Evidence of Continuing Declines in Fecundity of Steller Sea Lions in the Central Gulf of Alaska

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INTRODUCTION

From 2000 to 2004, index counts of western stock Steller sea lions (Eumetopias jubatus) in the Gulf of Alaska and Aleutian Islands increased by 10%, reversing a 30-year, 80% decline (Figure 1; Braham et al. 1980; Fritz and Stinchcomb 2005). Demographic changes associated with the steep population decline of the 1980s were a large drop (-20% to -40%) in the survival rate of juvenile sea lions accompanied by smaller declines in adult female fecundity and adult survival (York 1994; Holmes and York 2003). As the rate of decline slowed in the 1990s, modeling suggested that rates of juvenile and adult survival increased while fecundity eroded (Holmes and York 2003). Here we report that these trends continued through 2004, supporting the hypothesis that direct mortality sources (e.g., killer whale (Orcinus orca) predation) are not the current primary threats to recovery of the western Steller sea lion population.

METHODS

The historical data on Steller sea lions in the Central Gulf of Alaska which we used for this study were

- the juvenile fraction of the non-pup population obtained by measuring the relative length of animals on haulouts from aerial photographs as de scribed in Holmes and York 2002 (Figure 3a and 4)
- adult and juvenile (non-pup) sea lion counts at consistently-surveyed groups of haul-outs and rookeries (trend sites; Figure 3b)
- estimated pup counts at all five major rookeries (Figure 3c)

We fit this data using a time-varying model ($N_{t+1} = \mathbf{Y} \times N_t$) for Steller sea lion population dynamics 1976 to 2004. N_t is the vector of number of individuals at each age at time t. Y_t is the life history model at time t, which is specified as a modified Leslie matrix giving the survivorship from age *i* to *i*+1 and the number of pups born to females age *i* in year t. To understand the extent to which the results would be sensitive to changes in the underlying life history model, we used three different life history matrices estimated from age and fecundity data collected on Marmot Island in the 1970s, the matrix estimated by Calkins and Pitcher (1982), the matrix by York (1994), and a new matrix with York (1994) survivorships but re-estimated fecundities which included fecundity senescence for old females.

We allowed juvenile survivorship (age 1-3), adult survivorship (age 3+) and adult fecundity to change as a step-function, such that these demographic rates would be constant for a period of years and then change by a scaling factor to a new rate. Our first set of changes was based on the oceanographic periods identified in Benson and Trites (2002): 1970-1976, 1977-1988, 1989-1997, 1998-2004. The second time period combination was based on analyses Steller sea lion population trends which indicate distinct periods with different population dynamics (York et al. 1996, Holmes and York 2003): 1970-1982, 1983-1988, 1989-1992, 1993-1998, 1999-2004). We added two additional time periods by adjusting the late-1980s shift between 1988 and 1989.

The model was fit using maximum likelihood estimation as described in Holmes and York 2003. The different model fits were compared with AIC.

RESULTS

The first part of the population decline in the early to mid-1980s was associated with low juvenile survivorship and slight declines in fecundity, and was followed by increased juvenile survivorship offset by further declines in fecundity into the late 1990s. From 1998 to 2004, non-pup counts on CGOA trend sites declined (Figure 3b), although at a slower rate than in previous time periods. The model fits indicate that the most parsimonious demographic cause for this change is continued erosion of adult fecundity which is offset by a continuing increase in juvenile and adult survivorship (Figure 5). This pattern was robust across all life-history models for Steller sea lions that we compared (Figure 6).

Declines in fecundity mirror the steady declines in CGOA pup-to-non-pup ratios (Figure 7). These declines are due in part to greater juvenile survivorship, which increases counts of non-pups with no rise in pup production. According to the model, however, increased juvenile survivorship by itself cannot explain the decline in pup-to-non-pup ratios. Declines in fecundity must also be occurring to explain this pattern. There are several ways to decrease fecundity: lower early or late-term pregnancy rates, lower post-partum pup survival, increased average number of years between successful breeding, older average age of first reproduction, and a shift in the age-structure of reproducing females combined with a non-uniform age-specific reproduction, to name several (Pasqual and Adkison 1994; York 1994; Pitcher et al. 1998). A model incorporating solely changes in the age of first reproduction was unable to fit the data, suggesting that increased age of first reproduction alone cannot explain the drop in fecundity. However, determining which particular factors are causing or interacting to cause decreased fecundity is not possible using simply the pup, non-pup and juvenile fraction data described here, and will require additional research and field studies directed specifically at sea lion fecundity.

