR events and the wave index for days on which the wind direction was not from the south (r = + 0.129, p > 0.45).

There was no evidence of density-dependent pup survival. For each island, the effect of number of adult females per island on pup survival was not significant (p > 0.4, p > 0.5, for SEFI, WEI, respectively) given the inclusion of the 2 predictor variables, NPGO and the extreme wave index.

3.4. Weaning success

We repeated the analysis on pup survival, this time analyzing whether a female produced a weaned pup, irrespective of whether the female had given birth. Considering the same predictor variables as in the preferred model obtained analyzing pup survival (see Table 2), results were similar when analyzing weaning success: The effect of NPGO in fall–winter was highly significant and was of similar magnitude on the 2 islands (Table A1 in the Appendix). The effect of the extreme wave metric was significant for WEI (p = 0.031), but not for SEFI (p > 0.5). For the latter, the effect was estimated to be slightly positive. Finally, the effect of the extreme wave index differed significantly on the 2 islands (p = 0.004, Table A1).

4. DISCUSSION

4.1. Local variables influencing pup survival

We identified both local and basin-scale variables accounting for annual variation in pup survival on the South Farallon Islands. At the local scale, extreme waves during the pupping season were associated with reduced pup survival. The actual causes of death may have been several. In particular, biologists on the Farallon Islands have often observed pups washed out to sea, many of which presumably drowned (Berger 2015). In addition, pups, whether washed out or not, may have been separated from their mothers as the result of storm surges, and not reunited, as Le Boeuf & Reiter (1991) report, resulting in starvation or hypothermia. Severe storms may also degrade the breeding habitat, making pups more susceptible to mortality risks; erosion of beach habitat in relation to storms has often been observed (Berger 2015). Sepúlveda et al. (2020) demonstrated that extreme wave height and wave power of coastal storms impacted pup survival in South American sea lions. Major storm surges are associated with high pup mortality in Australian fur seals (Pemberton & Kirkwood 1994, Pemberton & Gales 2004).

There is significant concern about this cause of mortality, because extreme events such as coastal storms are predicted to increase in frequency and/or severity, especially in conjunction with a predicted increase in the severity of El Niño events (Cai et al. 2014, 2015). For the congener, the southern elephant seal, the effect of storm surges on pup survival has not been reported, but extreme snow events are a concern. McCann (1982) reported that unusual snowfall led to pup mortality in this species when pups were trapped in melt holes.

An important finding, confirming Hypothesis 3, was that the impact of extreme waves differed by island (Fig. 5A). This was the case whether all days with waves exceeding 4 m were enumerated or only days with winds from the southern sector (ΔAIC = +2.58, +2.94, respectively, comparing models with no interaction to models with an interaction with island). Analysis of maximum wave height provided some support for a difference between island (Table 3). Regarding tide height (i.e. water level), there was a significant effect on pup survival for WEI (p = 0.045), but not for SEFI; however, the AIC for the model without an island interaction was very slightly better (by 0.11 units) than the model with an island × MHHW interaction. The decrease in pup survival on WEI with increasing mean MHHW points to the im-

portance of inundation, acting directly or indirectly on pups. High water levels reflect effects of winter storms in conjunction with astronomically based extreme tides ('king tides').

Our findings regarding extreme waves and inundation point to the potential impact of winter storms on pup survival. To better understand the role of winter storms in regard to pup survival, we analyzed the incidence of AR events during winter months (Gershunov et al. 2017). We did not find that the frequency of AR events predicted pup survival. However, the frequency of AR events in January and February was well correlated with the extreme wave index, for days for which wind direction was from the south. In other words, years with frequent AR events were years with a greater number of days in which waves exceeded 4 m and winds were from the south. Thus, there is support for our *a priori*-determined criterion of enumerating days with extreme waves and with wind direction from the south. In any case, the association between extreme waves and pup survival was supported, whether days with wind directions not from the south were included or not.

