

Correlates of the decline of the Steller sea lion in the North Pacific

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Abstract

Correlates of the decline of the Steller sea lion in the North Pacific

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The decline of the Steller sea lion (*Eumetopias jubatus*) in the North Pacific is investigated using a statistical Bayesian model. Chapter one reviews current research into Steller sea lions and identifies the major hypotheses thought to be associated with their decline. Chapter two identifies correlates of changes in Steller sea lion life history parameters. This work builds on several previous models. The project fits annual estimates of Steller sea lion reproductive rates, first year survivorship, and non-pup survivorship at six rookeries in Alaska. Changes in these life are correlated with the June Pacific Decadal Oscillation (PDO) as well as an index of catch per unit effort of three species of Steller sea lion prey.

Results of the model include detection of an occasional, single-year crash in Steller sea lion pup survivorship in years with a very negative June PDO. Both fishing and the PDO were shown to be correlated with each of the Steller sea lion life history parameters, and those parameters were shown to be highly variable on an annual scale. Areas for improvement in error assumptions are identified as a means of improving the model fit and accuracy of the results. The result from this project add to the literature on the decline of Steller sea lions, as well as advance the modeling techniques used to investigate the problem.

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Chapter 1

BACKGROUND ON THE PROBLEM

The Steller sea lion, *Eumetopias jubatus*, is a large marine mammal inhabiting the North Pacific. The population abundance the western stock has declined more than 80% since the 1970s (National Research Council, 2003), resulting in legal protections including restrictions placed on fisheries. Despite being at the center of a large research effort (Dalton, 2005; Berman, 2008; Hogarth, 2005), there is little or no consensus on the cause or causes of the declines. This project compares two of these hypotheses for the decline: first, commercial fishing causing localized depletions of critical Steller sea lion prey and second, changes in the climate affecting the availability of critical prey species.

1.1 Introduction

The Steller sea lion is the largest extant otariid (Nowak, 2003). The family Otariidae is within the suborder Pinnipedia, which has an evolutionary history dating back to the Oligocene (Deméré et al., 2003). Steller sea lions may have evolved as early as the late Pliocene, and were well established in the Pleistocene (Loughlin et al., 1987; Harlin-Cognato et al., 2006). They presently inhabit the Pacific Rim, with rookeries in the Kuril Islands, Aleutian Islands, Alaska, the Pacific Coast of Canada and the United States.

The National Marine Fisheries Service recognizes two distinct population segments of Steller sea lions. The eastern segment, referred to here as a the eastern population, extends East from 144° W along the Pacific coast of the United States and Canada, while the western population extends west of this line (62 FR 30772, 1997).

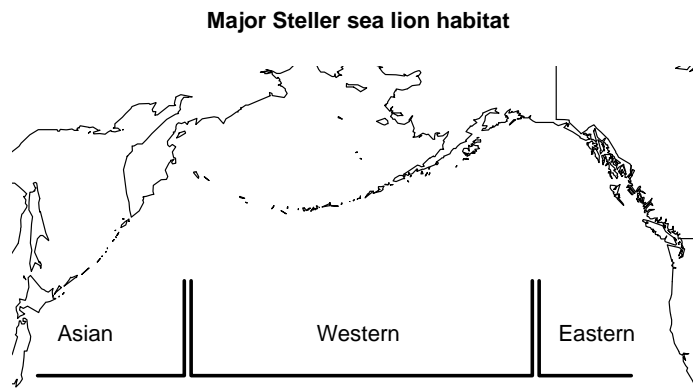


Figure 1.1: Range and stock differentiation of Steller sea lions.

Genetic work, particularly mitochondrial DNA (mtDNA), also shows a weaker differentiation of the western population, subdividing it further into western and Asian groups (Hoffman et al., 2006). Population boundaries are less evident in autosomal microsatellite markers (Trujillo et al., 2004). The current population boundaries (Figure 1.1) are thought to have been established by glacial refugia during the late Pleistocene (Harlin-Cognato et al., 2006).

Steller sea lions are gregarious animals, congregating on rocky and exposed coastlines throughout their range (Ban, 2005; Call and Loughlin, 2005), generally in ice-free regions. Sites where births and breeding occur are termed “rookeries,” while “haul-out” refers to sites where reproductive activities are rare. Reproduction is on an annual cycle with births occurring from mid-May to mid-July (Pitcher et al., 2001).

Both males and females reach reproductive maturity around 4 years (Pitcher et al., 1998). Although males will not generally have the opportunity to breed for several years after maturity, females start breeding at maturity (Raum-Suryan et al., 2002). Steller sea lions are sexually dimorphic and polygynous (Nowak, 2003). Males establish and defend a territory on a rookery against other males, giving them exclusive

reproductive access to the females in their territory. Males who are not large enough to maintain a territory are generally unable to breed, but occupy territory adjacent to the rookery during the breeding season.

Both males and females disperse widely after breeding. Dispersal distances are as much as 1500 km (Raum-Suryan et al., 2002). Between 50 to 80% of females return to their natal rookery to breed, with higher rookery fidelity in the southeast (Raum-Suryan et al., 2002). Other sources, using genetic data, indicate high rookery fidelity among females (Baker et al., 2005). Autosomal microsatellite markers, which are passed to offspring by both males and females, have not shown the population boundaries as strongly as mtDNA, possibly indicating sex-biased dispersal (Hoffman et al., 2006; Trujillo et al., 2004).

1.1.1 Population trend

Steller sea lions in the western population have declined more than 80% since the late 1970s (National Research Council, 2003). Smaller, but still substantial declines were also observed in the Asian population (Burkanov and Loughlin, 2005). Recent declines began in the 1970s and were most dramatic in the 1980s. There are indications, however, the endangered western population is rebounding since 2000 (National Marine Fisheries Service, 2008).

The decline of Steller sea lions has generated a great deal of discussion and research. Numerous hypotheses have been put forward for the decline (National Research Council, 2003); Each of eight categories of Steller sea lion decline are discussed below.

Fisheries competition

The rationale for the regulations of certain fisheries is based on the assumption that those fisheries may have a deleterious impact on the Steller sea lion. Fishing in the North Pacific, particularly the pollock fishery, has expanded dramatically since

the late 1960s (FAO, 2005). Pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), and Atka mackerel (*Pleurogrammus monopterygius*) are commonly consumed by Steller sea lions in the western stock (Sinclair and Zeppelin, 2002), leading some to suggest competition with pollock and other fisheries as a possible cause for declines (National Research Council, 2003).

Alverson (1992) has argued that, although heavily fished, the pollock stock in Alaska was increasing through the 1980s. He argued against fishing as the major causative factor behind Steller sea lion declines. Alverson further argued that by removing piscivorous fish, fisheries may be balancing any damage done to the Steller sea lion prey. Trites et al. (1997) has also argued that marine mammals diets in general have a relatively small overlap with fisheries, and the primary controls on prey availability may be piscivorous fish. Shima et al. (2000) makes a point similar to (Alverson, 1992), noting that with later declines in pollock abundance, Steller sea lions appeared to maintain pollock as a major component of their diet and reiterates the point made in Trites et al. (1997). The conclusion in Shima et al. (2000) with regard to fishing activity is “if commercial fishing activity is to have an influence on the decline of Steller sea lions, we need to further investigate how commercial fisheries may be affecting not just abundance but also the distribution and availability of prey to Steller sea lions” (pp116).

Several attempts have been made to demonstrate correlations of declines with fishing around rookery sites. Loughlin and Merrick (1989) and Ferrero and Fritz (1994) both looked at how rookery abundance data correlated with local fishing, neither finding clear results. Two later projects, Hennen (2006) and Dillingham et al. (2006), both found positive correlations with fishing.

Environmental change

Perhaps the most widely discussed hypothesis is changes in the climate. Environmental changes could have influenced or caused Steller sea lion declines through altering

their prey resources. Trites et al. (2007b) outlined the hypothesis as it is generally formulated. A shift in sea surface temperature in 1976-77 caused a “regime-shift” in western Alaskan waters from a ecosystem dominated by forage fish such as herring and eulachon to one dominated by gadids and flatfish. The shift lowered the quality, although not necessarily the quantity, of prey consumed by Steller sea lions. Examination of links in this hypothesized chain of event has been extensive stretching over multiple disciplines.

The first such link is in establishing that a climate shift occurred in the 1976-77. The shift is usually termed in the literature as a “regime shift” or the Pacific Decadal Oscillation (PDO)¹. It is usually used to denote an irregular, approximately decadal change in sea surface temperatures in the North Pacific. Mantua et al. (1997) found changes in the first principle component of sea surface temperature records, generally referred to as the PDO index, in the North Pacific in 1947 and 1977, with a non-significant shift in 1925. Other oceanographic indices show similar patterns of changes, although the underlying cause is not known (Mantua et al., 1997; Benson and Trites, 2002).

The different phases of the PDO, termed “warm” and “cold,” with the pre-1977 regime generally being referred to as cold, and the post-1977 regime being termed warm. These phases are associated with oceanographic changes including the location and magnitude of upwelling and mixing. Oscillation between warm and cold regimes has been examined in the past. With paleoclimate indicators, Verdon and Franks (2006) demonstrated changes in El Niño Southern Oscillation frequency consistent with regime shifts dating back 400 years. There is general agreement about a regime shift in 1977, however many of the other identified regime shifts have drawn criticism.

Since the definition of the PDO index (Mantua et al., 1997), oceanographic regime

¹In some contexts, it is not clear if a reference to “the PDO” indicates changes in the PDO index (which partially reflects sea surface temperature) or a general shift of a number of indicators which may be reflected in the PDO index. However using the term “regime shift” can also be problematic since there is no agreed definition of what constitutes a regime shift.

shifts have been linked with widespread biological changes in the North Pacific. Regime shift has been implicated in changes in the assemblages of fish. For example, Chavez et al. (2003) found cyclic behavior, alternating between sardines (warm regime) and anchovies (cold regime), while Benson and Trites (2002) report cyclic sequences between planktivores (which includes both sardines and anchovies) and piscivores. Conversely, Fritz and Hinckley (2005) have argued that there is little or no evidence of changes in the relative abundances at all. Biological indices, such as sizes of salmon runs, have also been incorporated into time series and have been used to identify regime shifts (Marzban et al., 2005; Hare and Mantua, 2000).

In the regime shift hypothesis, Steller sea lions are thought to have switched from a nutritionally sufficient diet to a deficient diet at the 1977 regime shift. The nutritionally poor diet is usually associated with pollock or Pacific cod, while the richer diet contains a greater diversity of species and includes lipid-rich species such as capelin or herring. The mechanism causing nutritional deficiency may be low caloric density (Trites and Donnelly, 2003) or deficiency in other nutrients (Litzow et al., 2006).

The pre-1977 diet of Steller sea lions is poorly known (Trites et al., 2007b; Fritz and Hinckley, 2005), however numerous efforts have been made to look for nutritional deficiencies. Merrick et al. (1997) found summer diet diversity was strongly correlated with regional declines in the western stock. Trites and Donnelly (2003) find Steller sea lions are physically smaller post-1977, however they find no evidence of nutritional stress in blood chemistry, and behavioral indicators seem to show they are finding adequate prey (although it is not certain whether the prey were nutritionally sufficient).

To assess the nutritional quality of pollock, Rosen and Trites (2000) conducted a captive feeding trial on six Steller sea lions. Although they were fed pollock *ad libitum*, all of the study animals lost weight. A later experiment demonstrated juvenile Steller sea lions did increase consumption to compensate for food with low nutritional

density (Rosen and Trites, 2004), which stands in contrast to those results. This later series of experiments, however, did support the hypothesis that some prey items may have sufficiently low nutritional density that fluctuations in their abundance could increase daily prey demand above the digestive capacity of juvenile sea lions. Fritz and Hinckley (2005) have also argued that the experiments may be unreliable due to naturally occurring formaldehyde in preserved fish. They also note that there is high variability in the nutritional value of fish within a species. There is also a natural seasonal variation in metabolic rates and consumption rate which could confound these results (Rosen and Trites, 2004; Kumagai et al., 2006).

