

Examination of the Relationship Between Seasonal Ice and Calf Production in the Eastern Pacific Population of Gray Whales.

Wayne L. Perryman, SWFSC, George Watters, PFEG, Lisa Schwarz, SDSU,

ABSTRACT: We developed indices of seasonal ice distribution relative to known feeding grounds for eastern Pacific gray whales. We used log linear models to describe calf production in this population as a function of a slow compensatory response to reduced prey biomass and a more rapid response to interannual variability in access to feeding grounds related to seasonal ice. We used the model to test a series of hypotheses and found that most of the observed variability in calf estimates between 1994 and 2001 could be explained by compensation to reduced prey and the distribution of seasonal ice during the first half of the feeding season prior to calf production. The effect of ice distribution during the feeding season prior to ovulation was eliminated from the model based on AIC_C criteria. Based on the distribution of seasonal ice between April and August 2001, we predict an increase in calf production for this population (349 or 703 depending on number of parameters in the model) in 2002. We suggest that the ability to terminate existing pregnancies when the nutritive condition of the females is not adequate to deal with the physiological challenge of fasting through much of lactation may be a significant factor in the reproductive strategy of gray whales.

Introduction

The recovery of the previously endangered eastern Pacific gray whale (*Eschrichtius robustus*) population is a success story, but a recent decline in calf production and a simultaneous increase in strandings have promoted the hypothesis that the population is rapidly compensating in response to food limitation (LeBoeuf *et al.* 2000). Moore *et al.* (2001) asked whether the gray whale population was “hitting K [carrying capacity] hard.” We propose an alternative hypothesis, that the recent decline in calf production and increase in strandings are the result of slow compensation (on a decadal scale) and fast physical forcing (on an annual scale). We neither believe that there is a single carrying capacity for gray whales nor that the population is hitting a current K hard.

Decadal processes seem to play a role in gray whale population dynamics. During the late 1980s and into the 1990s, the growth rate of the eastern Pacific gray whale population slowed (Breiwick in press, Wade in press), as the estimated biomass of their benthic prey in the Bering and Chukchi seas decreased (Highsmith and Coyle 1992; Coyle and Highsmith 1994; Grebmeier and Dunton 2000). These findings support the hypothesis that the gray whale population compensates for food limitation. Nevertheless, this compensation appears to have been on at least a decadal scale, and it is unclear whether other compensatory processes could have been rapid enough to explain the almost 10 fold increase in strandings and 70 % drop in calf production observed in 1998 (Moore *et al.* 2001; Perryman *et al.* 2002).

Annual processes also seem to play a role in gray whale population dynamics. Variations in calf production during 1994-2000 were correlated with the duration of the ice-free season over the Chirikov Basin (Perryman *et al.* 2002). The Chirikov Basin is an important feeding ground for eastern Pacific gray whales (Moore *et al.* 2000, Moore and DeMaster 1997), and adult females may terminate pregnancies if they cannot consume enough amphipods to later fast through the last two months of pregnancy and the majority of lactation (Perryman *et al.* 2002). Because the period of rapid fetal growth in rorquals coincides with arrival on the feeding grounds (Lockyer 2002), it seems likely that the impact of limited prey availability on existing pregnancies occurs early in the feeding season, before significant physiological investment in the fetus. Thus, interannual variation in ice cover and duration could limit access to important feeding grounds and ultimately lead to interannual variation in the number of pregnancies that are carried to term.

In this paper we develop a simple model that describes both a slow compensatory decline in calf production and fast modifications of this decline by physical changes in access to feeding grounds. We compare indices of seasonal ice distribution with gray whale calf production during 1993-2001. We consider relationships between calf production and ice distributions early and late in the summer feeding season to determine when the link between whales and ice was effected. We consider relationships between calf production and the temporal distribution of seasonal ice during the summers in which female whales were pregnant and prior to ovulation to determine which process was more affected by access to the feeding grounds. Based on the distribution of ice in 2001, we predict calf production for 2002.