Further study is needed to determine why winter storms/inundation may have had a larger impact on WEI pups than SEFI pups. We suggest that there is greater exposure to storms on WEI than SEFI, which is consistent with the finding that the mean slope of beaches on WEI is only about half that of SEFI. No significant differences between the islands with respect to elevation, aspect, or proximity to water were evident, however (N. Nur & J. Howar unpubl.). Information on actual water levels on each island (inundation) would be very informative.

In addition to differential impacts of extreme waves on pup survival, there are likely additional local influences, pertaining to specific habitat characteristics, spacing of females in the rookeries, greater spacing apparently leading to lower pup mortality (Berger 2015), etc. The specificity of local effects is further indicated by the weak concordance in interannual variation of pup survival between the 2 islands (Fig. 6). After adjusting for the effect of fall–winter NPGO, there was no significant association between annual pup survival on SEFI and on WEI (mixed-effects logistic regression, $p > 0.3$, LRT), suggesting that local effects are manifested differently on the 2 islands.

4.2. Basin-scale correlates of pup survival

The strongest predictor of pup survival was the basin-scale NPGO index. NPGO reflects primary
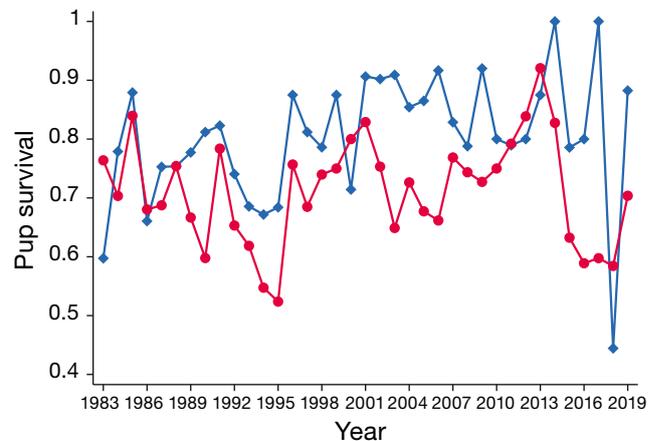

Fig. 6. Interannual variation in northern elephant seal pup survival probability for Southeast Farallon Island (blue diamonds) and West End Island (red circles). After adjusting for the effect of fall–winter North Pacific Gyre Oscillation, annual WEI pup survival was not correlated with SEFI pup survival, nor vice versa ($p = 0.18$, $p > 0.3$, respectively)

productivity in the Northeast Pacific — specifically, interannual and decadal variation in salinity, nutrient upwelling, and surface chl *a* (Di Lorenzo et al. 2008, 2009, 2013). Di Lorenzo et al. (2013) argue that in recent decades, the NPGO, rather than the PDO, has been driving most of the variability in the physical and biological realms of the North Pacific. The NPGO index has been shown to correlate with zooplankton abundance (Sydeman et al. 2013), and, of particular relevance, Kilduff et al. (2015) report that coho and Chinook salmon survival rates in western North America between 1980 and 2006 reflected NPGO rather than the PDO. Variation in the NPGO index was associated with changes in prey consumption by common murres *Uria aalge*, which then had implications for timing of breeding and reproductive success of this species (Gladics et al. 2015).

The strong link between the NPGO and pup survival likely reflects foraging conditions for females during the months prior to giving birth, a time during which they undertake 2 extensive foraging trips (Le Boeuf et al. 2000, Le Boeuf 2021). Recent studies have provided great insights into the locations of foraging trips and the prey that females consume (Robinson et al. 2012, Saijo et al. 2017, Goetsch et al. 2018). These studies show that females consistently forage at the boundary between the subtropical and subpolar North Pacific gyres (Robinson et al. 2012, Abrahms et al. 2018); it is therefore noteworthy that, as stated by Di Lorenzo et al. (2013), the NPGO specifically tracks changes in the strength of the 2 gyre systems.

