ARTICLE

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Environmental factors influencing eastern North Pacific gray whale calf production 1994–2016

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Abstract

This paper describes the relationship between eastern North Pacific gray whale calf production and environmental conditions in the Pacific Arctic where they feed. The results show how interannual variation in sea ice cover in the Bering and Chukchi Seas along with broader indices of North Pacific climate, such as Pacific Decadal Oscillation (PDO) and North Pacific Index (NPI), are linked to variation in gray whale reproductive output. Estimates of gray whale calf production were derived from 23 consecutive years (1994–2016) of shore-based visual surveys conducted off California during the northward migration. PDO and NPI in combination with ice cover in the Bering and Chukchi Seas during the early phase of gestation appear to be important in explaining the observed variability in calf production. Of the 2,285 time series linear models evaluated, the model of best-fit included PDO(July), Ice(June), NPI(February), and explained 60% of the observed variability in calf production. After elimination of two data outliers in calf production estimates (2013 and 2014) a model including Ice(May), PDO(May), and NPI(July) explained 90% of the variability. We conclude that access to prey early in the gestation period is critical to reproductive success in this population and may be important for other capital breeding mammals.

1 | INTRODUCTION

The life history of eastern North Pacific (ENP) gray whales *(Eschrichtius robustus)* follows a strategy typical of many baleen whales (mysticetes), which includes long annual migrations between seasonally productive high-latitude summer feeding grounds and lower-latitude winter calving and breeding grounds that have warmer and more oligotrophic waters (Rice & Wolman, 1971). Although gray whales feed opportunistically on benthic and pelagic prey during migration (Nerini, 1984) and a few hundred animals from this population feed during the summer between Northern California and Kodiak Island, Alaska (Moore, Wynne, Kinney, & Grebmeier, 2007), data showing that northbound gray whales weigh less (Rice & Wolman, 1971) and are thinner than those migrating south (Perryman & Lynn, 2002) suggest that the acquisition of energy stores for the 5–6 month migration occur primarily in the Arctic. This life history strategy places a large burden on reproductive females who must partition available resources firstly to support their own survival and secondly to support the demands of gestation and the much larger energy expenditure associated with lactation. Successful reproduction depends on the nutritive condition of the adult female and the availability of foraging opportunities to pregnant females following their northbound migration (Christiansen, Vikingsson, Rasmussen, & Lusseau, 2013; Lockyer, 2007). In preparation for this process, pregnant females are the first to return to the Arctic in boreal spring (Rice & Wolman, 1971) and their arrival in the Bering Sea coincides with the start of the seasonal retreat of sea ice (Stroeve, Markus, Boisvert, Miller, & Barrett, 2014).

Perryman, Donahue, Perkins, and Reilly (2002) found substantial interannual variability in estimates of the number of northbound gray whale calves each spring (1994–2000) off the coast of central California and reported a positive relationship between annual calf production and the length of the previous ice-free season in the Chirikov Basin of the northern Bering Sea, just south of the Bering Straits. Specifically, summer feeding seasons characterized by longer ice-free periods were followed in subsequent springs by higher estimates of calf production. The authors suggested that sea ice may represent a physical barrier potentially limiting access of pregnant females to important areas of prey resources. Reduced body condition related to a shorter feeding season may in turn impact the ability of females to bring pregnancies to term.

Since the publication of Perryman et al. (2002), significant changes have been reported in the Pacific Arctic, impacting both the seasonal sea ice cycle, as well as the location of important feeding habitats and the overall availability of benthic prey to gray whales (Grebmeier et al., 2015; Moore, 2008; Moore, Grebmeier, & Davies, 2003; Schonberg, Clarke, & Dunton, 2014). The Arctic is warming at a rate between two and three times the global average (Post et al., 2013) and reductions in the extent of seasonal and multiyear ice cover in the boreal summer are amongst the clearest signals of global climate change (Stammerjohn, Massom, Rind, & Martinson, 2012). However, the observed regional patterns of the sea ice system embedded within this Arctic-wide climatic trend are both temporally and spatially complex (Francis & Hunter, 2006; Frey, Moore, Cooper, & Grebmeier, 2015; Serreze, Crawford, Stroeve, Barrett, & Woodgate, 2016). In the Bering Sea, through which northbound gray whales must pass on their way north to Arctic feeding grounds, ice area during the beginning of the melt season in mid-April to May has remained at a comparable level and even shown episodic increases over the past few decades (Brown & Arrigo, 2012; Post et al., 2013; Serreze et al., 2016; Wendler, Chen, & Moore, 2014).