METHODS

Based on published sources (Berzin 1984; Nerini 1984; Moore 2000 Moore *et al.* 2000) and personal observations in the Arctic, we produced a composite chart of feeding grounds for gray whales, covering an area of about 49,418 km² (Figure 1). We realize that Figure 1 is not an all inclusive representation of areas in which gray whales feed. Our goal was to develop a broad spatial model that would serve as a tool for detecting the impacts of relatively subtle shifts in ice cover feeding opportunities for gray whales. In the analyses that follow, all feeding sites were considered to be of equal importance to the population.

We constructed a digital model of Figure 1 within the GIS program ARC/INFO and then converted this model to a Lambert equal-area azimuth projection. We obtained composite weekly charts of ice type, extent, and thickness from the National Ice Center (NIC) (1977-1994, and 1997-2001) and the National Snow and Ice Data Center (NISIDC) (1995-1996), imported them into ARC/INFO, and converted their projections to match the feeding grounds model described above. Each ice chart was then overlaid with the feeding grounds model and intersect points were used to determine the areas of the feeding grounds that were free of ice. We considered regions that were reported to have <10% concentrations as ice-free. After ARC/INFO calculated the area of feeding habitat that was free of seasonal ice, each chart was visually inspected to insure that isolated polynyas were not interpreted as available feeding

habitat. We calculated the percent of the feeding grounds that were ice free for each chart and developed a plot for these values for each year (Figure 2). The area under the curve was used as our index of seasonal ice (SI) for that year.

Modeling Strategy

We used log linear models to describe calf production as a function of a relatively slow compensatory process and relatively fast variations in access to feeding grounds. Our approach was to specify a saturated model designed to consider all hypotheses of interest and then to reduce this model by removing terms that were not useful from an information theoretic standpoint. We considered four hypotheses in the saturated model.

1. Calf production was affected by compensation.
2. Calf production was affected by access to feeding grounds during the entire feeding season prior to ovulation.
3. Calf production was affected by access to feeding grounds during the first half of the feeding season in which female gray whales were pregnant.
4. Calf production was affected by access to feeding grounds during the second half of the feeding season in which female gray whales were pregnant.

Motivations for hypotheses about the importance of compensation and access to feeding grounds during pregnancy are provided in the Introduction. It has also been suggested that physical conditions during the summer in which female gray whales ovulate would affect calf production (Rice and Wolman 1971). Given these four hypotheses, the systematic component of our saturated model had five parameters.

$$\ln(Ct) = a + \lambda(t-1) + \lambda SI_{t-2,1+2} + \beta_1 SI_{t-1,1} + \beta_2 SI_{t-1,2}. \quad (1)$$

We used the year t to denote the year of northbound migration, $t-1$ to denote the year of pregnancy, and $t-2$ for the year of ovulation. Ct is the estimate of northbound calves in year t , and $SI_{t,p}$ is the seasonal ice index in period p of year t . Period 1 covers April 7-August 18 (the first half of the feeding season), and period 2 covers August 19-December 31 (the second half of the feeding season). An entire feeding season is denoted by the subscript 1+2. a is an intercept, and the λ and β parameters determine the degree to which seasonal ice indices affect calf production. We use the year of pregnancy ($t-1$) as a proxy for an unobserved suite of ecological and environmental conditions to which the gray whale population might respond in a compensatory manner. The parameter γ determines the strength of this compensatory response.

We fitted models with negative binomial likelihoods, and removed terms from the saturated model with a bias-corrected modification of Akaike's Information Criterion (AICc) (Burnham and Anderson 1999). We motivated the negative binomial structure by assuming that calf production in any given year is distributed as a Poisson random variable, and that the mean of this Poisson distribution is itself distributed as a gamma random variable. This motivation

seems consistent with our view that the expected calf production (not simply calf production itself) should vary with changing ecological and environmental conditions (*e.g.* with long-term changes in benthic amphipod production). The Poisson-gamma mixture leads to the negative binomial distribution (McCullagh and Nelder 1989). We calculated AICc for all possible models nested within the saturated model (*i.e.* we considered all possible combinations of the four hypotheses listed above) and selected the model with the lowest AICc.