Bypassing questions about diet, Marzban et al. (2005) found correlations between environmental variables and Steller sea lion trends. Due to the relevance to the present project, Marzban et al. (2005) is discussed in more detail below.

Environmental change, along with fisheries competition, form the two leading hypotheses for Steller sea lion decline (Trites et al., 2007b). Despite extensive investigation, the evidence does not appear to strongly favor one of these hypotheses over the other. These two hypotheses are further investigated in chapter 2.

Predation

Several species have been examined as potential predators on Steller sea lions. The Pacific sleeper shark (*Somniosus pacificus*) and salmon shark (*Lamna ditropis*) have been examined, however no definitive conclusion has been reached (Sigler et al., 2006). The killer whale (*Orcinus orca*) has received substantial attention in the literature as a possible Steller sea lion predator.

Springer et al. (2003) put forward the hypothesis, termed the sequential megafaunal collapse (SMC) hypothesis, that transient killer whales switched from a diet of great whales to marine mammals after the declines due to harvest of the former. The SMC has been assailed on several fronts recently. Trites et al. (2007a) argues that the trends in other marine mammals from the western stock are not replicated in the east-

ern populations. Since killer whales would exploit prey populations without regard for the prey's population boundaries, this is a counterintuitive result. DeMaster et al. (2006) shown statistically that the declines were not in fact sequential as Springer et al. (2003) argued. Mizroch and Rice (2006) presented data which indicated that most of the great whales assumed to be food in the SMC probably were not consumed in quantity by killer whales. Wade et al. (2007) provides perhaps the most extensive review of marine mammal trends, draws similar conclusions: (i) the different declines in different regions are contrary to the SMC hypothesis, (ii) even if great whales were important prey, they would have continued to be available in sufficient numbers to support killer whales (iii) great whales are not important prey (iv) the declines were not sequential.

In contrast, Williams et al. (2004) has argued, based on bioenergetics, that a decline in marine mammals which Springer et al. (2003) notes could be caused by very few killer whales. Whitehead and Reeves (2005) suggested that killer whales may not have been preyed upon great whales *per se*, but feeding on the detritus from whaling expeditions. The cessation of whaling, under this hypothesis, would cause those individuals to seek pinnipeds as a prey source.

Anthropogenic effects

Marine mammal exploitation for food and resources has been part of human existence for nearly the entire Holocene (Ackerman, 1988). Although a traditional harvest continues today, there is no reason to think it has changed recently, thus may not be attributable as a cause for the decline (ADF&G, 1997). Estimates of the total number of Steller sea lions taken in a traditional hunt are in the low hundreds per year (ADF&G, 1997; Loughlin and York, 2000).

There was a 13 year directed commercial harvest of Steller sea lion pups in Alaskan waters which ended with the passage of the Marine Mammal Protection act in 1972. Although a directed harvest has been the primary cause of many pinniped declines

in other species (Gerber and Hilborn, 2001), and the Steller sea lion harvest was substantial, averaging approximately 3500 pups per year (Alverson, 1992)), Pascual and Adkison (1994) showed that this harvest was unlikely to be responsible for the sustained decline observed.

Incidental harvest related to other commercial activities may have played a more sustained role in depleting Steller sea lions. There was a substantial taking of Steller sea lions in Japanese waters throughout the 20th century related to fisheries activity, as well as taking to improve the commercial northern fur seal (*Callorhinus ursinus*) harvest (Uni, 2006). In Alaskan waters, Steller sea lions were sometimes killed to prevent fouling of commercial fishing gear or perished accidentally after becoming tangled in fishing gear. Up until the late 1980s, an estimated 1000-2000 animals were taken each year incidental to commercial fishing activity in the United States (Alverson, 1992; Fritz et al., 1995).

Limitations were placed on incidental killing in US fisheries since 1988 under an amendment to the Marine Mammal Protection Act. Since 1990, the Steller sea lion has been protected under the Endangered Species Act. Regulations pursuant this protection include restrictions placed on some fisheries near Steller sea lion critical habitat (Fritz et al., 1995; National Marine Fisheries Service, 2008). Russian protection was instituted in 1994 with an endangered listing in Russian Red Book (Waite and Burkanov, 2006).

Disease

Disease has been responsible for large-scale die-offs of other marine mammals. There is some evidence of possible disease agents: antibodies have been found to a variety of potential illnesses in Steller sea lion blood, as well as elevated haptoglobin which may be an indication of infection, but no direct evidence of an epidemic has been found (National Research Council, 2003). A review of serological data found no evidence for infection being the cause of Steller sea lion declines (Burek et al., 2005). A study of

possible disease-causing parasites in Steller sea lions likewise found nothing to suggest infection was a primary cause of the decline (Yurakhno and Stryukov, 2006).

In starvation or disease mortality events, it is likely that there would be observations of dead or dying sea lions. Neither is evident for Steller sea lions (Calkins et al., 1999). Nevertheless, it is difficult to rule out disease entirely. Disease may hasten or worsen problems caused by other factors and the disease agent may have yet to be identified.

Contaminants

No conclusive evidence has been found, but there are many sources of possible contamination, any of which may have an impact on Steller sea lion physiology or reproduction. Heavy metals accumulate in Steller sea lions (Saeki et al., 1999; Ando et al., 2005; Kim et al., 1996). Toxic levels of chromium were found in some Steller sea lion pups, but results are limited due by few data (Wise Sr. et al., 2006). High, potentially toxic levels of DDT and PCBs have been found in Steller sea lions (Barron et al., 2003; Myers et al., 2006; Hoshino et al., 2006). Further examination of this hypothesis is warranted, but is outside of the scope of the present project.

Synergies

The underling “cause” of a population decline is difficult to pin down. Ultimately, any decline in population abundance in a closed system is caused by mortality rates exceeding reproductive rates. The death of an individual can be caused by multiple factors and the population mortality rate is the summation of all of these individual mortality events. Likewise reproduction is the net result of many factors, and is further complicated by attempting to assign meaning to the cause of non-events (such as reproductive failure). So perhaps a designation of specific “causes” of Steller sea lion declines is misleading; instead, focus should be put on the relative contribution of various factors.

The National Research Council (2003) identified models as one method at determining the contribution of multiple factors. To this end, several ecosystem models have been developed to examine Steller sea lion declines under multiple hypotheses. Two ecopath models, Gu  nette et al. (2006) and Trites et al. (1999) examined fishing, competition, climate, and direct predation as possible influences on Steller sea lion declines. Both identified climate shifts as having the greatest effect, with some influence of other factors. Wolf and Mangel (2004), which is discussed more extensively below, models Steller sea lions using an age-structured model. They find climate impacts having the most influence on the declines, while killer whale predation plays a more minor role.

All three models suffer from unquantified uncertainty in model specification which prevents reliance on the results. The specifics of how each hypothesis should influence model components is not specified in the hypothesis (Fay and Punt, 2006), and as a result, it is not clear that the outcome would be different if the model were differently specified. Fay (2004) and Fay and Punt (2006) model population trends, but do not link specific outcomes to hypotheses, as discussed below.

1.2 Review of related projects

1.2.1 Wolf and Mangel (2004)

Wolf and Mangel (2004) develop a model, also used in Wolf et al. (2006), for Steller sea lion interactions with fisheries, climate, and killer whales. Fishing data from NOAA standardized trawl is used to estimate the CPUE of fished populations. Changes due to climate are measured with the total pollock abundance near each rookery, as measured in the standardized trawl. Since there are few data available for killer whale abundance, the count of nearby harbor seals is used as a proxy for killer whale predation pressure. For each rookery in the model, a two-stage age-structured model predicts the population trend. The elements of the Leslie matrix are each multiplied

by functions linking observed counts to environmental variables. Free parameters within each function control the degree to which environmental factors influence the elements of the Leslie matrix. The free parameters are fit to the data, giving an indication of which factors play an important role in the decline.

Their investigation found total prey available and pollock available have strong effects on certain elements of the Leslie matrix, while harbor seal density (killer whale predation) had moderate effects.

Much of the model used by Wolf and Mangel (2004) is fairly general, it does rely on specific functions which link the hypotheses to the life history parameters. There is an unquantified uncertainty in the results, therefore, due to uncertainty in the choice of these functions. The specific functional form is not intrinsic to a given hypothesis. Wolf and Mangel (2004) discuss reasons for the specific choice of functions, based on views on the way in which the ecosystem functions, however there is not enough information to make a more compelling case.

The strength of the approach used in Wolf and Mangel (2004) is the testing of multiple models simultaneously, specifically linking hypotheses to model outcomes. This approach is replicated in the project developed in chapter 2.

1.2.2 Fay (2004)

Fay (2004) examines the effect of “impact scenarios” on modeled sea lion populations. The purpose of the work was to elucidate the cause or causes of the sea lion decline, however the scenarios themselves were not linked to any specific hypothesis for the decline. Fay and Punt (2006) indicated there was insufficient information about how a specific cause of the decline, climate or the PDO for instance, would be manifested in spatial and temporal changes in the vital rates.

The age and sex structured population model included Steller sea lion counts in six subpopulations of the western population, and allows for movements between subpopulations. No single factor affected all the subpopulations and there was no

clear conclusion that would implicate one of the hypotheses.

One outcome of the work is the potential importance of movement. Although the model developed in chapter two does not permit less than 100% site fidelity, this is a nontrivial assumption which does not entirely reflect biological reality. Further consideration of this point is warranted in future work.

1.2.3 Hennen (2006)

Hennen (2006) examines the correlation between the slope of linear best-fit lines (for various intervals of time) of Steller sea lion adult count data against time, and fishing and fish abundance which occurred at various distances from each rookery (ranging from 10-100km).

To assess the declines at 32 Steller sea lion rookeries, a linear best fit line was regressed to the adult counts at two time intervals: before 1991 and between 1991 and 2000. The line of best fit was then correlated against a first principle component of three measures of fishing effort in the region of the rookeries. There was a strong association found between the fisheries in the earlier time, and a weaker association in the later.

The relevance to the present project, developed in the second chapter, is the use of principle components analysis as a technique of data reduction. This limits the number of parameters which need to be fit, as well as allows for consideration of composite predictors which may have more biological meaning.

1.2.4 Dillingham et al. (2006)

Dillingham et al. (2006) examined correlations between commercial fishing effort, groundfish abundance as measured by trawls, and Steller sea lion abundance. A radius of 74km around each rookery was used to define the “local” fishing in both correlation analyses. Pollock abundance was found to be inversely correlated with Steller sea lion rates of population change (calculated for adult counts N_t as $\ln \frac{N_t}{N_{t-1}}$).

Fisheries had mixed effects, with trawl fisheries positively correlating with sea lion growth and longline fisheries negatively correlated. Missing data was handled using a statistical interpolation technique.

1.2.5 Loughlin and Merrick (1989); Ferrero and Fritz (1994)

The Loughlin and Merrick (1989) paper looked for correlation between sea lion abundance and commercial harvest of Pollock near six rookeries. Ferrero and Fritz (1994) update this work by introducing Kendall’s concordance, a scale-free estimator of correlation, and looked at longer time-series and at more rookeries. This change of statistics results in correlations found to be significant in the first paper changed to not significant in the second. Both papers use multiple time-lags, up to 5 years, to examine a delayed effect. The spatial scale of the analysis was pollock harvest ranged from 20 nm to 120 nm.

1.2.6 Marzban et al. (2005)

The goal in Marzban et al. (2005) is to uncover the long-term trend in Steller sea lion populations. Unlike a simple linear de-trending, they use a lag-1 scale-free correlation as measured by Kendall’s concordance measure. They find significant downward trends everywhere but southeast Alaska (where an increase is found) and eastern Aleutian Islands (where the decline is not significant at 99%).

They next present a tentative analysis looking for “self-organized criticality” (SOC). The SOC is measured by qualitative examination of various indicies of climate, fishing, and Steller sea lions looking for power distributions. They conclude the Steller sea lion data do show some possibility of an uncaused (self-critical) decline. While this is an interesting, under-explored possibility, in their own words “the qualitative nature of these findings cannot be over-emphasized.”

Their third analysis is a nonlinear principle components analysis using neural networks. In addition to confirming the 1977 and 1989 years as regime shift, they

find 1969, 1984, and 1994 regime shifts as well.