In contrast to the pattern of ice retreat reported for the Bering Sea, there has been a linear trend of earlier ice retreats and later ice formation in the Chukchi Sea from 1979 to 2014 (Serreze et al., 2016). Along with the overall reduction of seasonal ice cover in this region during the summer, primary production is reported to have increased by 30% between 1998 and 2012 (Arrigo & van Dijken, 2015). These increases are largest on the inshore shelves of

the Chukchi and Beaufort Seas and are fueled to a large extent by nutrient rich waters flowing northward through the Bering Strait (Brown & Arrigo, 2012). The significant increase in current flow through the Strait bringing warm surface waters into the Chukchi Sea results in more rapid seasonal ice melts along with longer open water seasons which, in turn, extend periods of rapid primary production (Woodgate, Stafford, & Prahl, 2015). There has also been a significant loss of thicker multi-year ice which adds to the overall all reduction in ice cover (Parkinson & Comiso, 2013) and is likely responsible for a significant increase in under ice primary production (Arrigo et al., 2012, 2014). In the absence of large pelagic communities of zooplankton, strong pelagic-benthic coupling contributes to exceptionally high benthic biomass in four "hot spots" in the northern Bering and Chukchi Seas (Grebmeier et al., 2015). Gray whales are still observed feeding within the Chirikov Basin of the northern Bering Sea (Moore et al., 2003) an area reported to have had historically high benthic infaunal biomass (primarily *Ampelisca* amphipods). However, it appears that there has also been a substantial shift of feeding effort farther north into the Chukchi Sea and extending to an area of persistently high productivity off Barrow, Alaska (Brower, Ferguson, Schonberg, & Clarke, 2017; Dunton, Grebmeier, & Trefry, 2014; Grebmeier, 2012; Grebmeier et al., 2015; Moore et al., 2003). These changes in the Pacific Arctic are contributing to what has been described as a "boom time" for baleen whales in this region (Moore, 2016).

This paper presents results from a substantially longer time-series of northbound gray whale calf production estimates than was previously analyzed in Perryman et al. (2002), and examines in greater detail the relationship between calf production and environmental conditions in the Pacific Arctic. We specifically address how interannual variation in sea ice area in the Bering and Chukchi Seas, along with broader indices of North Pacific climate (Pacific Decadal Oscillation, North Pacific Index) may contribute to variation in reproductive output. We further examine the timing of environmental variation in the context of the gray whale reproductive cycle and its potential impact on calf production.

2 | METHODS

2.1 | Shore-based surveys

Counts of northbound gray whale calves have been collected annually by observers from the Piedras Blancas Light Station, located on the central California coast, for 23 consecutive years (1994–2016). Survey effort began in mid- to late March each year and typically ended as counts of northbound calves reached insignificant levels (<1 calf/day) in late May. Data collection and calf production estimation were consistent throughout the study period and followed methodologies reported in Perryman et al. (2002). Weather permitting, counts were conducted by a team of two observers for 12 hr/day, 6 days/week (1994–2003 and 2005) or 5 days/week (2004 and 2006–2016). Primary search effort was carried out with unaided eye but 7×50 and 25×150 binoculars were also used to search farther from the watch site to confirm calf presence and identify individuals within groups. This time series of estimates is consistent in counting and estimation methodologies and several observers participated in all or nearly all of the surveys.

Following analyses presented in Perryman et al. (2002), it was assumed that the number of gray whale calves passing the survey site far enough offshore to be undetectable by the observers was negligible and that daytime and nighttime passage rates were the equivalent. To account for imperfect probability of detecting calves by the observation team we corrected the observer counts of northbound calves by the average detection probability estimates from seven consecutive years of replicate counts which found that the team missed about 11% of the calves passing the site (mean = −0.889, SE = 0.06375). Each day's effort was divided into four 3-hour periods and passage rates during these periods were calculated from the observed counts multiplied by the inverse of the detection function. To correct for periods when observers were not on effort, we used a population model that was stratified by week

to account for varying passage rates (Cochran, 1977). A Taylor series expansion (Seber, 1982) was used to calculate the variance of the estimates.

2.2 | North Pacific environmental indices

2.2.1 | Seasonal ice cover

Ice cover data used in this analysis were derived from Nimbus-7 SMMR and DMSP SSM/I-SSMIS satellite passive microwave data converted to ice cover (Fetterer, Knowles, Meier, Savoie, & Windnagel, 2017) and provided by the NASA National Snow and Ice Data Center Distributed Active Archive Center (https://doi.org/10.5067/EYICLBOAAJOU). These satellite products convert passive microwave brightness temperatures into sea-ice concentration values and used a 15% ice concentration threshold to delimit the area of sea ice coverage. We used the 15% threshold because it is the most commonly used standard for tracking broad area sea ice coverage in the north Pacific. Seasonal sea ice in the Pacific sector of the Arctic typically reaches its greatest areal coverage by mid-March and begins to retreat substantially in May (Stroeve et al., 2014). We summed the area covered by sea ice in the Bering and Chukchi Seas, and evaluated the relationship between monthly ice area and calf production with a lag time of 0 years (ice values during pregnancy) and 1 year (ice cover leading up to ovulation). In addition, we examined seasonal and annual averages of sea ice coverage, as well as day-of-the-year values corresponding to the latest retreat and earliest advance dates of 15% sea ice concentration contour across the Bering Strait, as well as the total duration (in days) that the Bering Strait remained open (data from Serreze et al., 2016). These variables indicating the timing of ice changes in the Bering Strait were only included in models of calf production based on seasonal and annual averages.