$$\text{AICc} = -2\ln(L) + 2p + \frac{2p(p+2)}{n-p-1}. \quad (2)$$

n is the number of observations, and p is the number of parameters in the model. The log negative binomial likelihood is $\ln(L)$.

$$\ln(L) = \sum_i (\ln[\Gamma(\theta + y_i)] - \ln[\Gamma(\theta)] - \ln[y_i!]) + y_i \ln[\mu_i] + \theta n[\theta] - [\theta + y_i] \ln[\mu_i + \theta]. \quad (3)$$

y_t is the observed log calf estimate in year t ; μ_t is the predicted log calf estimate in year t ; and θ is a parameter that determines how the variance in log calf estimate changes as a function of the mean. Estimates of θ were made for each of the candidate models. We used AICc (rather than AIC) because the number of parameters in our saturated model was relatively large compared to the number of calf-estimate observations (Burnham and Anderson 1999). We used the negative binomial modeling functions provided by Venables and Ripley (1999).

RESULTS

After removing terms from the saturated model (Table 1), we estimated that

$$\ln(C_t) = 29141 - 0.14(t - 1) + 0.05SI_{t-1,1}. \quad (4)$$

The fit of (4) is illustrated in Figure 3A (note that the fit is shown on the original scale of the observations). Given the sign of the $SI_{t-1,1}$ effect in (4) and our definition of SI , our model predicts that calf production is increased when less ice covers the feeding grounds during the first half of the summer in which females are pregnant (Figure 3B). The relative contributions of the $t-1$ and $SI_{t-1,1}$ effects to variation in observed calf production are illustrated in Figure 3C. The $t-1$ effect suggested a slow compensatory decline in calf production, and the $SI_{t-1,1}$ effect suggested that more rapid variations in access to feeding grounds caused calf production to vary around this declining trend.

Although we selected (4) as our final model, residuals from this model were not randomly distributed. Six of the eight residuals from (4) were negative, including the three residuals for 1998-2000 (Figure 3A-B). The relative abundance of negative residuals from (4) suggested that we did not identify an important predictor of calf counts or that the AICc may have been overly

stringent. We found that the models listed prior to (4) in Table 1 had residuals that were better behaved, but such a difference might be expected because the former models had more parameters. We acknowledge that it was difficult to unequivocally resolve the apparent discrepancy between model selection based on AICc and consideration of residual patterns.

We made two predictions of calf production in 2002, and we expect about 350 or 700 calves to pass Pt. Piedras Blancas during their northbound migration in 2002 (Table 2). The first prediction was made from (4) using $t-1 = 2001$ and $SI_{2001,1} = 73.85$. The second was made from the fifth model listed in Table 1;

$$\ln(C_t) = 292 + 0.05SI_{t-1,1} \quad (5)$$

Note that the $SI_{t-1,1}$ effects estimated in (4) and (5) were equivalent. We predicted calf production from both (4) and (5) because the $t-1$ effect in (4) cannot account for the possibility that environmental and ecological conditions in 2001 may be reversed from those that apparently caused a compensatory decline in calf production during 1993-2000. For example, (4) might not be appropriate if benthic amphipod production decreased during 1993-2000 but increased in 2001. We also estimated two prediction intervals from (4) and (5) (Table 2). The intervals from both models overlapped substantially, and suggest that the interval (160, 1600) would include calf production in 2002 more than 50% of the time.

Table 1: Selection from the saturated model. The table is structured to show a sequence of single-term deletions, but all possible subsets of the hypotheses described by the saturated model were considered.