In contrast to fecundity, the model fits indicate that to be most consistent with the pup, non-pup, and juvenile fraction trends, juvenile and adult survivorships are likely near or above levels estimated in the late 1970s. Increases in juvenile survivorship, particularly since 1999, could be a delayed density-dependent response in the population, or have resulted from improvements in foraging conditions related to changes in climate (Bond et al. 2003) or groundfish fishery management regulations (McBeath 2004). Alternatively, increased juvenile survival could be due to extended maternal care (nursing) of an existing pup/yearling as a result of a decline in fecundity (e.g., loss of fetus, greater number of years between successful breeding), a circumstance reported in adult female Australian sea lions (Neophoca cinerea; Higgins and Gass 1993). Pitcher et al. (1998) hypothesized that decreases in body condition of adult female Steller sea lions in the 1980s led to greater rates of spontaneous abortion, and hence lower birth rates and fecundity, than in the 1970s. Again, analysis of the detailed factors leading to increased juvenile survivorship is not possible simply with the data we have available for this analysis. Determining whether better foraging conditions or longer maternal investment is primarily responsible for the increases in juvenile survivorship will require specific data and research on juvenile sea lions.

DISCUSSION

Researchers have consistently pointed to low survivorship, particularly for juveniles, as the primary ultimate cause of the steep decline of the western Steller sea lion population that occurred in the 1980s (York 1994; Pascual and Adkison 1994; Chumbley et al 1997), but a drop in fecundity is likely to have occurred as well (Holmes and York 2003; this study). This suggests that both direct (e.g., predation, illegal shooting, incidental take in fisheries) and indirect (e.g., disease, pollutants, nutritional stress related to climate change or the competitive effects of fisheries) sources of mortality negatively affected the population at this time (Calkins and Goodwin 1988; NRC 1996; Pitcher et al. 1998; NRC 2003; Springer et al. 2003; Trites and Donnelly 2003; Fritz and Hinckley 2005). What has been the subject of considerable controversy, however, is which direct and indirect factors were important in the population's decline and which continue to be inhibiting recovery. In the 1980s, the most prominent direct factors may have been shooting (legal and illegal) and incidental take in fisheries (Alverson 1992; Trites and Larkin 1992; NRC 1996), but these were likely greatly reduced in the 1990s (NRC 2003; McBeath 2004). Recently, new attention has been focused on possible increased rates of killer whale predation in the 1980s that may still be affecting recovery (NRC 2003; Springer et al 2003; Williams et al 2004). While diseases (Burek et al. 2003) and contaminants (Reijnders 1984) may be involved, nutritional stress from fisheries-induced or natural environmental changes in prey abundance, distribution or quality is the indirect factor cited most often for its involvement in the sea lion decline (NRC 1996; Trites and Donnelly 2003; Fritz and Brown 2005; Fritz and Hinckley 2005).

The patterns of Steller sea lion demographic changes described here are consistent with the hypothesis that direct sources of mortality have not had major impacts on this population since the early 1990s, nor do they appear to be major threats to the recovery of this endangered species, at least in the CGOA. Our findings point to indirect factors, perhaps nutritional stress (Trites and Donnelly 2003) as the largest threats to recovery. However, rather than juveniles being the group affected, as suggested by Rosen and Trites (2004), our results and those of Pitcher et al (1998) suggest that it is adult females that are experiencing a nutritional bottleneck, a bottleneck that is limiting their reproduction rather than their survivorship.

The western stock of Steller sea lions has experienced a 30-year decline throughout its range in the North Pacific Ocean, and is now at only 20% of pre-decline levels. The past four years have seen an encouraging abatement of the decline across much of the Gulf of Alaska and Aleutian Islands, and slight increases in non-pup counts in some areas. However, pup-to-non-pup ratios remain well below the pre-decline levels of the 1970s, and the most parsimonious explanation is that fecundity has been steadily declining in the CGOA population and is currently well below 1970s levels. As a consequence, it is premature to conclude from the small recent increases in non-pup counts alone that the endangered western Steller sea lion is on the road to long-term recovery.

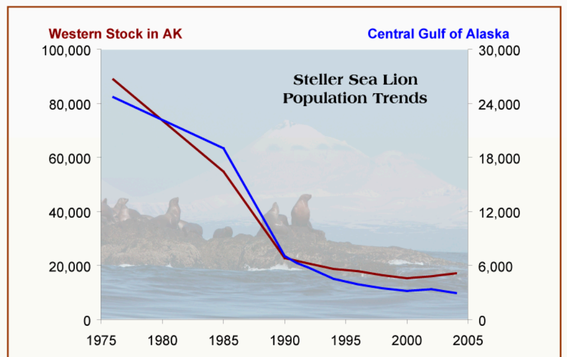

Figure 1. Counts of adult and juvenile Steller sea lions on western stock trend sites, 1970s to 2005.