2.3 | Other indices of Arctic climate variability

In our exploration of environmental factors potentially influencing interannual variability in northbound gray whale calf estimates, we also examined monthly, seasonal, and annual mean values of two North Pacific climatic indices: Pacific Decadal Oscillation (PDO) Index and the North Pacific Index (NPI). The PDO Index, corresponding to the first principal component (or empirical orthogonal function) of monthly sea surface temperature anomalies (SSTa) over the North Pacific, provides an indicator of basin scale patterns of sea surface temperature north of $20°N$ latitude (Mantua, Hare, Zhang, Wallace, & Francis, 1997). Shifts in this index have been linked to warming/cooling trends and changes in ice concentrations (Zhang, Woodgate, & Moritz, 2010; Wendler et al., 2014). In contrast, the NPI corresponds to the area-weighted sea level air pressure over the region $30°N–65°N$, $160°E–140°W$, and tracks the intensity of the Aleutian Low (Trenberth & Hurrell, 1994). Strength and position of the Aleutian Low has been linked to advection of warm air northward with impacts on ice cover and inclusion of this factor provides some additional breadth in our consideration of factors impacting climate in the North Pacific (Bond, Overland, Spillane, & Stabino, 2003).

2.4 | Analyses: exploratory single-factor correlation analyses

The timing of environmental variation was examined in the context of the gray whale reproductive cycle by calculating Pearson correlation coefficients (ρ) between annual calf production estimates and (1) monthly combined sea ice area in the Bering and Chukchi Seas, (2) the monthly PDO index, and (3) the NPI index. Single-factor correlation analyses were examined at time lags between 0 and 27 months from the April mid-point of annual calf productions

surveys. The period 5–16 months (0 year lag) corresponded approximately to the gestation period in the breeding phenology of gray whales, while the period 17–26 months (1 year lag) corresponded to the prebreeding period during which reproductive females were either nursing a calf from the previous breeding cycle or building up energy reserves prior to breeding. Note that correlations during the +1 year period were based on one less year of data than the +0 year correlations.

2.4.1 | Time series linear models (monthly, annual, seasonal)

To develop a predictive model of calf production as a function of environmental covariates (e.g., sea ice area, Bering Strait timing, and climatic indices) we compared a variety of least squares time series linear model fits on the basis of Akaike's Information Criterion adjusted for small sample size (AICc), using the function *tslm* from the *forecast* package (v.8.2; Hyndman & Khandakar, 2008) in the statistical program R (v. 3.3.2; R Core Team, 2018). Time series linear models of annual calf estimates were fitted to possible combinations of monthly covariates within a time frame of 0–16 month lag prior to the calf survey such that each index (sea ice area, PDO, NPI) was represented only once in each model. This approach minimized possible multicollinearity issues resulting from the inclusion of multiple monthly representations of sea ice area, NPI, or PDO indices which showed strong intercorrelation between sequential months. We also investigated the possibility of multicollinearity between sea ice area, NPI, and PDO indices by calculating a variance inflation factor (VIF) for each combination of covariates. In addition, we fitted models of calf production based on all possible combinations of annual and seasonal mean sea ice area, NPI, and PDO indices, as well as variables representing the timing of the Bering Strait opening. Models were ranked on the basis of predictive performance in relation to model complexity using Akaike's weights (wAICc), which represents the probability that given model optimally minimized AICc out of a set of candidate models.

2.4.2 | Examination of residuals

Following the approach suggested by Hyndman and Athanasopoulos (2014), the validity of the top ranked models were evaluated by examining the standard residual plots for multiple linear regression models, as well as time-series specific metrics, including autocorrelation function plots and Breusch-Godfrey tests for serial correlation (Breusch, 1978; Godfrey, 1978) to evaluate potential temporal dependencies in the residuals that might necessitate more complex dynamic regression models (i.e., linear models with ARIMA errors). In several of the highest-ranking models, calf production estimates in 2013 and 2014 exhibited large positive residuals that exerted an unbalanced, highly leveraged influence on least squares parameter estimates, based on Cook's distances (D) (Cook,1977). These residuals also pulled the residual vs. fitted plot away from a homogeneous linear fit indicated by nonuniformly distributed residuals (i.e., nonhomoskedasticity). Therefore, an alternate set of candidate models was fitted with 2013 and 2014 removed, and model performance and validity, including tests of potential residual autocorrelation, were subsequently reexamined.