Model	Residual df	2ln(L)	AICc
$\ln(C_t) = a + \psi(t - 1) + \lambda SI_{t-2,1+2} + \beta_1 SI_{t-1,1} + \beta_2 SI_{t-1,2}$	3	-94.0	134.0
$\ln(C_t) = a + \psi(t - 1) + \lambda SI_{t-2,1+2} + \beta_1 SI_{t-1,1}$	4	-94.4	115.7
$\ln(C_t) = a + \psi(t - 1) + \beta_1 SI_{t-1,1}$	5	-98.1	110.1
$\ln(C_t) = a + \beta_1 SI_{t-1,1}$	6	-110.7	117.1
$\ln(C_t) = \varepsilon$	7	-119.6	122.5

Table 2: Predicted calf estimates during the 2002 northbound migration.

Model	Expected calf count	Approximate 51% pred. interval	Approximate 95% pred. interval
$\ln(C_t) = a + \psi(t - 1) + \beta_1 SI_{t-1,1}$	349	(165, 740)	(26, 4672)
$\ln(C_t) = a + \beta_1 SI_{t-1,1}$	703	(335, 1476)	(60, 8286)

DISCUSSION

We found that most of the observed variability in calf estimates for eastern Pacific gray whales could be explained by compensation to processes acting over both decadal and interannual time scales. The long term factor is likely a reflection of the gray whale population response to the well documented decline in the biomass of benthic amphipods in the northern Bering and Chukchi Seas. However, most of variability in calf estimate appears to be related to interannual differences in the spatial and temporal distribution of seasonal ice. Specifically, it was the extent of seasonal ice during the first half of the feeding season that was linked to the number of calves produced in the following winter. A factor representing the impact of seasonal ice on ovulation (year $t-2$) was included in the saturated model but removed based on AIC_C criteria (Table 2). Thus, our results support the hypothesis that observed changes in gray whale calf production were related to impacts on existing pregnancies (Perryman *et al.* 2002).

While it is likely that ovulation rates for adult female gray whales, and probably all baleen whales, are linked to adult female nutritive condition (Rice and Wolman 1971; Lockyer 2002) our results suggest that the termination of existing pregnancies is also likely to be a significant factor in the reproductive strategy for gray whales. The link between the adult female condition and the probability that existing pregnancies are carried to term has been demonstrated for some pinnipeds (Testa 1987; Pitcher *et al.* 1998) and was suggested for fin whales by the correlation between estimated pregnancy rates and prey availability in the same season Lockyer (1987). Because lactation is the most physiologically demanding aspect of reproduction and female gray whales rely on stored fats to support them through most of this period, it seems likely that they have evolved a mechanism to protect them from producing calves that they cannot support. Unless an adult female gray whale was significantly under nourished, it would seem most efficient for her to ovulate, become pregnant and then make a “decision” on whether to carry the pregnancy to term based on her condition early in the feeding season while her physiological investment in the foetus was still small.

Based on the distribution of seasonal ice between April and August of 2001, we predict that there will be an increase in calf production for gray whales in 2002 (Table 3). The scale of the increase depends upon whether the factor for long-term compensation for reduced prey abundance should be included in the model. We acknowledge that the model that we have developed is a simple one, that we don't know how long the link between ice and gray whale calf production has been in effect, and that its predictive capacity is limited. In an attempt to address the history of the link between ice distribution and calf production, we developed SI indices back through the years prior to the estimate of northbound gray whale calves published by Poole (1984).

Figure 4 shows normalized values for SI indices from 1976 through the present. Poole (1984) estimated the number of northbound gray whale calves in 1980 and 1981 were essentially the same. These years follow the two most disparent years for seasonal ice in our record and thus suggest that the link between ice and gray whale reproduction was not present in the early 1980s. It is interesting to note that the period of ice shortened feeding seasons during the late

1980s and early 1990s coincide with periods when pregnancy rates reported from the Russian fishery showed a downward trend (Reilly 1992). This longer perspective also seems to indicate that the period from 1993 through 2001 was characterized by relative long feeding seasons (large positive SI indices). This suggests that the large calf estimates for the 1996 - 1998 seasons may represent the anomalies in reproduction for this population rather than the very low estimates reported for 1999-2001 (Perryman *et al.* 2002; Perryman and Rowlett 2002).