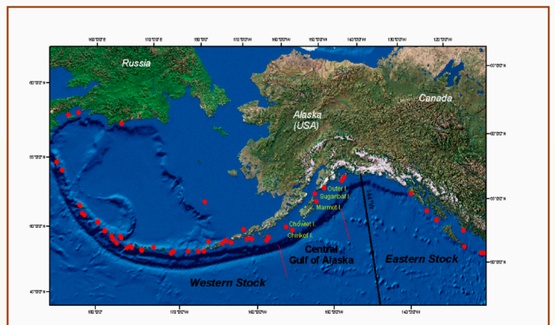

Figure 2. Principal breeding locations (rookeries) in Alaska, USA, of the western (W of 144°W) and eastern stocks of Steller sea lion. Names of islands with rookeries in the central Gulf of Alaska are shown.

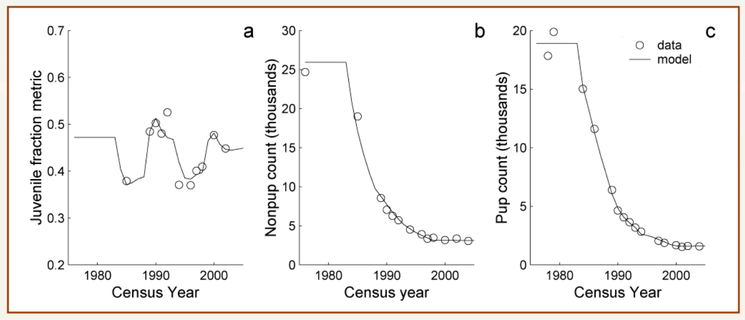

Figure 3. Historical trends in juvenile fraction, non-pup, and pup counts in the central Gulf of Alaska. a) Index of juvenile fraction from all photographed trend and non-trend haul-outs with a large male. The vertical lines show the 95% confidence intervals on the measured juvenile fractions. b) Adult and juvenile (non-pup) counts on rookery and haul-out trend sites. c) Pup counts on the five major central Gulf of Alaska rookeries. The circles show the observed data. The lines show the maximum likelihood fit of the temporally varying Leslie matrix model (Eq. 1) to the data. In this model, juvenile survivorship, fecundity and adult survivorship were allowed to change in 1983, 1988, 1993, and 1998.

Figure 4. Aerial photograph of Steller sea lions on a haulout showing relative length measurements used in the demographic analysis. The photo was taken on June 23, 2002 at Nagai Rocks in the Central gulf of Alaska.

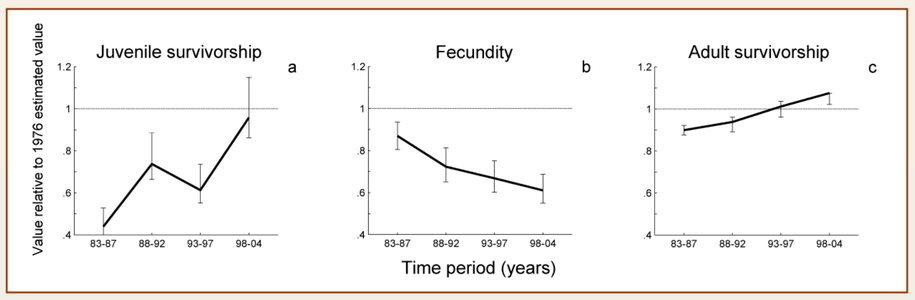

Figure 5. Maximum likelihood estimates of juvenile survivorship, fecundity and adult survivorship for 1983-87, 1988-92, 1993-97 and 1998-2004 relative to 1976 levels (shown by the dotted line at 1.0). 95% confidence intervals were determined by one-dimensional likelihood profiling allowing all other parameters in Eq. 1 to be free (cf. Holmes and York (2003) for details).

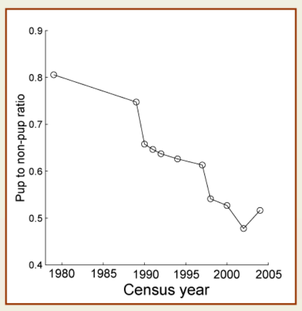

Figure 6. Ratio of pup-to-non-pup counts at trend haul-out and rookery sites in the central Gulf of Alaska.

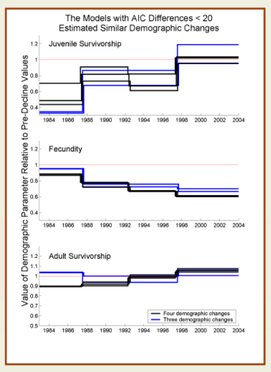

Figure 7. Estimated demographic changes from 1983 to 2004 for the 5 models with (AIC- min AIC) < 20. The models with 4 temporal changes fit the data best (the number of time changes was treated as a free parameter for penalizing in the AIC calculation). The re-estimated York 1994 matrix with fecundity senescence was the best life-table model. The maximum likelihood estimates for juvenile survivorship, adult survivorship, and fecundity are shown as relative to pre-decline estimates. The red-line at y=1 is the pre-decline estimate, so that 0.9 on the y-axis is 90% of pre-decline levels.

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