To assess the relative predictive performance of models based on the full data set, when compared with models fitted with the 2013 and 2014 outliers removed, a hv-block cross-validation analysis was used (Racine, 2000). This analysis allowed the mean squared predictive error (MSPE) to be assessed when comparing fitted values to observed data not used in fitting the model (including 2013 and 2014 calf estimates), while preserving the correlation structure inherent in the calf production time series data. The hv-block cross-validation procedure successively removed five test data sets of length $h = 5$, such that each data point was represented once as test data. A buffer region of $v = 2$ data points before and/or after each test data set was also excluded to account for possible autocorrelation between test and training data sets. Models were fitted using the remaining training data with or without the 2013 and 2014

outliers removed, and then the resulting model fits were used to predict to each test data set (including 2013 and 2014 calf estimates when these fell within the test data set).

3 | RESULTS

3.1 | Calf estimates

One of the clearest characteristics of the calf estimate time series was the high degree of interannual variability (Table 1), ranging from a high estimate of 1,528 calves in 2004 to a low of 254 calves in 2010. Using the closest published abundance estimates (16,033 for 2002 from Laake et al., 2009; 20,990 for 2011 from Durban, Weller, Lang, & Perryman, 2015) this equates to swings in calf production from 9.5% to 1.2%. Partially as a result of this high interannual variability there was no discernable secular trend in the calf production estimates over the 23-year period examined herein (Figure 1), despite an estimated 22% increase in the underlying adult eastern North Pacific gray whale population over the same period (Durban, Weller, & Perryman, 2017). There was, however, a trend in median migration dates, indicating that the midpoint of the migration is now occurring approximately 1 week later than in the mid-1990s. The slope parameter of this index of migratory timing was significant ($F = 6.030$, $p = .023$), however, only after excluding an outlier from the 1999 migration, the first year of an unusual mortality event for this population (Figure 2).

TABLE 1 Effort, counts and estimates of total northbound gray whale calves from shore-based surveys for northbound gray whale calves passing the Piedras Blancas Light Station.

| Year	Effort (hr)	Calf count	Calf estimate	SE
1994	671	325	945	68.21
1995	610	194	619	37.19
1996	694	407	1,146	70.67
1997	709	501	1,431	82.02
1998	554	440	1,388	94.84
1999	737	141	427	41.10
2000	704	96	279	34.79
2001	722	87	256	28.56
2002	711	302	842	78.60
2003	686	269	774	73.56
2004	562	456	1,528	96.00
2005	669	343	945	86.90
2006	531	285	1,020	103.30
2007	469	117	404	51.20
2008	498	171	553	53.11
2009	476	86	312	41.93
2010	487	71	254	33.94
2011	500	246	858	86.17
2012	435	330	1,167	120.29
2013	483	311	1,122	104.14
2014	529	429	1,487	133.35
2015	522	404	1,436	131.01
2016	436	367	1,351	121.38
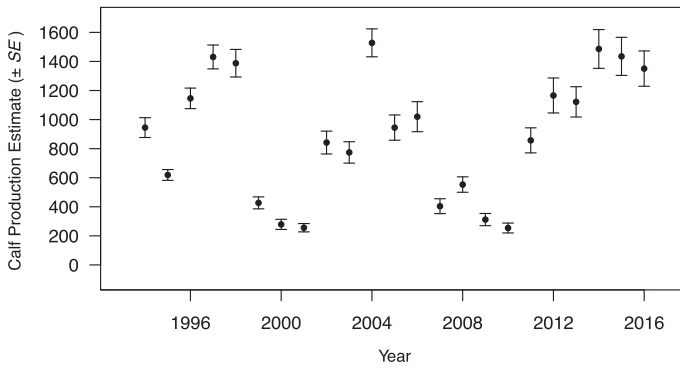
FIGURE 1 Estimates of northbound gray whale calves passing the Piedras Light Station during shore-based surveys 1994–2016.
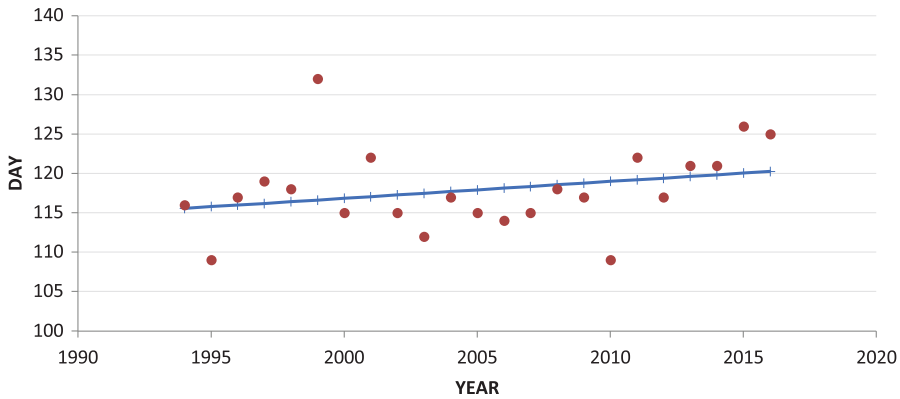

FIGURE 2 Plot of median migration dates for northbound gray whale calves surveyed from the Piedras Light Station. Slope of linear regression line is significant if 1999 point deleted.