NPGO indices for all seasonal periods, and for various intervals, were highly significant predictors of pup survival (p < 0.001, in all cases). PDO indices were significant predictors as well (0.01 < p < 0.05 in all cases), but the predictive ability of the NPGO indices was substantially greater (Table 3). The strongest predictor of all was the NPGO of the fall and current winter (i.e. September–February). This 6 mo period corresponds to the 2 mo of pupping, plus the 4 mo prior to arrival at the breeding grounds; it includes most, but not all, of the long, gestational foraging trip that females make prior to the pupping season (Robinson et al. 2012). With regard to the 3 mo periods evaluated, the strongest predictor was the fall prior to the pupping period (September–November), with the winter (December–February) NPGO index the second strongest, followed by summer (June–August).

The strong relationship between pup survival and NPGO during the fall points to the latter statistically predicting conditions for pregnant females during the critical period when they must accumulate extensive energy reserves prior to arriving at haulout locations (Le Boeuf & Crocker 2005). Interestingly, fall and winter NPGO values provided better predictive ability than summer and fall (ΔAIC = +4.39 comparing the latter to the former). Thus, NPGO values for the month prior to pup birth and the 2 mo of pupping contributed more to explaining annual variation in pup survival than the NPGO values in the initial phase of the female's pre-breeding foraging trip (i.e. during June–August). In fact, the September–February interval was the superior predictor compared to all other possible 6 mo intervals (lowest AIC among all ten 6 mo windows evaluated, including August–January, July–December, etc.).

That winter (December–February) NPGO values contributed to predicting pup survival led us to explore whether winter NPGO might be associated with a driver that had a more direct effect on pup survival, such as thermal stress, or that may interact with mortality risks. We investigated potential thermal stress on pup survival by analyzing pup survival in relation to either mean daily high temperature by month or maximum monthly temperatures on SEFI in January and February. However, we did not find evidence to support such an effect (p > 0.2 for the temperature indices examined). Nevertheless, mean daily high temperature was negatively correlated with the fall–winter NPGO (r = −0.400, n = 37, p = 0.014), suggesting there may be weather-related impacts on pup survival associated with NPGO; e.g. the lower the NPGO, the greater thermal stress.

Whatever the mechanism underlying the strong correlation between NPGO and pup survival, the similarity of effect on WEI and SEFI, as determined from our analysis, suggests that the effect is manifest at a spatial scale beyond that of the individual island, i.e. at the basin scale, which reflects the extensive area in which female elephant seals forage prior to breeding.

Le Boeuf & Crocker (2005) provide evidence that ocean climate, as indexed by PDO in their study, influences maternal behavior and, ultimately, weaning mass. Several studies on northern elephant seals have identified the impacts of strong El Niño events on the ecology and behavior of elephant seals (Huber et al. 1991, Le Boeuf & Reiter 1991, Crocker et al. 2006). In particular, Crocker et al. (2006) show that in 2 strong El Niño years (i.e. 1983 and 1998), females gained much less mass in the post-breeding foraging trips than in other years, which may be impacting their condition up to and including pup rearing. The authors note that reduced success in foraging could have resulted from reduced prey abundance, changes in prey distribution or patch characteristics, as well as changes in the cues used by the seals to locate their prey.

Abrahms et al. (2018) found that in the northern elephant seal, the PDO influenced the relationship between the female's foraging strategy and her mass gain during the gestational foraging trip. In turn, Robinson et al. (2012) linked mass gain during the gestational foraging trip to subsequent natality for the same study population. Holser et al. (2021) found that, for this study population, oceanic indices (including PDO and MEI), as well as female condition and colony size, influenced weaning mass.

Taken together, these studies indicate how oceanic conditions may be influencing maternal condition and possibly maternal behavior of northern elephant seals, which potentially can influence pup survival. Similar linkages were demonstrated by Lee & Sydeman (2009), who found that both the Northern Oscillation Index (NOI) and PDO correlate with pup sex ratio for the Farallon population, likely through the mechanism of climatically induced nutritional stress on gestating females.