Although our model does not directly include factors to account for the complex shifts that have been reported in the Arctic ecosystem, we feel that we have proposed a plausible mechanism for the relationship between seasonal ice cover and calf production for gray whales. While it is possible that seasonal ice is only the visible reflection of some other correlated environmental parameter, the simple obstruction of feeding grounds by ice provides a reasonable explanation to the rapid changes in reproduction in response to environmental change.

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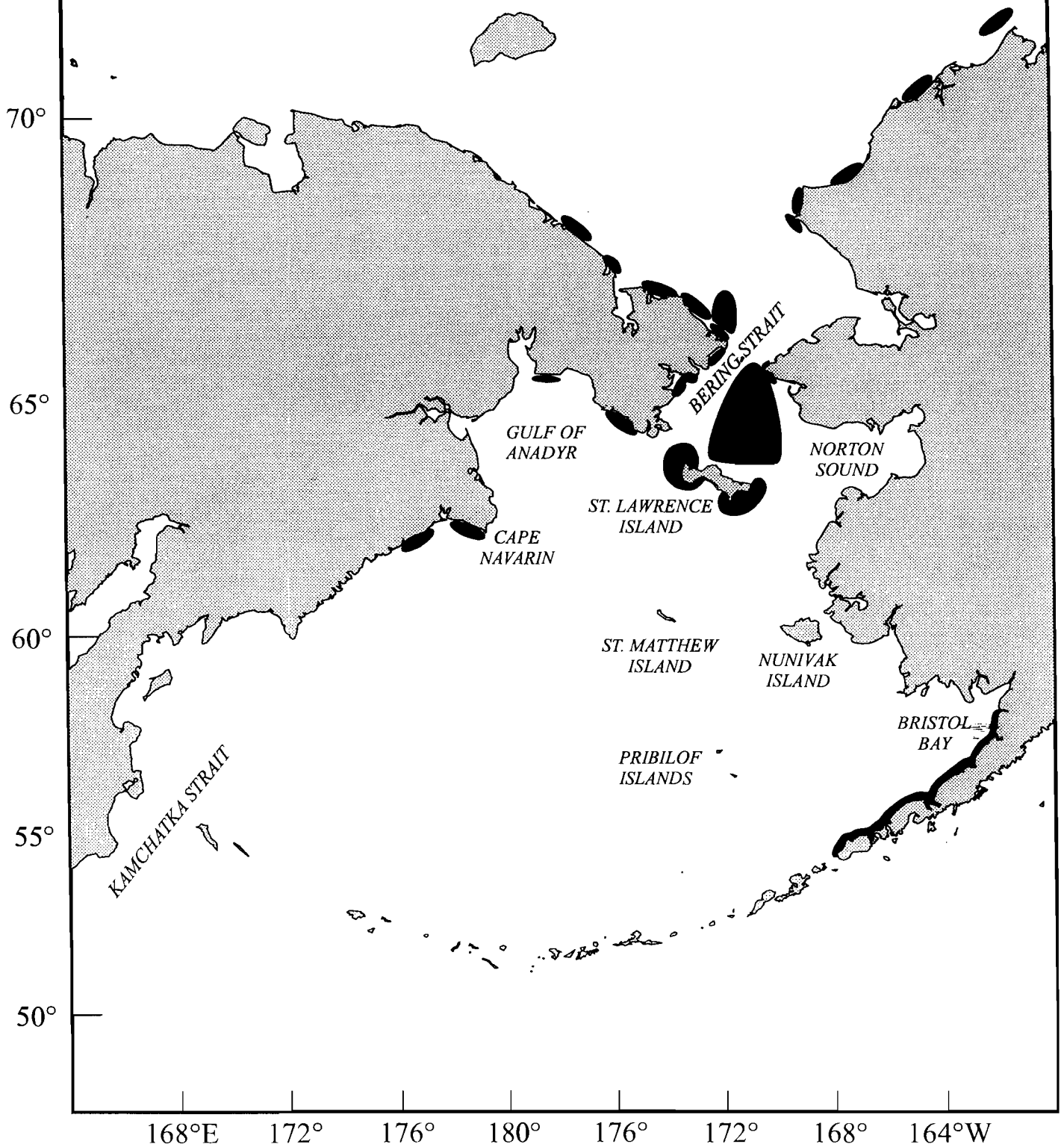
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FIGURE 1