3.2 | Relationships between calf estimates and environmental variables

Examining single factor correlation coefficients between calf estimates and monthly indices of Bering-Chukchi sea ice area, PDO, and NPI, we found consistently higher negative correlations with sea ice and NPI and positive correlations with PDO during the pregnancy or gestation phase of gray whale reproductive phenology, relative to the prebreeding and ovulation phase (Figure 3). In particular, we found that correlations between calf production and ice area ($\rho_{ice,May + 0}$ = −0.60) and PDO ($\rho_{PDO,May + 0}$ = 0.53) both peaked during May of the +0 year, a period when reproductive females first return to high-latitude feeding grounds during early pregnancy, and when sea ice extent in some years covers a substantial portion of the summer feeding grounds (Figure 4).

3.3 | Time series linear model selection results

Fitting time series linear regression models to all possible combinations of Bering-Chukchi ice area, PDO, and NPI, where each monthly index was represented only once, resulted in n = 2,196 least squares model fits. Annually and seasonally averaged Bering-Chukchi ice area, PDO, and NPI, as well as dates representing the retreat, advance, and open season values for the Bering Strait, contributed an additional 89 models for a total of n = 2,285 models represented in the subsequent AICc model comparison analysis. Based on the full data set, the model that minimized AICc (Calves ~ Ice$_{June}$ + PDO$_{July}$ + NPI$_{January}$), explained a substantial proportion of the variance in calf production
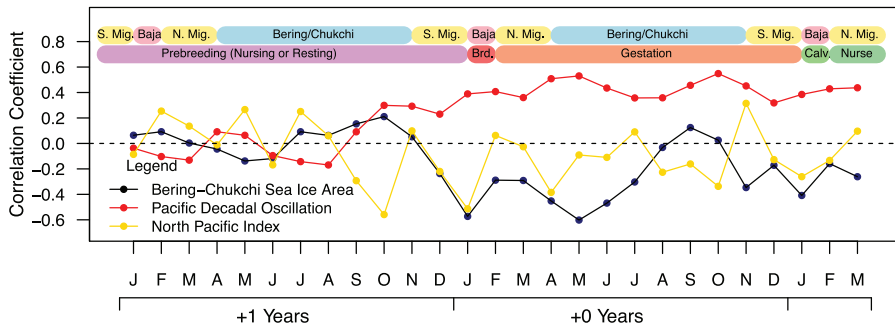
FIGURE 3 Correlation coefficients of calf production estimates (Table 1) and the extent of combined Bering-Chukchi Sea ice, PDO, and NPI mean values for the seasons of ovulation and calving.
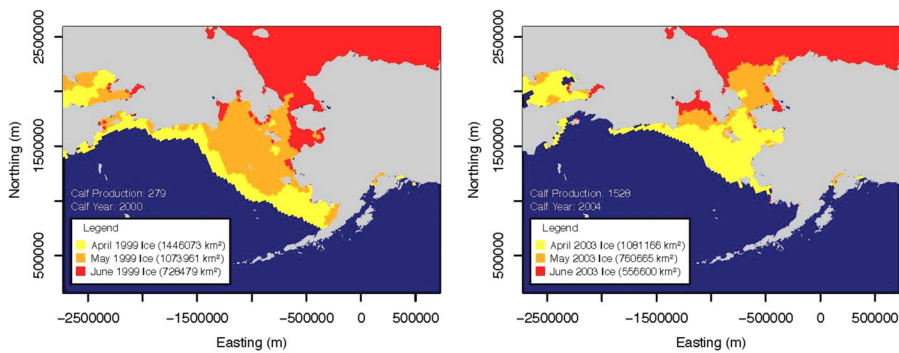

FIGURE 4 Comparison of two contrasting seasons of seasonal ice cover, 1999 with extensive ice in April–June and 2003 with much less ice, and estimates of northbound calves that followed these ice events.