Our results regarding pup production are consistent with the findings of Lee (2011), who analyzed an earlier time series for the Farallon population (1974–1994) and found that the NOI was correlated with weaning success. Warmer ocean conditions during the time of pregnancy were associated with poorer weaning success, with similar relationships exhibited by primiparous and multiparous females (see Lee 2011, their Fig. 2A).

The congener, southern elephant seal *Mirounga leonina*, also demonstrates strong linkages between ocean climate, maternal condition, and condition of the pup (Fedak et al. 1996, McMahon & Burton 2005). Clausius et al. (2017) showed that ocean climate conditions (specifically, sea ice extent) influenced maternal condition (i.e. body mass), which in turn was correlated with mass of the weaned pup (see also McMahon et al. 2017). Furthermore, annual sea ice extent had an effect on weanling mass over and above the estimated effect of maternal body mass (Clausius et al. 2017). Not only sea ice extent, but variation in the Southern Annular Mode (SAM) and chl *a* concentration are also associated with variation in weanling mass (Oosthuizen et al. 2015, McMahon et al. 2017). These latter 2 studies report on weanling body condition, which may be correlated with survival of the pup to weaning as well. In this species, survival of pups to weaning was greater for mothers of greater body mass, indicating the importance of maternal condition (Arnbom et al. 1997).

4.3. Implications and further studies

The Farallon elephant seal breeding population has only been reestablished since 1972; maintaining a robust population in the face of climate and anthropogenic threats is therefore a high conservation and resource-management priority. The decline in number of pups produced that survive to weaning is a concern, providing motivation for this study to examine whether changes in pup survival probability can account, in part, for the decline in the number of pups successfully reared as well as to better understand factors that influence pup survival probability.

We have identified 2 sets of factors that influence pup survival probability on the South Farallon Islands: environmental conditions, especially in the months immediately prior to pup birth, which may, in turn, be affecting maternal condition during pup rearing, and which act at large spatial scales; as well as local factors impacting survival probability acting on a very local (island-specific) scale.

Our findings regarding specificity of impact with respect to extreme waves and/or inundation suggests value to 2 sets of follow-up studies to investigate the mechanism involved. First are fine-scale studies of the timing of pup mortality in relation to the timing of extreme waves or inundation within the pupping season. Le Boeuf & Reiter (1991) make the point that pup mortality was especially high in 1983 at the Año Nuevo colony not just because of extreme water levels, but

also because of the timing of the event in late January. Had a comparable storm event occurred substantially earlier or later in the pupping season, the impact would have been much reduced, they maintain. We were able to identify the significance of extreme waves in both January and February, but our results provide the impetus for a more detailed study of the timing of pup mortality in relation to extreme events, using, for instance, survival analysis, also referred to as time-to-event analysis (Hosmer et al. 2008, George et al. 2014; see example in Nur et al. 2004).

The second avenue of study concerns analyzing the within-island risk of mortality due to storms and extreme waves. Whereas we show that the effect of extreme waves/storms differs by island, monitoring of elephant seal rookeries suggests that the effect of storms may act on even smaller scales, such as specific haulout locations (Berger 2015). There is an opportunity to examine how conditions at individual breeding locations (elevation or slope of the beach, extent of sandy habitat, etc.) influence pup survival, especially in years with extreme events during the pupping season. Information on inundation of beach habitat during the pupping season would be invaluable.

In addition, our findings provide motivation for further study to elucidate how oceanic conditions in the months prior to, and including, arrival at haulout locations, ultimately influence pup survival. While the relationship between the mass of the mother at parturition and the mass of the weanling has been well studied, the relationship of maternal condition to pup survival has not been analyzed in the same detail. In addition, oceanic conditions in the fall and winter may influence the level of parental investment by the female (Ortiz et al. 1984, Arnbom et al. 1997); we hypothesize that under more benign conditions, females shift their resource allocation more to the pup, and therefore reserve less for their own self-maintenance. Clausius et al. (2017) report that environmental conditions in the month before the breeding season commences influenced weanling mass in southern elephant seals, over and above the direct effect of maternal mass on weanling mass, similar to findings by Holser et al. (2021) for the northern elephant seal.