Their analysis which is most relevant to the present effort, however, is the correlation of the Steller sea lion pup and adult counts with various climate indices at multiple time lags. They use Kendall's concordance, as with the trend analysis, to determine correlations. They find a number of strong correlations, and do some preliminary analysis (using negative time lags) to address the issues of multiple comparisons. Their discussion of the various indices is lacking, however, leading to some difficulty in interpretation of these results.

The present project is different in that it looks principally at correlations of the PDO index with Steller sea lion vital rates rather than counts. Marzban et al. (2005) is a useful source, however, in identifying useful data to examine.

1.2.7 Holmes and York (2003)

The analysis presented by Holmes and York (2003) is aimed at determining the timing of changes in Steller sea lion vital rates. They fit four models which allowed for vital rate changes at various times. Their model is age-structured, with vital rate changes modeled as multipliers on a baseline Leslie matrix. In addition to the pup and adult counts used in this project, they additionally use measurements taken from archived photographs to estimate the juvenile fraction. Their models do not incorporate movement, and allow only for observation error.

They conclude there were significant changes to the juvenile survivorship in the early 1980s, with some less (or non) significant changes in fecundity. While juvenile survivorship rebounded in the 1990s, adult survivorship declined (although not nearly as dramatically).

There are several ways in which the present project differs from this approach. The data used are different, since the juvenile fraction data are not available from all rookeries. They also do far less post-model analysis, neither correlating the changes with any climate or fishing variables nor analyzing the trend across regions. They are

also estimating a few changes in life history parameters in particular years, chosen *a priori*, whereas the present project estimates a time series (resulting in an estimate of the vital rates each year).

1.2.8 *Holmes et al. (2007)*

Holmes et al. (2007) extend Holmes and York (2003), but use a similar framework. The authors fit matrix population models to pup, juvenile, and adult count data. The models had up to four years in which the Leslie matrix parameters can change. Those years are selected by the Akaike Information Criterion. The model is fit using maximum likelihood, estimating the vital rate parameters over the intervals specified in the model.

They conclude there was a crash in juvenile survivorship in the mid-1980s, which recovered and increased steadily, reaching pre-decline levels in the 1990s. They find birth rates, on the other hand, underwent a steady decline since the mid-1970s. They discuss possible factors which could lead to this pattern, including moderate food limitation, contaminants, or disease.

The present project explicitly ties the hypotheses to changes in the vital rates, which can narrow the possible causes. It also differs from Holmes et al. (2007) in the temporal resolution; yearly estimates of Leslie matrix parameters are derived. Holmes et al. (2007) does, however, include a higher resolution in the ages of Steller sea lion counts than were included in the present project.

1.3 ***Further work***

The next chapter develops a project related to the conservation of Steller sea lions. This project examines the relationship between Steller sea lion life history parameters and two possible causes for the decline, the PDO and an index of fishing. The project uses a simple Leslie matrix model, fit to pup and adult count data from rookeries in western population. It is a novel investigation into Steller sea lion ecology, as well as

a development in methodology building on existing models and work.

The project models Steller sea lion counts at six rookeries in the North Pacific. The project estimates variables linking the June PDO and an index of fishing to the life history parameters: reproductive rate, pup survivorship, and adult survivorship. One result, indicating occasional and dramatic crashes in the first year survivorship, is verified in the raw count data. Interpretation of the results is hampered somewhat by some suspiciously narrow posterior confidence intervals, the cause of which is not certain.

The results of this project have some management implications, suggesting a component of the cause for the decline. The identification of the causes is necessary to effective management. Although the magnitude and mode of each of the two possible causes is also determined, the interpretation of these results is more limited given some uncertainty in the modeling results. The questions surrounding how best to manage Steller sea lion populations is at the center of a multi-million dollar research effort (Dalton, 2005; Berman, 2008; Hogarth, 2005). This work contributes information to the body of literature on these animals.

Chapter 2

IMPACTS OF FISHING AND THE PDO ON THE DECLINE OF STELLER SEA LIONS (*EUMETOPIAS JUBATUS*)

2.1 Introduction

The decline of Steller sea lions in western Alaska, beginning in the 1970s and continuing through the 1980s, has been the subject of a great deal of research. Possible triggers for the decline are numerous and varied, but two major hypotheses have emerged as likely causes: climate, as reflected in the Pacific Decadal Oscillation (PDO) and fisheries causing a localized depletion of Steller sea lion food resources. Both hypotheses act through changes in the prey quality or quantity available to Steller sea lions, and thus separating these hypotheses poses difficulty. This project examines the correlation of the PDO and a fishing index with the changes in life history parameters at rookeries and haul-outs in the western population of Alaska. A model is developed which uses data from six sites, examining the hypotheses by looking at the annual impact of fisheries and the PDO have on each site.

The results show an occasional crash in the pup survivorship through the 1990s, predicted by the June PDO. The other life history parameters are shown to be highly variable between years and sites, and are correlated with both the PDO and fishing. Although methodological issues limit the interpretation, the strongest of these results is demonstrated in the data directly. These results are presented in the context of previous work on the changes in the life history parameters of Steller sea lions.

Steller sea lions (*Eumetopias jubatus*) are large marine mammals which inhabit the north Pacific Ocean. They have been the subject of an intensive investigation

since their decline starting in the 1970s (Dalton, 2005; Berman, 2008; Hogarth, 2005). While these projects have been informative, they have not definitively concluded the cause or causes of Steller sea lion declines.

Under the Endangered Species Act (1973), Steller sea lions are divided into two populations: western and eastern (Alaska Region Sustainable Fisheries Division, 2001). The western population extends westward from 144° longitude and is classified as endangered while the eastern population, extending along the western coast of Canada and mainland United States, is classified as threatened. Genetic work, particularly on mtDNA, has also demonstrated the western population consists of two subgroups: the Alaskan and Asian populations with only a few individuals moving between the populations each year for reproduction (Baker et al., 2005). This result is at odds with autosomal microsatellite DNA loci, which indicate mixing of the populations. This might be due to sex-biased dispersal (Trujillo et al., 2004).

Steller sea lions are protected under law in the United States, and their decline has motivated a series of fisheries regulations. Steller sea lions are protected under the Endangered Species Act and Marine Mammal Protection Act, which prohibit hunting or otherwise taking them. Additionally, several Alaskan groundfish fisheries have been identified as potentially altering food availability. Since 1993, 20 nautical mile “aquatic zones” were established around rookeries and key haul-outs (National Marine Fisheries Service, 2008). Pollock, Pacific cod, and Atka mackerel fisheries, which might interfere with Steller sea lion feeding, are subject to additional regulation or prohibition in these aquatic zones. Transit is further prohibited within three nautical miles of critical habitat (50 CFR 679.22).

Western population Steller sea lions declined dramatically in the 1970s to 1990s, from an estimated 220,000-265,000 in the 1970s reaching a low of approximately 50,000 in 2000 (National Marine Fisheries Service, 2008). Since that time, however, the western population has shown a 12% increase in non-pups. Trends in the eastern population have not shown a similar decline but instead show a 3% average annual in-

crease since the 1970s. Despite the genetic distinctiveness of the population, the Asian population (which is managed as one group with the western population) suffered a decline similar to the western population in the 1980s. Since the 1990s, the Asian population has remained constant or increasing (National Marine Fisheries Service, 2008).

The cause or causes for the decline of the western population has been widely investigated. Many hypotheses have been advanced to explain the decline (National Research Council, 2003). Chief among these are changes in whaling patterns lead to killer whales (*Orcinus orca*) switching to marine mammal consumption (Springer et al., 2003; Whitehead and Reeves, 2005), fishing causing depletion of Steller sea lion prey (Loughlin and Merrick, 1989), climate changes, reflected in the the Pacific Decadal Oscillation (PDO), changing the prey availability (Trites et al., 2007b), and pollutants interfering with Steller sea lion health (Hoshino et al., 2006). While there are adherents and critics of all of these views, two of these stand out as most probable: fishing and the PDO.

The hypothesis that killer whales are responsible for Steller sea lion declines is part of a larger hypothesis about ecosystem interactions in the North Pacific. Dubbed the sequential megafaunal collapse (SMC) hypothesis, proponents argue a subset of killer whales formerly subsisted on a diet of great whales (Springer et al., 2003). The great whales' decline through the 20th Century lead, the argument goes, to these killer whales depredating other marine mammals, particularly seals, sea otters, and sea lions, switching prey as each species became depleted (Stephens and Krebs, 1984). A slightly different formulation, Whitehead and Reeves (2005), argued it was not killer whale predation on living great whales but on the whale remnants left by commercial whaling. Both views received wide criticism (DeMaster et al., 2006; Mizroch and Rice, 2006; Trites et al., 2007a) for being biologically infeasible with unsupported underlying assumptions. DeMaster et al. (2006) demonstrated that the declines of the prey were not sequential. Numerous authors have pointed out there is no evidence

of substantial killer whale predation of great whales.

The possibility of pollution causing declines has been suggested, singling out heavy metals or organochlorides as possible causes (National Research Council, 2003; Saeki et al., 1999). Myers et al. (2008) found polychlorinated biphenyl (PCB) and dichlorodiphenyltrichloroethane (DDT) in blood collected from pups throughout all three Steller sea lion populations. The highest concentrations were found in the Asian populations, which is incongruent with the severity of the decline. Moreover, although higher concentrations have been reported in some Steller sea lions (Myers et al., 2006), the average concentrations found in Myers et al. (2008) were at or below the levels required to produce physiological effects in harbor seals (Myers et al., 2008). Holmes et al. (2008) found heavy metals in both eastern and western populations, possibly implicating mercury in the decline. The work, however, is preliminary and interpretation is limited by the lack of information on safe exposure levels.

Commercial fishing has been responsible for direct Steller sea lion mortality in the past through gear entanglement and direct taking (Loughlin and York, 2000; Pascual and Adkison, 1994). These have decreased dramatically with the implementation of fishing regulations in the United States (Perez, 2003). Nevertheless commercial fishing may still be having an impact on Steller sea lion recovery through the removal of Steller sea lion prey items (National Marine Fisheries Service, 2008).

The PDO is an indicator of a large scale ecological regime in the North Pacific (Grebmeier et al., 2006), which some have indicated may result in changes in the quality or quantity of prey resources for Steller sea lions (Trites et al., 2007b). The PDO, defined as the first principle component of an array of biological and climatological indicators (Mantua et al., 1997), is correlated with a shift in fishing resources known to be high quality prey items (Benson and Trites, 2002). The necessity of these prey items in the Steller sea lion diet and other assumptions of this hypothesis are debated (Fritz and Hinckley, 2005).

Previous work has identified several patterns in Steller sea lion reproduction and

survivorship which are relevant to the Steller sea lion decline and prospects for recovery. Holmes et al. (2007) identified a steady decline in reproduction, even while survivorship was increasing in the 1980s, as the life history parameter change which best accounts for the age and sex structured count data from western population. Pendleton et al. (2006) used mark-resight methods to demonstrate that juvenile survivorship dropped at Marmot Island in a period of the decline, while juvenile survivorship was stable at Forrester island during a period of increase.

2.2 Methods

This project aims to provide a meaningful test of two major hypothesis for the decline: changes in fishing near sea lion critical habitat or changes in the climate as represented by the Pacific Decadal Oscillation (PDO).

An age structured model is developed for six rookeries in the western population of Alaska (Figure 2.1). The Steller sea lion reproductive rate, and survivorships are dependent on the PDO and an index of fishing though rate parameters fit to the data. Bayesian methods (Gelman et al., 2004) are used to estimate posterior distributions for the parameters in each model. Magnitudes of the parameters are interpretable as relative effects of the hypothesized causes: the PDO and fishing.