(R^2 = 0.60; Figure 5a). However, support for this model out of the range of candidate models was diffuse (wAIC = 0.11), and an examination of the residuals plot revealed two large positive residuals associated with the 2013 and 2014 calf production years. These outlying residuals resulted in a nonuniform distribution of the residuals with respect to the fitted values, and were shown to have highly leveraged influence on the least squares parameter estimates ($D_{Cook's}$ = 0.19, 0.36). Refitting all the candidate models with the 2013 and 2014 outliers removed, resulted in the selection of Calves ~ Ice_{May} + PDO_{May} + NPI_{July} as the most parsimonious model, explaining a high proportion of the observed variance in calf production (R^2 = 0.90). The strength of this model fit, which included four parameters, can also be seen in the close alignment of the predicted and observed calf production in Figure 5b. Moreover, based on Akaike's weights there was substantially greater support for this individual model (wAIC = 0.40) out of the set of candidate models, as well as greater consistency between the covariates selected across all of the highest ranked models. All fifty of the highest ranked models (representing 96.6% of wAIC probability), contained Ice_{May} and more than half of these models (n = 27) also contained a term representing PDO in April, May, or June.

Excluding the 2013 and 2014 calf estimate years from the training data sets but not the test data sets in the hv-block cross validation analysis also resulted in substantially lower prediction error ($MSPE_{full\ data}$ = 117,310, $MSPE_{2013,2014excl.}$ = 101,169), in the highest ranked model as well as more generally across all candidate models. Further examining the residuals of the highest ranked models revealed consistent variance with respect to the fitted values, and based on an examination of autocorrelation functions and Breusch-Godfrey tests there was no indication of significant temporal dependency in the residuals that would suggest the need for dynamic regression models with ARIMA errors. Finally, it is notable that annually or seasonally averaged indices, which might be expected to smooth
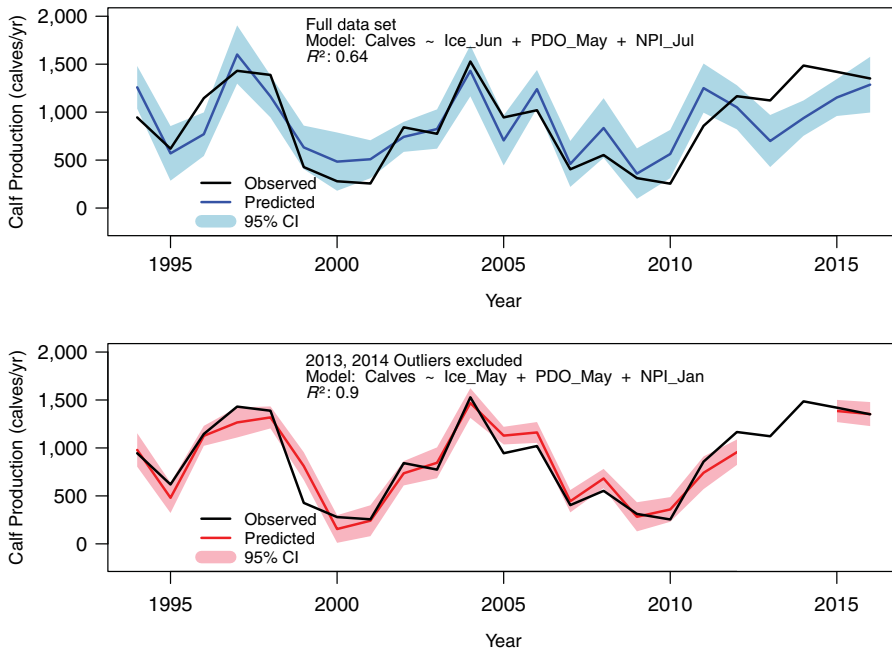
FIGURE 5 Best multiple linear regression fits of calf estimates for models based on the full data set (a) and for the models excluding the two outlier years, 2013 and 2014 (b).

month-to-month volatility in ice area, PDO, and NPI indices, performed substantially worse than monthly indices of ice area and PDO in the April–May–June time period when pregnant females first arrive back on the feeding grounds.

4 | DISCUSSION

Over the 23-year time series reported in this study, estimates of northbound eastern North Pacific gray whale calves displayed a degree of variability that cannot be explained solely on the basis of recruitment to or mortality/senescence from the breeding age population. Overall, the correlation analysis as well as the inference from the model selection process developed in this study both point to environmental conditions during this early phase of gestation as potentially important factors in the high interannual variability in ENP gray whale calf production. Specifically, in years of negative PDO and/or extensive sea ice cover in important gray whale feeding habitats in the northern Bering and southern Chukchi Seas in May and June, counts of north-bound migrating calves are lower in the following spring.

This variability may also be consistent with the life history strategies of other long-lived mammals, in which females must weigh the immediate energetic costs of pregnancy and lactation against their own survival and potential future reproductive output (Wade & Schneider, 1992; Wasser & Barash, 1983). Females faced with the natural fluctuations in prey/food resources may not ovulate, behaviorally avoid pregnancy, or may not carry a pregnancy to term unless they are in physically robust condition and/or feeding opportunities are favorable (Wade & Schneider, 1992; Williams et al., 2013). These reproductive tradeoffs are likely particularly acute in ENP gray whale females, which rely on stored energetic capital to meet their basal metabolic requirements during approximately half of each year, as well as incurring the simultaneous energetic costs of a demanding 14,000+ km round trip migration along with the provisioning of early fetal development. These considerations raise the intriguing question of when

during the reproductive phenology of female gray whales does environmental variability play the most direct role in influencing reproductive outcomes?