Pup survival is an important demographic parameter underlying population viability and any management actions that can reduce pup mortality should be considered, for example, with regard to maintaining optimal physical condition of the pupping location. Regarding the demographic implications of pup survival, it does not appear that changes in pup survival probability have led to the long-term decrease in

number of surviving pups on the South Farallon Islands. If anything, there has been a slight, non-significant tendency for increasing pup survival over time (p > 0.3). However, the recent decline in pup survival on SEFI, observed in 2015–2019, is a cause of concern and provides motivation for further study.

That said, over the entire time series, the primary determinant of the reduction in number of surviving pups is the statistically significant decline in the number of females attending breeding colonies on the South Farallon Islands, an average decline of $3.42 \pm 0.42\%$ yr^{-1}, from 1983 to 2019. Identifying the causes of the decline is beyond the scope of this study, but such an investigation should consider habitat conditions at potential and actual breeding locations on the 2 islands, as well as considering suitability of habitat at other breeding locations within the region, including the Point Reyes peninsula (Sydeman & Allen 1999), the Año Nuevo colony (Le Boeuf 2021), as well as further north, such as in Humboldt County. Two possible mechanisms to consider with regard to reduction in the number of attending females are: reduced probability of local recruitment for Farallon-born elephant seals and/or reduced breeding fidelity for adult females. Reduction in the probability of local recruitment could be due to increased emigration of pups from the Farallon Islands or due to decreased survival of juveniles to adulthood (Condit et al. 2014). It is also possible that survival of adults has decreased during this time, though Lee (2011) found no evidence that oceanic conditions were correlated with adult female survival.

Identifying the causes of the decline in numbers of adult female northern elephant seals at the South Farallon Islands and addressing these causes are important objectives, but success will require a regional approach to the issue to determine if females are shifting their locations or whether there are region-wide population trends.

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Appendix.

Table A1. Determinants of northern elephant seal reproductive success (1 if a female reared a pup to weaning age; 0 if no pup was born or did not survive to weaning) on Southeast Farallon Island (SEFI) and West End Island (WEI). Results of the preferred model of reproductive success in relation to environmental variables, including main effect of island (SEFI vs. WEI, base level), fitting mixed-effects logistic regression on reproductive success. Model assumes outcomes are clustered by year (random intercept). Estimate of variance due to random effect (year) = 0.245 ± 0.040; likelihood ratio test that this differs from 0: $\chi^2(1)$ = 56.67, p < 0.0001. Effect of extreme wave index differed between the 2 islands (comparing WEI to SEFI: difference = −0.0529, SE = 0.0182, z = 2.90, p = 0.004); model output shows estimated slope coefficients for each island. Effect of fall–winter North Pacific Gyre Oscillation (NPGO) did not differ between the 2 islands, hence only a single slope was fit

Model statistics: no. of observations = 7548; no. of groups = 37
Log likelihood = −4775.607; Wald $\chi^2(4)$ = 56.06; p < 0.0001

Variable	Coeff.	SE	z	p > |z|	95% CI
NPGO fall–winter	0.2373	0.0442	5.37	0.000	0.1507 to 0.3238
Effect of island					
SEFI	−0.3869	0.0706	−5.48	0.000	−0.05253 to −0.2484
Effect of wave index by island					
SEFI	0.0106	0.0198	0.53	0.593	−0.0282 to 0.0494
WEI	−0.0424	0.0197	−2.15	0.031	−0.0809 to −0.0038
Intercept	0.9450	0.0775	12.20	0.000	0.7932 to 1.097