The parameter distributions which form the results of this project are estimated in a Bayesian framework (Gelman et al., 2004). This approach allows the incorporation of prior information about the parameters in the form of the prior distribution, representing the uncertainty in knowledge of the parameters. The specific algorithm used is the Metropolis-Hastings algorithm, a form of Markov Chain Monte Carlo (MCMC) which repeatedly draws values of the parameters based on the last set of accepted parameters. Each draw, termed a jump, is accepted or rejected with a probability based on the ratio of their likelihood and priors. The jump function, $J(\theta|\theta^*)$, is a distribution which gives the probability of making a jump from θ^* to θ . By repeatedly jumping and accepting according to the rule, the parameters approximate their

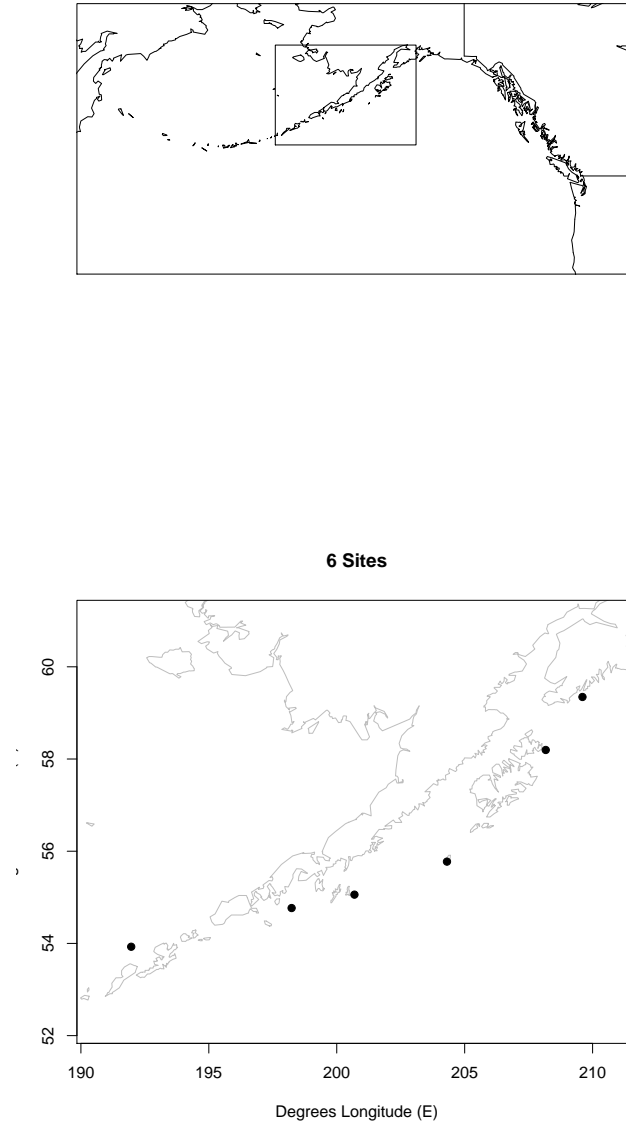


Figure 2.1: (Top) A map of the North Pacific, showing the region studied in this project. The rectangle indicates the boundaries of the lower map. (Bottom) A map of the sites included in the model (solid circle).

Bayesian posterior distribution, reflecting knowledge of the parameters given the new data being modeled.

This project builds on work done previously, relating the decline to climate and fishing predictors. Starting with Loughlin and Merrick (1989), updated in Ferrero and Fritz (1994), a correlation between fishing and decline was examined at multiple lags. Marzban et al. (2005) similarly examined the relationship between sea lion trend and the PDO, finding a strong correlation. Dillingham et al. (2006) and Hennen (2006) related Steller sea lion population trends to fishing near the rookeries, both demonstrating a significant correlation on different spatial scales.

As with these previous works, the model used in this project explicitly includes life history parameters of the population. The goal is to determine the extent to which two variables, the PDO and an index of fishing localized around each rookery, influence each of the life history parameters: reproduction and survivorship at age. A Bayesian approach allows the incorporation of information already drawn from other datasets, such as the estimates of the life history table for Steller sea lions. The results are a series of nine parameter Bayesian posterior distributions, from which parameter estimates and uncertainty can be derived representing the degree to which that factor (PDO or fishing) influences the three life history parameters in the model: first year (pup) survivorship, juvenile and adult (non-pup) survivorship, and reproductive rate. An additional set of auxiliary parameters are also estimated: initial pup and non-pup counts at each site and a parameter to account for incomplete observations.

The model developed below is similar in form to Wolf and Mangel (2004): an age structured matrix population model. Two possible predictors for Steller sea lion declines are included in the model: The PDO, and an index of fishing. Rookery-specific fishing catch per unit effort (CPUE) information, derived from observer data, and region-wide PDO information are used as data sources for the model. This investigation covers years from 1989 to 2006, which is a period of less dramatic declines than were experienced earlier, and includes some years over a period of western population

growth (National Marine Fisheries Service, 2008). Holmes et al. (2007) suggested that separate causes might be responsible for the initial decline and the subsequent failure to recover.

2.2.1 Data

Counts of Steller sea lions, both of pups (less than one year) and non-pups (greater than one year), have been made at rookeries and haul-outs across the North Pacific (National Marine Mammal Laboratory, 2006a,b). Six of these sites (Table 2.2) were selected, based on the number of years in which counts were made. All the sites selected for this project were rookeries.

The counts did not identify gender, counting both males and females. Pups were counted in separate expeditions, leading to many years where only pup or non-pup counts are available. Pup counts were uniformly made during summer months, so for comparability only adult counts made in June, July, or August were included in the model. Observations were primarily performed by aerial survey, although other methods were employed in counting adults.

To verify that the counts did not differ significantly by counting method, instances of multiple counts made at the same site and at nearly the same time using different methods. There were 524 observations made of non-pup counts which were made within three days of another count at the same site. Included in this analysis were sites not included in the model, since observation error is expected to be the same at those sites.

A comparison of counting methods using analysis of variance (Table 2.1) shows the count type is a non-significant predictor, indicating count types do not vary systematically. Counts were classified into 113 groups in which each count was made within three days of another count in the same group at the same site. The group therefore consists of a series of observations of the same site, at approximately the same time. This most directly identifies variation due to differences in counting

Table 2.1: Analysis of variance table to verify observations did not vary systematically by count type, as indicated by the non-significance of the count type predictor.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Observational groups	112	89592776	799936	3.8534	$< 2 \times 10^{-16}$
Count type	4	450319	112580	0.5423	0.7047
Residuals			407	84489848	207592

Table 2.2: Sites included in the model, together with coordinates. Larger sites are described with two sets coordinates indicating their boundaries.

Site	Longitude	Latitude
Atkins	-159.31	55.06
Bogoslof/Fire Island	-168.03	53.93
Chirikof (Boundary 1)	-155.66	55.78
Chirikof (Boundary 2)	-155.72	55.77
Marmot (Boundary 1)	-151.8	58.23
Marmot (Boundary 2)	-151.87	58.17
Outer (Pye) Island (Boundary 1)	-150.38	59.34
Outer (Pye) Island (Boundary 1)	-150.41	59.35
Pinnacle Rock	-161.76	54.77

method versus differences in counting methods. These group predictors were the first to enter the model. The second term to enter was the count type, which indicated the observational method used to make the count.

The PDO is a widely used (Trites et al., 2007b) index of climate, defined as the first principle component of a variety of biological and climatological factors in the North Pacific (Mantua and Hare, 2002). These data are complete and are treated as applicable to the entire North Pacific. Data are available monthly however only the month of June is used in this project. June is the dominant period of pupping for Steller sea lions (Pitcher and Calkins, 1981) as well as being the time in which most of the observation counts were made.

Fishing data were drawn from the observer database, a collection of observations of fishing catches made by National Marine Fisheries Service (NMFS) observers aboard fishing vessels. Data drawn were all hauls which either started or ended within 50km of each site. Trawl data was standardized by length of trawl in time to get an estimate of the CPUE near each rookery. CPUE is taken as reflective of the local abundance, and since abundance varies by site, each site has a unique fishing index. This index is defined as the first principle component of the estimated CPUE of cod, Atka mackerel, and pollock. These species were identified in National Marine Fisheries Service (2008) as being key prey resources for the Steller sea lion. Although reports from observers cover only a fraction of the fishery, this CPUE index represents an estimate of the effects of fishing on SSL foraging ecology at certain rookeries and haulouts.

The principle component was used as a means of data reduction (Faraway, 2006). A unique principle component vector is used at each site. This approach has the advantage of using an index of prey CPUE which is unique to each site, since the prey field is known to vary in both quality and quantity between sites (Schauffer et al., 2006). The use of a principle component, particularly one which is site-dependent, limits the interpretability and predictive value of the model. The fishing effect on Steller sea lions is expected to be not linked to a particular species, but rather the variation in prey items common to that site. By taking the first principle component of several of these CPUEs, the fishing index is a proxy for this loss of prey as well as reducing the number of parameters which must be estimated in the model.

Sites were selected based on the available yearly counts. The model was run from the first year there was both count and fishing data at the site. This results in potentially different starting years for each site. The earliest start year was taken to be 1989, which is just prior to both a substantial change in fishing regulation and a strong negative June PDO (which was found in early simulations to have a substantial impact). Fisheries data was also much more intensively collected in more recent times. The balance struck to choose 1989 was between the inclusion of all the

relevant events and as much data as possible, without ignoring unmodeled changes which might dilute the effect of a factor within the model.

2.2.2 Model

Bayesian posterior distributions are obtained for parameters (Table 2.3) in a Leslie matrix model. Notably this model is for individuals of both sexes, not just females. Six of these parameters show the influence of fishing and PDO on the life history parameters of Steller sea lions contained in the Leslie matrix for each site. These parameters are $\beta_{\phi 1}$, $\beta_{\phi 2}$, $\beta_{\rho 1}$, $\beta_{\rho 2}$, $\beta_{\sigma 1}$, and $\beta_{\sigma 2}$. Each is a coefficient of either the fishing (parameters with a subscript of 1) or the PDO (subscript of 2) in a linear combination to predict life history parameters of the model (Equations 2.4 through 2.6).

The Leslie matrix is a matrix of life history parameters, showing the reproduction (number of offspring per individual) and survivorship (number of individuals surviving from one year to the next) for a species (Caswell, 2000). This model uses a three parameter Leslie matrix model, with parameters which vary by both site and year. The specific values of the parameters are determined by the value of the PDO for that year, the value of the fishing index at that year and site, and estimated β parameters which do not vary by site.

The Leslie matrix transitions the Steller sea lion counts in year t at site i , P_{it} for newborn and A_{it} non-pup counts, to year $t + 1$ according to a Leslie matrix with parameters ϕ_{it} , ρ_{it} , and σ_{it} . These parameters represent the reproductive rate, the first year to second year survivorship, and the non-pup survivorship, respectively. The non-pup survivorship can be thought of as the weighted average of survivorships for

Table 2.3: Estimated parameters of the model. The priors for the β parameters were derived from Wolf and Mangel (2004), assuming there was no influence of the PDO or fishing on the each parameter. The pup and adult count priors were taken to be normal, with a mean set to be the actual observation in that year. The variance of the priors is set to be the same as the observational variance, 407, drawn from Table 2.1.

Parameter	Prior	Description
$\beta_{\phi 0}$	$N(\text{logit}(.197), 2)$	The baseline reproductive rate.
$\beta_{\phi 1}$	$N(0, 3)$	The effect of fishing on reproductive rate.
$\beta_{\phi 2}$	$N(0, 3)$	The effect of the PDO on reproductive rate.
$\beta_{\rho 0}$	$N(\text{logit}(.776), 2)$	The baseline first year survivorship.
$\beta_{\rho 1}$	$N(0, 3)$	The effect of fishing on first year survivorship.
$\beta_{\rho 2}$	$N(0, 3)$	The effect of the PDO on first year survivorship.
$\beta_{\sigma 0}$	$N(\text{logit}(.858), 2)$	The baseline 2+ year survivorship.
$\beta_{\sigma 1}$	$N(0, 3)$	The effect of fishing on the 2+ year survivorship.
$\beta_{\sigma 2}$	$N(0, 3)$	The effect of the PDO on the 2+ year survivorship.
P_{it_0}	$N(\mu_i, 407)$	The initial first year count, where μ_{pi} is the first year observation at site i , and t_0 is the first year of observation.
A_{it_0}	$N(\mu_i, 407)$	The initial 2+ year count, where μ_{ai} is the first year observation at site i , and t_0 is the first year of observation.
C	$N(2, 2)$	Count inflation of adult animals not observed, presumed to be at sea.

all ages greater than one. These parameters are combined,

$$\begin{pmatrix} P \\ A \end{pmatrix}_{it+1} = \begin{pmatrix} 0 & \phi \\ \rho & \sigma \end{pmatrix}_{it+1} \begin{pmatrix} P \\ A \end{pmatrix}_{it}, \quad (2.1)$$

giving the population in year t given the previous year's estimate at site i .