The exploration of correlations at different time lags in this study revealed stronger relationships between estimates of total northbound calves and the three selected environmental variables during gestation as opposed to the season prior to ovulation (Figure 3). Because of the strong intercorrelation between ice conditions and climatic indices across successive months, examining the correlation of calf estimates with environmental indices in any single month in isolation should be approached with caution. For example, the elevated correlation between calf production and sea ice area in January of the +0 year when reproductive female gray whales were breeding 7,000+ km to the south and east of Bering and Chukchi Seas, likely resulted from the correlation between January ice area and conditions later in the spring when gray whales were actually present in these habitats. However, we contend that the broad scale differences in strength of correlation with multiple environmental metrics between major phases of the breeding cycle likely reflect real biological differences in the timing of environmental influence on reproductive outcomes. With these important caveats in mind, we also note that correlation coefficient values peaked during the period when pregnant females were returning to the feeding grounds and confronting highly variable ice conditions, rather than during the ice advance period prior to ovulation. Our cautious interpretation is that the ability to rapidly replenish energetic capital reserves following the lengthy migration may play a more important role than female prebreeding condition in regulating calf production variability.

These results are consistent with those reported by Perryman et al. 2002 on the basis of a smaller data set from this population. They are also consistent with a growing body of results demonstrating the link between prey availability during pregnancy and reproductive suppression in baleen whales and other large terrestrial and marine mammals (Christiansen et al., 2013; Guinet, Roux, Bonnet, & Mison, 1998; Knowlton, Kraus, & Kenny, 1994; Leaper et al., 2006; Pitcher, Calkins, & Pendleton, 1998; Russell, Gerhart, White, & van de Wetering, 1998; Seyboth et al., 2016; Testa & Adams, 1998; Williams et al., 2013). While it is likely that all aspects of the reproductive cycle of female gray whales are impacted by their nutritive condition (Lockyer, 2001; Rice & Wolman, 1971), it appears that for this species, and likely for the other capital breeding large cetaceans, energy availability during gestation plays a critical role in the health and survival of the fetus.

The results of the model selection process in this study also support the importance of a negative relationship with Bering and Chukchi sea ice area and the positive relationship with elevated temperature anomalies over the western North Pacific and Pacific Arctic (i.e., positive PDO) during the late spring (April–May–June) period when females are first experiencing sea ice conditions and prey availability on the foraging grounds following migration. May ice area alone explained over 80% of the variability in calf estimates and was selected in all of the top 50 models. This finding supports the hypothesis that, under the conditions prevalent over our study period, in years where seasonal ice is slow to melt in the Bering and Chukchi Seas reproductive output is reduced in the ENP gray whale population. It is unclear whether the relationship with seasonal sea ice will continue into the future, however, the overall highest ranked model that also included May Ice Area, May PDO, and January NPI, proved remarkably successful in predicting observed calf production using only four parameters (including the intercept) linked to high-level physical indicators of oceanographic and atmospheric variability.

While our research has identified a particular sensitivity of gray whale calf production to changes in ice conditions over several decades between 1994 and 2016, ongoing climate change in the Arctic and Pacific basin will perhaps alter this pattern. For instance, the exceptionally low estimate of calf production in 2019 (Stewart & Weller, 2020) does not correspond with extensive spring sea ice and, in fact, was preceded by a nearly ice-free Bering Sea and extensive ice-free areas along the Alaskan Chukchi shelf in May 2018. Taken together with the high northbound calf estimates in 2013 and 2014, despite a relatively late ice retreat in 2012 and 2013 feeding seasons, suggests additional factors may be affecting mortality and reproduction, including potential effects of a changing climate and possibly intraspecific competition from a population that has substantially increased in abundance during the time period reported here. These events serve as a reminder that the link between gray whale calf production and environmental drivers should not be viewed as static, especially given the highly dynamic changes being
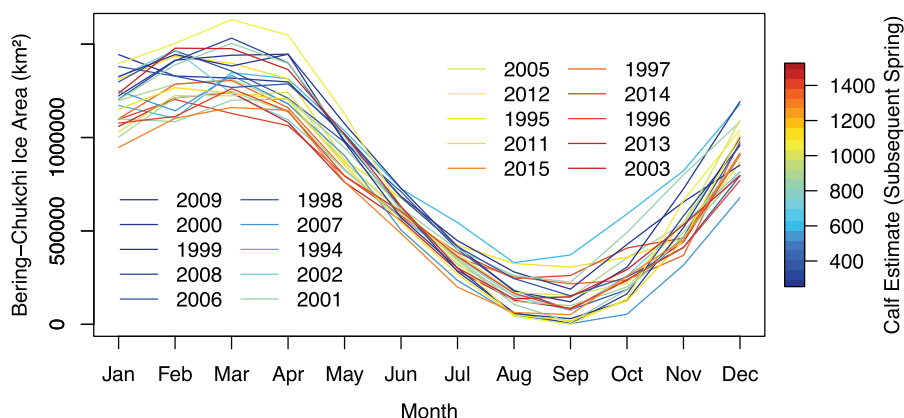
FIGURE 6 Plots of monthly combined values for sea ice area in the Bering and Chukchi Seas based on data published by the National Snow and Ice Data Center. Note pattern of separation between extensive ice years and those with less ice during the critical month of May.