Primary Feeding Grounds for Gray Whales



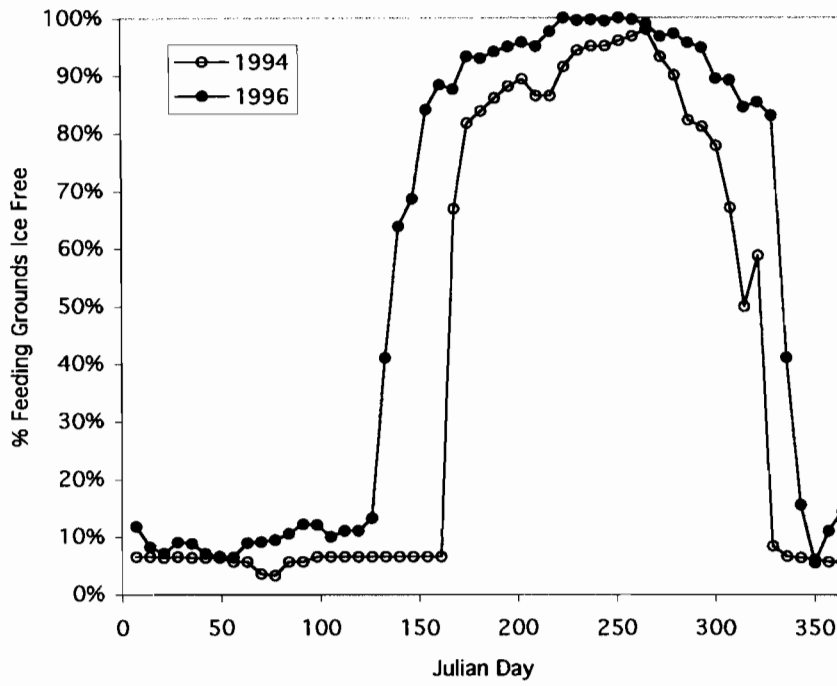


Figure 2. Calculated percentage of gray whale feeding grounds (see Figure 1) that were free of seasonal ice in 1994 (open circles) and 1996 (closed circles). Icedistribution based on charts published by the NIC and NISIDC.