At any given rookery, a given year's population estimate $(P_{it} \ A_{it})'$ is generated recursively by the previous year's population estimate multiplied by the Leslie matrix. Observational error is then added to each estimated count as a normally distributed error term ϵ_{it} . The estimated adult count is also multiplied by an estimated parameter C , representing the number of animals at sea during the count. This term is denoted the “at-sea inflation” factor. Few if any pups are expected to be at sea, however, so there is no corresponding term for pups. The values of the elements of the Leslie matrix are given by an inverse-logit transform of an affine combination of the PDO value X_t and a site-specific fishing index, F_{it} .

The joint likelihood for the pup and non-pup counts made at one site is shown in (2.2). The number of years since the initial counts P_{i0} and A_{i0} (which are estimated parameters) is t , and the variance on the observational error is τ^2 . The variance τ^2 is fixed at 407 for both pup and adult counts, at all sites. The value of 407 was chosen from the mean squared residual in an anova performed on portions of the count data (Table 2.1). It was chosen to be fixed after initial runs of the model showed a tendency for τ^2 to increase without an upper bound if estimated as a parameter. Due to the normal error structure ϵ_{it} added to predicted counts, the likelihood of the counts A_{it} and P_{it} given the previous year and transition matrix is a multivariate normal density with observations modeled as independent given the estimate (Casella and Berger, 2001):

$$p(P_{it}, A_{it} | \text{parameters}) = \frac{1}{2\tau^2\pi} \exp \left(- \frac{\begin{pmatrix} P_{it} - \hat{P}_{it} & A_{it} - C\hat{A}_{it} \end{pmatrix} \begin{pmatrix} P_{it} - \hat{P}_{it} \\ A_{it} - C\hat{A}_{it} \end{pmatrix}}{\tau^4} \right). \quad (2.2)$$

The predicted values for the pup and non-pup counts, \hat{P}_{it} and \hat{A}_{it} respectively, are generated by repeated matrix multiplication of the initial values P_{i0} and A_{i0} . The Leslie matrix changes every year, according to the values of the predictors. The model iteratively applies 2.1 to yield the estimated counts at any site i in year t :

$$\begin{pmatrix} \hat{P}_{it} \\ \hat{A}_{it} \end{pmatrix} = \left[\prod_{z=t}^1 \begin{pmatrix} 0 & \phi \\ \rho & \sigma \end{pmatrix}_{iz} \right] \begin{pmatrix} P_{i0} \\ A_{i0} \end{pmatrix}. \quad (2.3)$$

The error on the observations is taken to be independent, so the joint likelihood for all observations is the product of the individual likelihoods for each pup or adult count made.

The matrix in 2.3 has components given by

$$\text{logit}(\phi_{it}) = \beta_{0\phi} + \beta_{1\phi}F_{it} + \beta_{2\phi}X_t, \quad (2.4)$$

$$\text{logit}(\rho_{it}) = \beta_{0\rho} + \beta_{1\rho}F_{it} + \beta_{2\rho}X_t, \quad (2.5)$$

$$\text{logit}(\sigma_{it}) = \beta_{0\sigma} + \beta_{1\sigma}F_{it} + \beta_{2\sigma}X_t, \quad (2.6)$$

which varies as F_{it} and X_t vary.

All values of β parameters are estimated parameters in this model. The logit is

the log odds ratio and is a bijective map of $(0,1)$ onto $(-\infty, \infty)$. This ensures that ϕ , ρ and σ are all between 0 and 1. The logit function in this model is used in a similar fashion to the logit link in a binomial generalized linear model (Faraway, 2006). Prior distributions for $\beta_{\star 0}$ values were chosen to be centered around the parameter values used by Wolf and Mangel (2004), assuming the same survivorship for males and females. The priors for β_1 and β_2 are both centered at 0 with a variance of 3, chosen to be a value significantly larger than the expected magnitude of the parameters.

The logit transformation is a widely used function for mapping $(0,1)$ onto $(-\infty, \infty)$ (Faraway, 2006):

$$\text{logit}(x) = \log \left(\frac{x}{1-x} \right). \quad (2.7)$$

Although the survivorships, ρ and σ , are by definition a number between zero and one, the reproductive rate need not be. However since the reproductive rate of Steller sea lions is averaged over non-pup males and females, and twinning is very rare, it is unlikely that Steller sea lions would have a reproductive rate greater than one.

The first year counts for any given site is taken to be the year where the first count data are available, 1989 or later, where fishing CPUE estimates can also be made. The first year counts are taken to be estimated parameters, adding two parameters for every site in the model, which have a prior taken to be the first year of observed data, with a variance of 407, taken from the mean squared error in Table 2.1. Since the residuals of the anova (Table 2.1) can be thought of as observational error, the mean squared error is a natural choice to approximate the variance of the observational error. The uncertainty in the initial count (which is based around observed pup and adult counts for the first year), is also due to observational error. Thus both the prior for the counts and the observation error variance set on subsequent observations share the same value of 407. There are a total of 22 parameters to be fit in the model,

including initial values at the sites (Table 2.3).

2.2.3 Bayesian parameter estimation

Since there were pre-existing data available on the life history parameters used in this model, Bayesian statistics are used to gain further confidence in the parameters conditioned on the count data. Bayesian methods allow for the incorporation of prior knowledge of parameters through the specification of prior distributions (Gelman et al., 2004). In Bayesian statistics, the probability function associated with a parameter represents the uncertainty in its value, as opposed to frequentist statistics wherein probabilities represent the value of the parameter approached by increasing amounts of data (Jaynes, 2003).

The Metropolis-Hastings algorithm, which is an implementation of the MCMC method, was used to find the posterior distribution of the parameters. Starting from an initial value of the parameters, the parameters were perturbed or “jumped” to new values, the probabilities of which are determined by a jump function. The likelihood of the data given the new values, $f(D|\theta)$, times the prior distribution evaluated at the new parameter values, $g(\theta)$ is calculated. This is divided by the likelihood of the data, given the original parameters θ^* , times the prior distribution evaluated at the original values. This quantity is in turn multiplied by the ratio of the probability of the jump from the old values to the new, over the probability of jumping from the new values to the old using the jump function J . This is the acceptance ratio W :

$$W = \frac{f(D|\theta)g(\theta)J(\theta|\theta^*)}{f(D|\theta^*)g(\theta^*)J(\theta^*|\theta)}. \quad (2.8)$$

If the acceptance rate W is greater than 1, the new values are accepted and the

results are appended to the sequence of values. If the ratio is less than one, the new values are accepted with a probability equal to the value of the ratio. If the new value is not accepted, the value prior to the jump is appended to the sequence of parameter estimates. Whether the old or the new value is retained, that value is the starting point for another jump. Each of these cycles is termed a scan. This process is repeated for millions of scans. The resulting parameter values, if the simulation is run long enough and the parameters are thinned to remove autocorrelation among scans, are drawn from the posterior distribution, (Gelman et al., 2004).

To assess whether the simulation has run long enough, the stationarity of the solutions is assessed. Stationarity is defined as a lack of directionality in the scans, as well as constant variance. The jump function is the main controlling factor on the speed of convergence. To speed convergence, some tuning to the jump function is done after the model is run for an initial “burn-in” period. The burn-in period is an initial run of the MCMC used to roughly approximate a solution and provide information for fine tuning the jump function. The jump function used here is a multivariate normal. It is run for an initial burn-in period with independent jumps for each parameter, with variance on each of parameters roughly tuned to find an acceptance rate of approximately 23% (Cappe and Robert, 2000). A correlation matrix is taken from the burn-in scans which is used in the jump function of subsequent scans. This matrix was then re-tuned by a univariate scale factor to achieve an acceptance rate of approximately 23% (Cappe and Robert, 2000). All simulations in this model were written in Python 2.6.

2.3 Results

The computational approach used to estimate the posterior distributions for the model, MCMC, approximates sampling the posterior distribution of parameters through randomization and specific rules for acceptance (Gelman et al., 2004). The results of an MCMC are a joint distribution of all the parameters. The marginal distribution for the parameters are considered first, followed by correlations between parameter estimates. The initial estimates are usually poor, but converge to the true distribution through repeated sampling according to the Metropolis-Hastings algorithm. This process takes time to converge, usually scaling with the size of the model. A critical indicator of convergence is stationarity—the mean and variance of the estimates do not change with additional scans.

Stationarity was achieved for the parameters, indicating the scans were drawn from the posterior distribution of the parameters (Figures 35-37, 41-43, and 47-49). The model run contained slightly more than 6.5 million scans. Due to memory limitations, only 1 in 500 were saved by the computer; these were subsequently thinned further to removed autocorrelation.

Although stationarity does not necessarily imply convergence, it is a good indicator. There is an ever-present risk of programming errors as well, however this was minimized by simulations of posterior distributions on test data with known values.

The key model parameters (Table 2.4) show a large effect of PDO on the first year survivorship. All of the parameters fit to values away from zero, based on their 95% credible intervals, indicating that both the PDO and fishing do have some level of impact on each of the Steller sea lion life history parameters. The parameters have an effect on the life history parameters of Steller sea lions through an inverse logit function (equations 2.4 through 2.6) so the effect that each parameter has on the

Table 2.4: The means and 95% Bayesian intervals of the posterior distributions for the nine β parameters, representing the baseline reproductive rates and effects of the PDO and fishing.

	Mean	Lower bound	Upper bound
$\beta_{\phi 0}$	2.2762	2.2525	2.2947
$\beta_{\phi 1}$	0.2726	0.2692	0.2756
$\beta_{\phi 2}$	-0.6417	-0.6485	-0.6325
$\beta_{\rho 0}$	4.1646	4.1276	4.1992
$\beta_{\rho 1}$	0.6112	0.5929	0.6338
$\beta_{\rho 2}$	5.6686	5.6123	5.7300
$\beta_{\sigma 0}$	-0.8445	-0.8563	-0.8339
$\beta_{\sigma 1}$	-0.5756	-0.5853	-0.5658
$\beta_{\sigma 2}$	-1.0781	-1.0871	-1.0693

life history parameters is nonlinear and interactive with the other parameters. These results can be translated into the life history parameters using the values of the PDO and fishing at each site.

2.3.1 Posterior predictive distributions

Sampling from the joint posterior distribution gives parameters which can then be run though the model. The posteriors fits can be repeatedly resampled and the model run using those parameters forming a predictive distribution for the observation made at a particular site in a particular year. Although the β parameters are shared across all sites, each site has a different set of predictors and different initial pup and adult counts (Table 2.3). Since sites start at different points and each site has unique predictors, each site also has a unique posterior predictive distribution for each year (Figures 2.2 through 2.13). The predictive interval can be found then by repeatedly resampling the posterior distribution, running the simulation at each site, and adding the observational error.