recorded in the Arctic ecosystem. Understanding new and dynamic changes in the relationships reported here, if they occur, will require additional long-term data extending long enough to differentiate short-term responses from long-term patterns.

Although this paper primarily focuses on environmental factors correlated with reproductive output, there has also been considerable discussion of carrying capacity in the ENP gray whale population, particularly surrounding an Unusual Mortality Event (UME) in 1999 and 2000 (Gulland et al., 2005), and a more recent UME in 2019. The poor body condition observed for both living and dead whales, elevated stranding levels, and a subsequent drop in estimated population levels following the 1999/2000 UME has been previously interpreted as being due to exceeding carrying capacity (Moore et al., 2001) with negative top-down effects on benthic prey populations (Coyle, Bluhm, Konar, Blanchard, & Highsmith, 2007; Grebmeier & Dunton, 2000; Highsmith & Coyle, 1992). However, it is notable that 1999 and 2000, which also corresponded with very low estimates of calf production, were preceded by extensive sea ice in the Bering and Chukchi during the spring and early summer (Figure 6).

Conditions in the Pacific Arctic are rapidly changing including warmer temperatures, earlier onset of the melt season, open water leading to reduced ice-albedo effect, and longer ice-free seasons (Perovich et al., 2007; Stammerjohn et al., 2012; Stroeve et al., 2014), as well as an increased flow of nutrient rich waters from the northern Bering Sea into the Chukchi (Brown & Arrigo, 2012). The latter is contributing to significant increases in primary production and longer feeding seasons in important gray whale foraging areas. These changes are likely reflected in a pattern of slowly shifting towards a later migration of reproductive females with calves, which is analogous to the findings for southbound gray whales reported by Rugh, Shelden and Schulman-Janiger (2001). They are likely also reflected in the pattern of positive residuals over three of the past five years in our time series and indications of increased abundance for this population (Durban et al., 2017).

The direct cause of the anomalously high calf estimates for 2013 and 2014 are not fully understood, but these estimates coincided or followed anomalous weather and ice conditions in the north Pacific and Arctic. The warm water "blob" was the result of a marine heatwave that began during the winter of 2013 and lasted through 2015 (Di Lorenzo & Mantua, 2016). The 2013 and 2014 counts of gray whale calves also followed the summer 2012 season which represented the lowest recorded Arctic-wide sea ice extent during the satellite era dating back to 1978 (Parkinson & Comiso, 2013). The pattern of ice cover in that year may also have been important because while ice cover in May, an apparently critical time for gray whales, was indistinguishable from the median values for 1981–2010, ice melted rapidly in June, soon exceeding the open water area of the previous record low year of 2007

(Figure 6). It is also interesting to note that 2013 also appears to have been an exceptionally high year for bowhead whale reproduction, suggesting that they may also benefit from years with low ice cover (Clarke, Ferguson, Brower, & Willoughby, 2018)

It is clear now that the transition to a seasonally ice-free state in the Arctic will occur in the near future (Holland, Bitz, & Tremblay, 2006). This comparatively abrupt climatic shift is likely to create winners and losers as multiyear and seasonal ice cover continue a general pattern of decline. Pagophilic marine mammals, including many ice seals, walruses (*Odobenus rosmarus*), polar bears (*Ursus maritimus*), narwhals (*Monodon monoceros*)and possibly beluga whales (*Delphinapterus leucas*) are likely to face challenges in adapting to the "new climatic normal." The results of this study and other recent findings (e.g., Brower, Clarke, & Ferguson, 2018; George et al., 2018; Moore & Laidre, 2006) suggest that gray whales, bowhead whales, and other baleen whales that are becoming more common in Arctic waters, may increase in abundance, at least in the short term.

AUTHOR CONTRIBUTIONS

Wayne Perryman: Conceptualization; data curation; funding acquisition; methodology; project administration; supervision; writing-original draft; writing-review and editing. **Trevor Joyce:** Formal analysis; methodology; visualization; writing-review and editing. **David Weller:** Funding acquisition; investigation; methodology; writing-original draft; writing-review and editing. **John Durban:** Formal analysis; investigation; validation; writing-original draft; writing-review and editing.

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