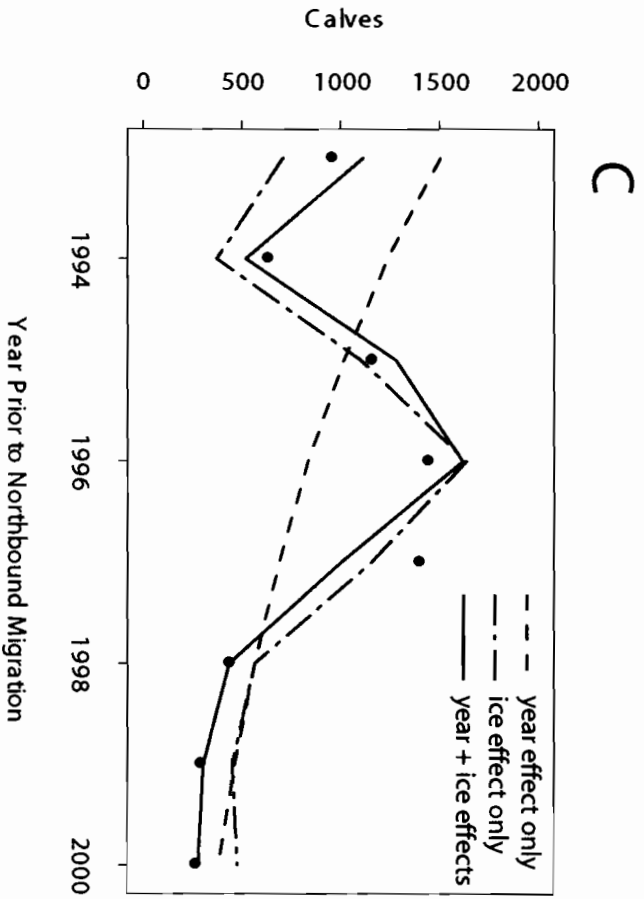
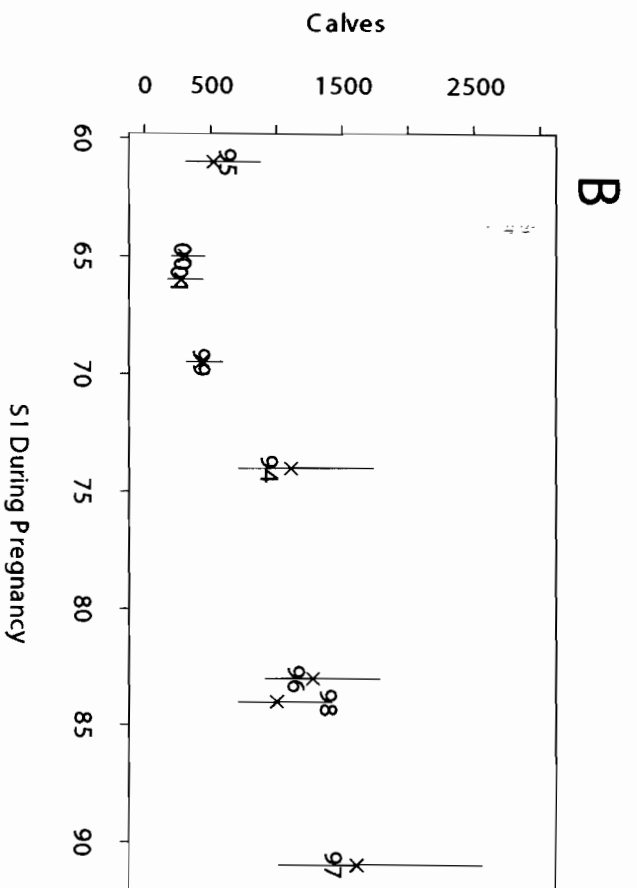
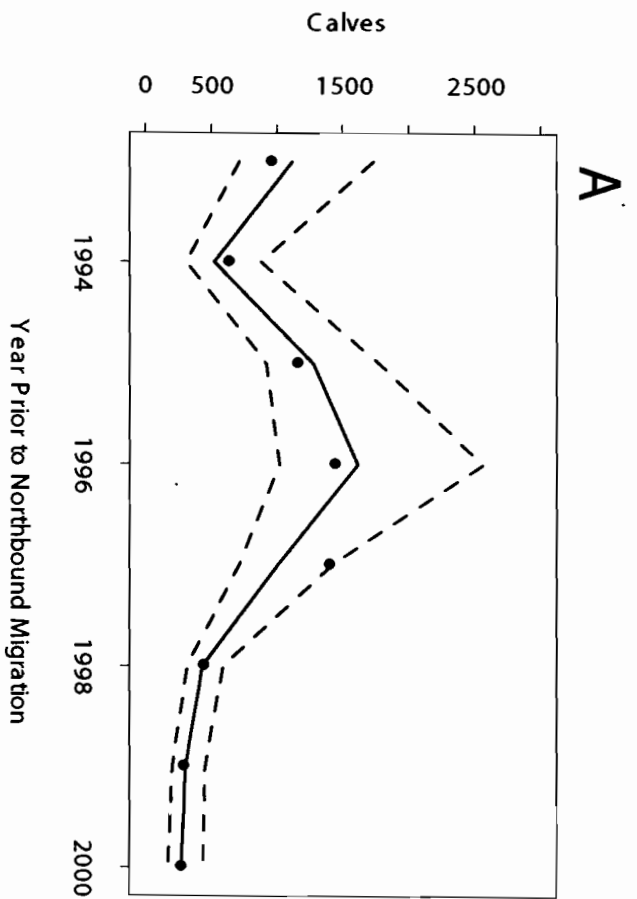