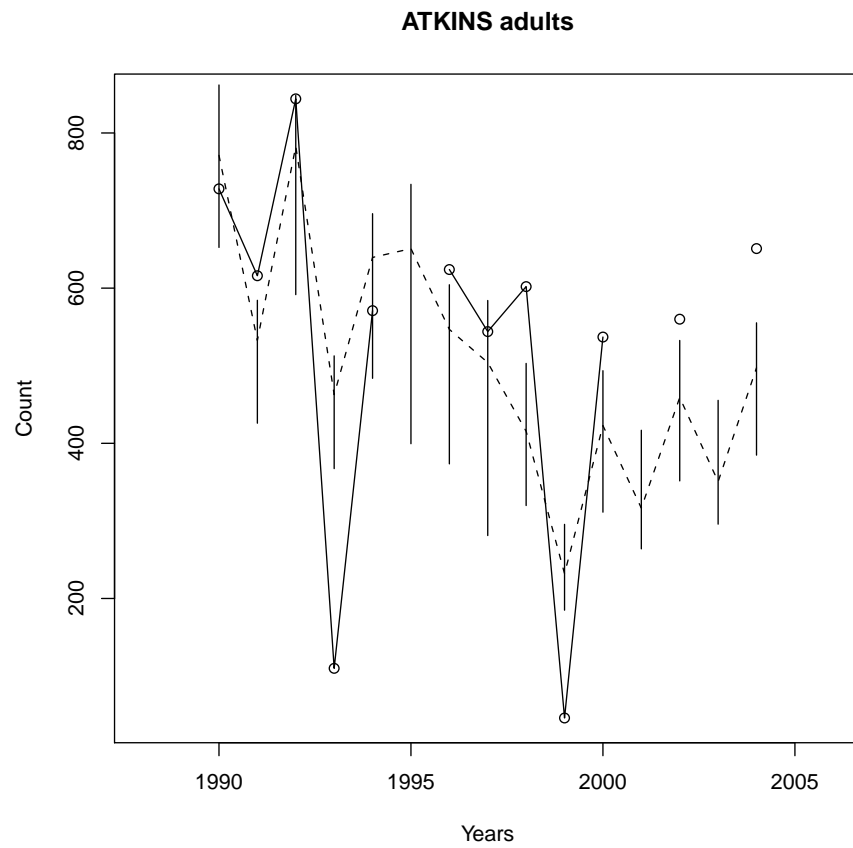


Figure 2.2: The posterior population trend (dotted line) and observations (open circles, solid line) for adults at Atkins. Vertical bars for each year represent the error margin of the prediction plus observational error.

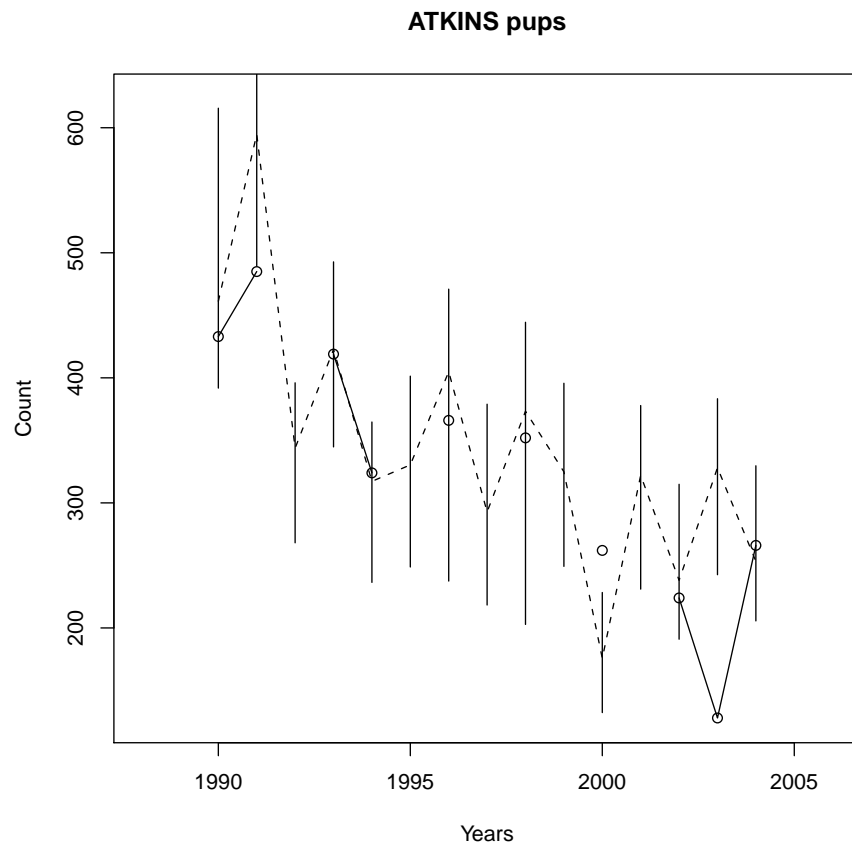


Figure 2.3: The posterior population trend (dotted line) and observations (open circles, solid line) for pups at Atkins. Vertical bars for each year represent the error margin of the prediction plus observational error.

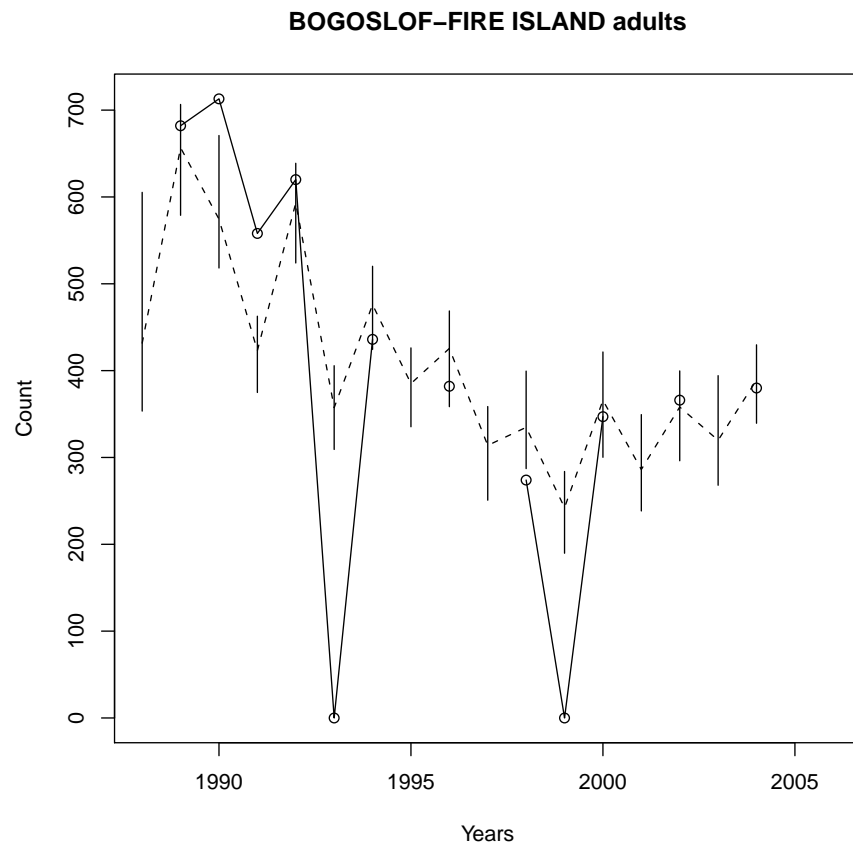


Figure 2.4: The posterior population trend (dotted line) and observations (open circles, solid line) for adults at Bogoslof/Fire Island. Vertical bars for each year represent the error margin of the prediction plus observational error.

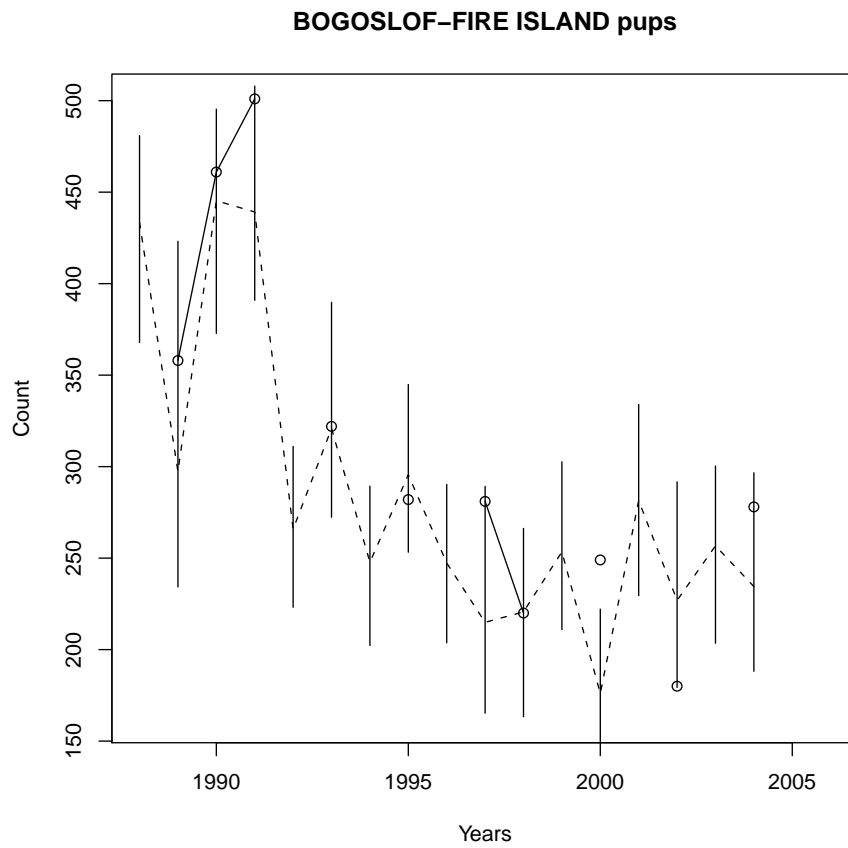


Figure 2.5: The posterior population trend (dotted line) and observations (open circles, solid line) for pups at Bogoslof/Fire Island. Vertical bars for each year represent the error margin of the prediction plus observational error.

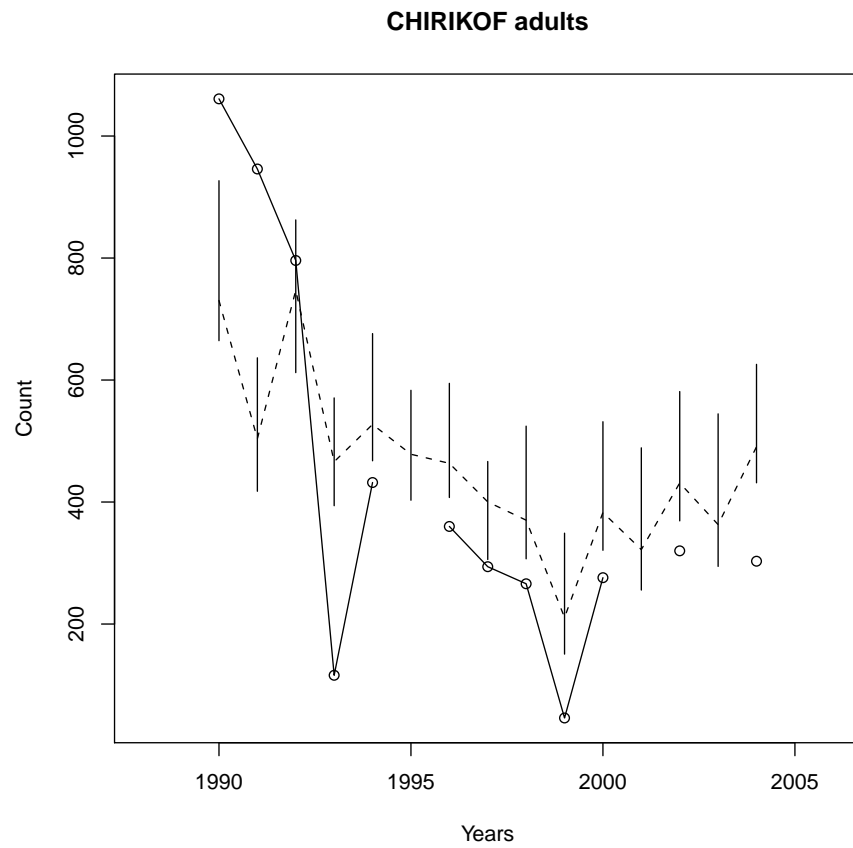


Figure 2.6: The posterior population trend (dotted line) and observations (open circles, solid line) for adults at Chirikof. Vertical bars for each year represent the error margin of the prediction plus observational error.

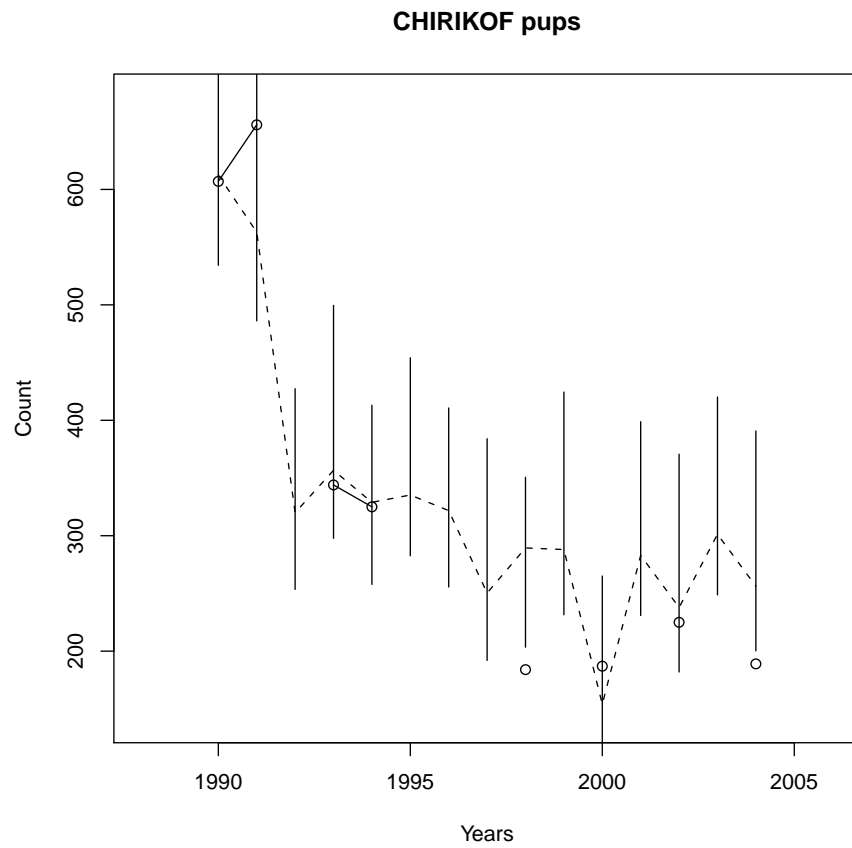


Figure 2.7: The posterior population trend (dotted line) and observations (open circles, solid line) for pups at Chirikof. Vertical bars for each year represent the error margin of the prediction plus observational error.

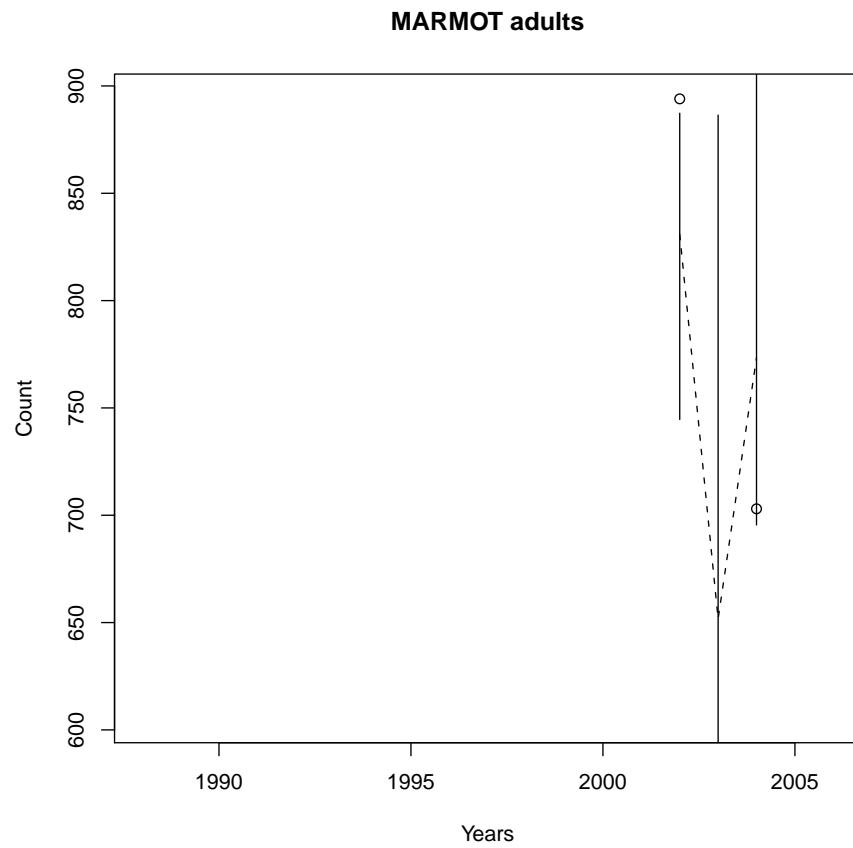


Figure 2.8: The posterior population trend (dotted line) and observations (open circles, solid line) for adults at Marmot Island. Vertical bars for each year represent the error margin of the prediction plus observational error.

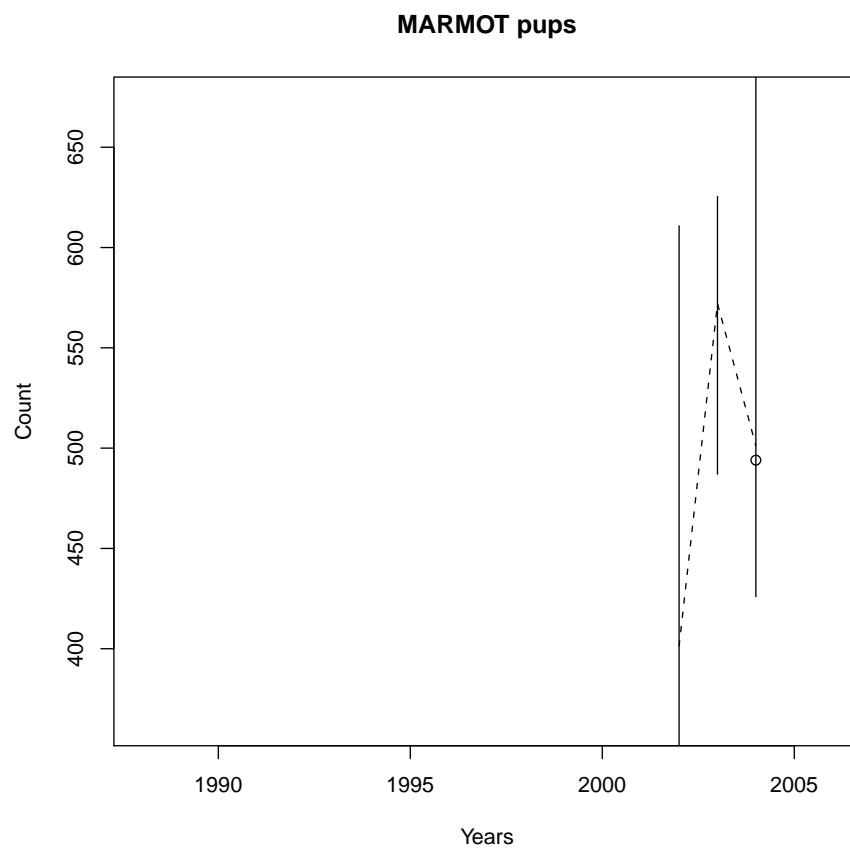


Figure 2.9: The posterior population trend (dotted line) and observations (open circles, solid line) for pups at Marmot Island. Vertical bars for each year represent the error margin of the prediction plus observational error.

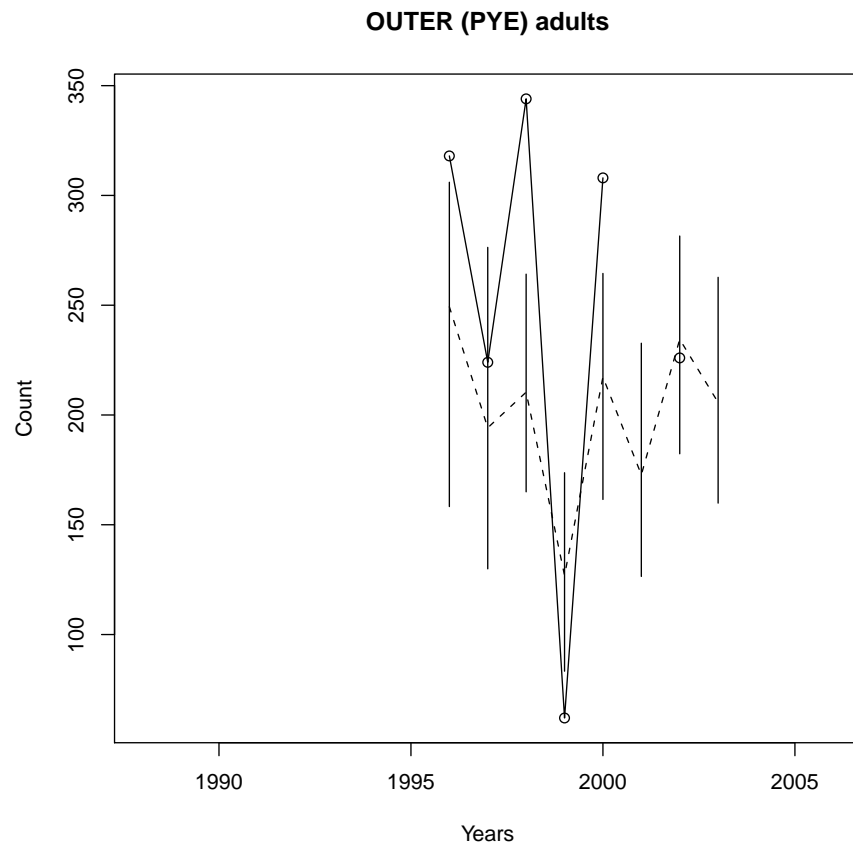


Figure 2.10: The posterior population trend (dotted line) and observations (open circles, solid line) for adults at Outer (Pye) Island. Vertical bars for each year represent the error margin of the prediction plus observational error.

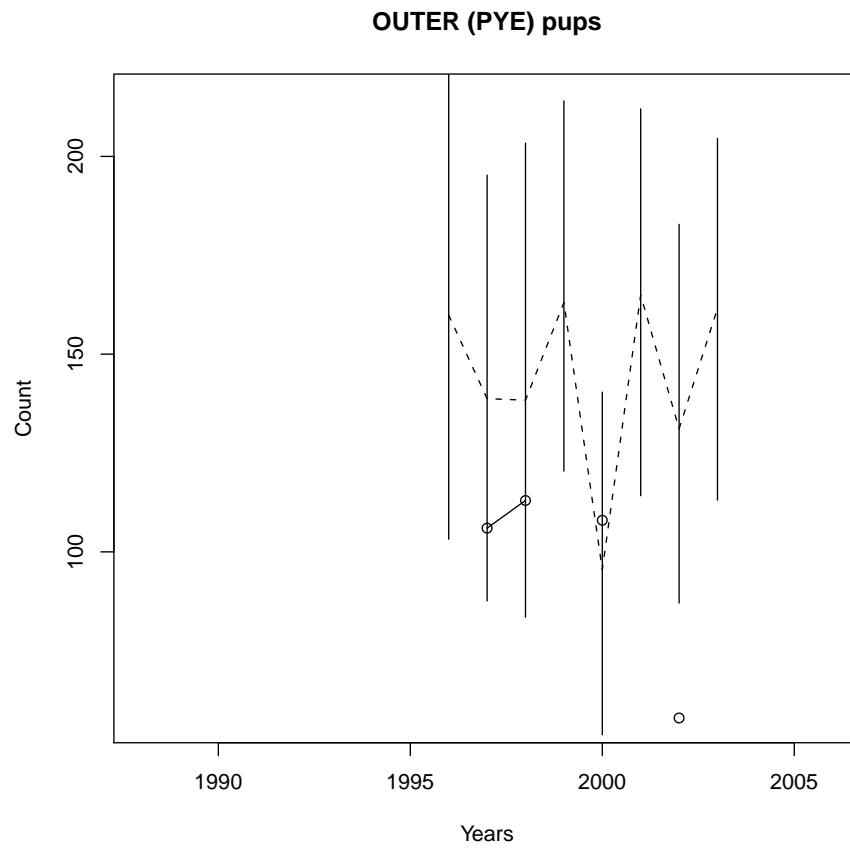


Figure 2.11: The posterior population trend (dotted line) and observations (open circles, solid line) for pups at Outer (Pye) Island. Vertical bars for each year represent the error margin of the prediction plus observational error.