Figure 3 Fits of log linear models to gray whale calf estimates. A) Fit of model by equation 4. The solid circles are the observed calf estimates; the solid line is the expected estimate; the dashed lines are the approximate 95% simultaneous confidence bounds. B) Visualization of SI effect from equation 4. The digits indicate the calf estimate for the year of the northbound migration; the "x" symbols indicate the expected calf estimate; and the bars represent approximate 95% confidence bounds. C) Visualization of "slow" compensatory and "fast" physical forcing effects on calf production. The solid line is the expected calf estimate from equation 4; the dashed-dotted line is the expected calf estimate from equation 5; and the dashed line is the expected calf estimate from a model that has only an intercept and a year effect.

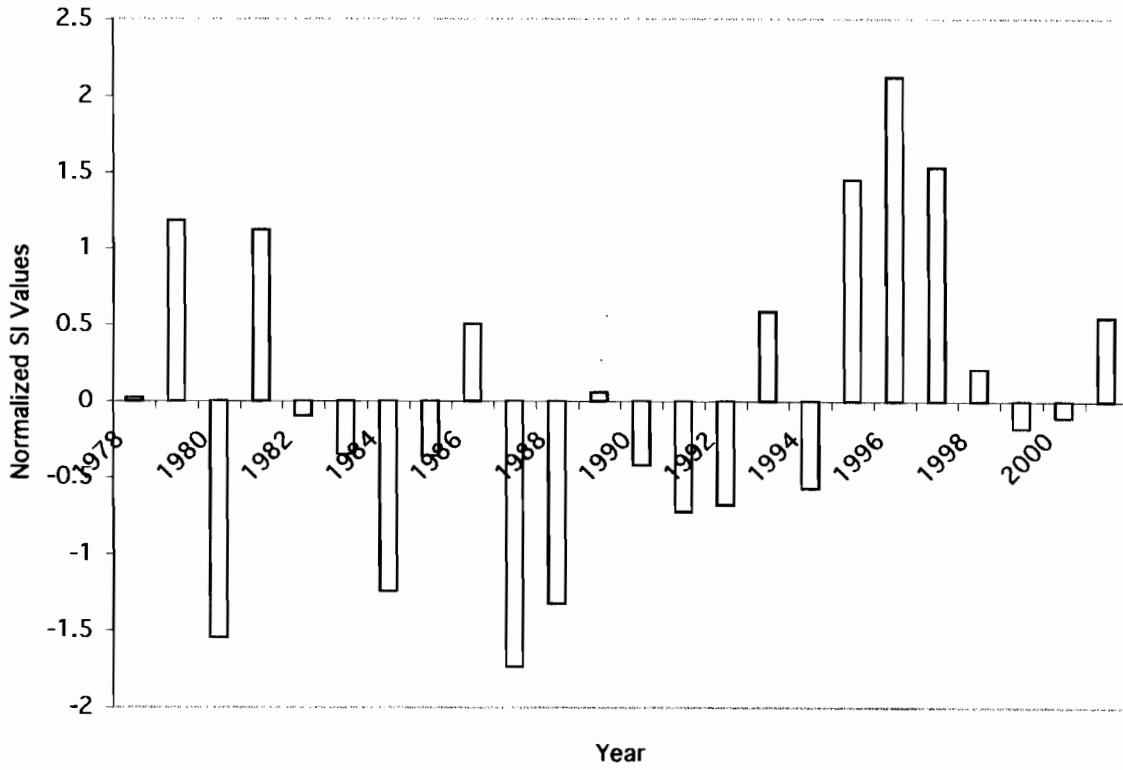


Figure 4 Normalized values of seasonal ice indices from the period 1978 through 2001.