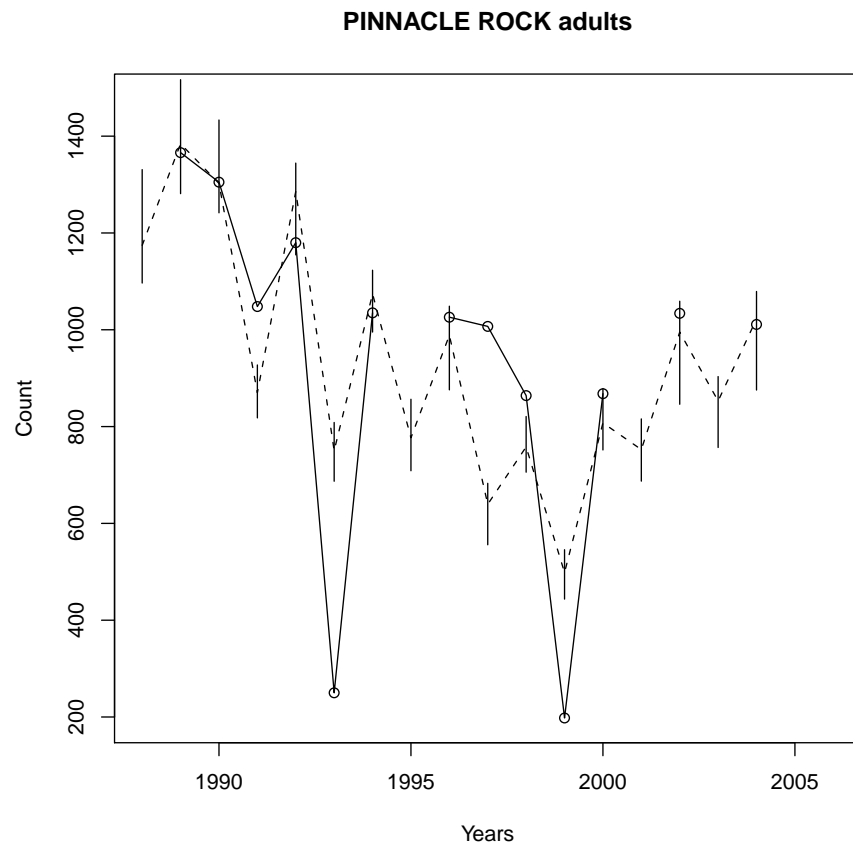


Figure 2.12: The posterior population trend (dotted line) and observations (open circles, solid line) for adults at Pinnacle Rock. Vertical bars for each year represent the error margin of the prediction plus observational error.

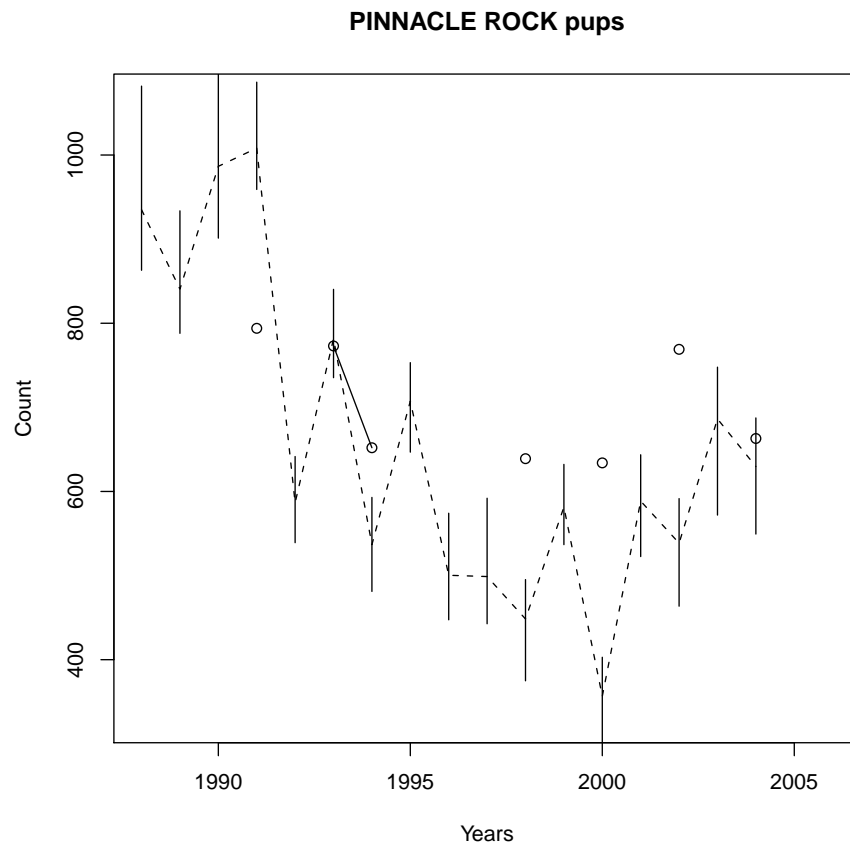


Figure 2.13: The posterior population trend (dotted line) and observations (open circles, solid line) for pups at Pinnacle Rock. Vertical bars for each year represent the error margin of the prediction plus observational error.

The results from these plots show several features. The posterior predictive intervals often do not intersect the points which should be included. This is discussed further below in section 2.3.8. Despite this, however, the predictions do, in some sense, follow the general trends of the data at all of the sites.

2.3.2 *Reproductive rate*

The parameters controlling the reproduction rate, defined here as the number of offspring per adult (not female, as is more frequently the definition) show opposite impacts of fishing and the PDO. A higher fishing index has the result of increasing the reproductive rate, while the PDO has the effect of decreasing the reproductive rate by approximately the same order of magnitude (Table 2.4). The convergence shows stationarity of the solutions (Figures 35-37), with small variances around the parameter estimates (Figures 38-40). Reconstructing the estimates of ϕ at each site via equation 2.4 (Figures 2.14-2.19), using the means of the posterior distributions of $\beta_{\phi 0}$, $\beta_{\phi 1}$, and $\beta_{\phi 2}$ (Figures 2.14-2.19) shows the reproduction rates are surprisingly high. The values are unusually high since the values of the reproduction rate is averaged over both males and females. With the known rarity of twinning (Loughlin et al., 1987), a reproduction rate over 0.5 is biologically problematic. This could be indicative of one of several possible patterns, including systematic under counting of males, a skewed sex ratio represented in the counts, or an artifact of the model structure.

A rookery may not have an equal sex ratio since males defend harems of multiple females (Loughlin et al., 1987). The younger males who are unable to defend a harem often are near the rookery and may be missed in the count, resulting in a systematic overcount of females on rookeries.

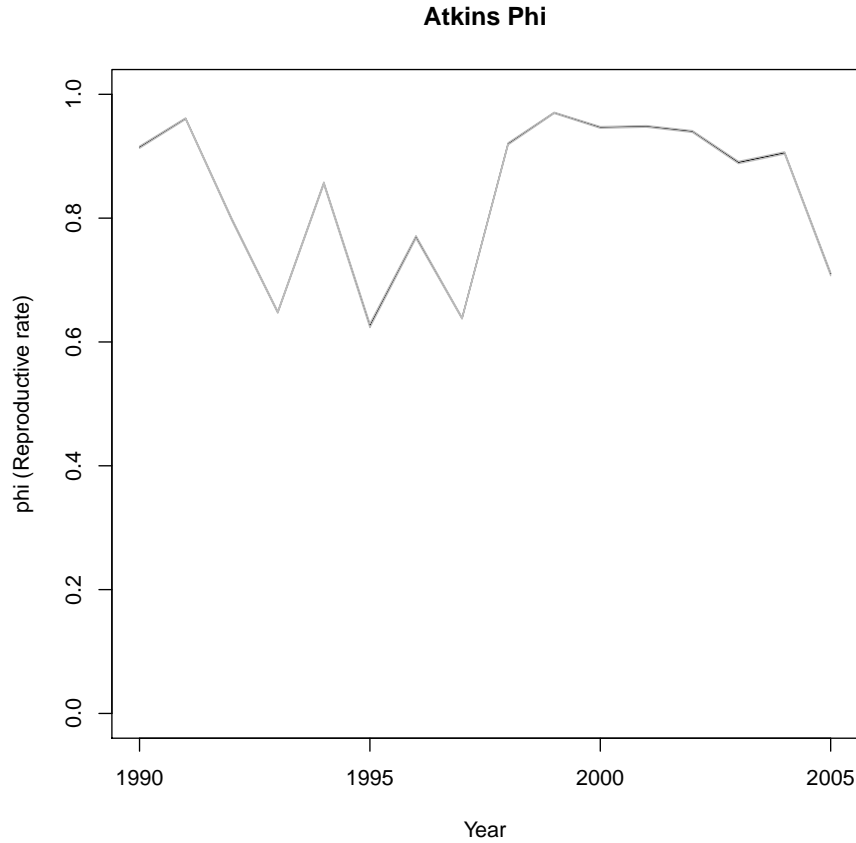


Figure 2.14: The reproductive rate ϕ at Atkins, reconstructed using the time series of fishing near Atkins and the June PDO. The estimated parameters β parameters are taken to be the mean of their posterior distributions. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.



Figure 2.15: The reproductive rate ϕ at Bogoslof/Fire Island, reconstructed using the time series of the fishing index near Bogoslof/Fire Island and the June PDO. The estimated parameters β parameters are taken to be the mean of their posterior distributions. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

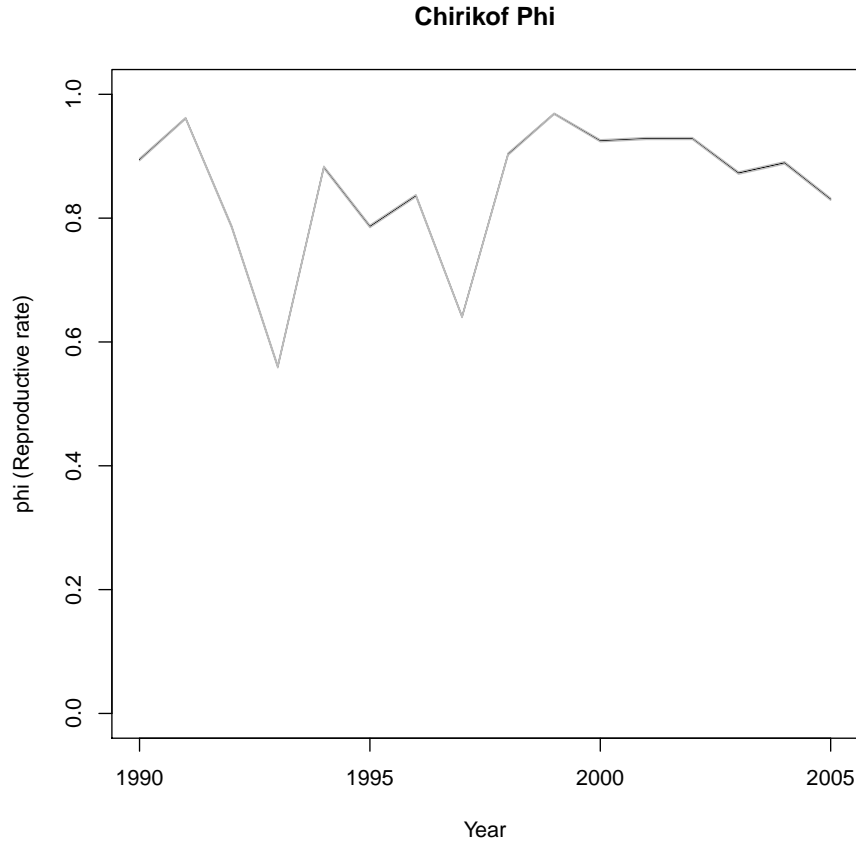


Figure 2.16: The reproductive rate ϕ at Chirikof, reconstructed using the time series of the fishing index near Chirikof and the June PDO. The estimated parameters β parameters are taken to be the mean of their posterior distributions. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

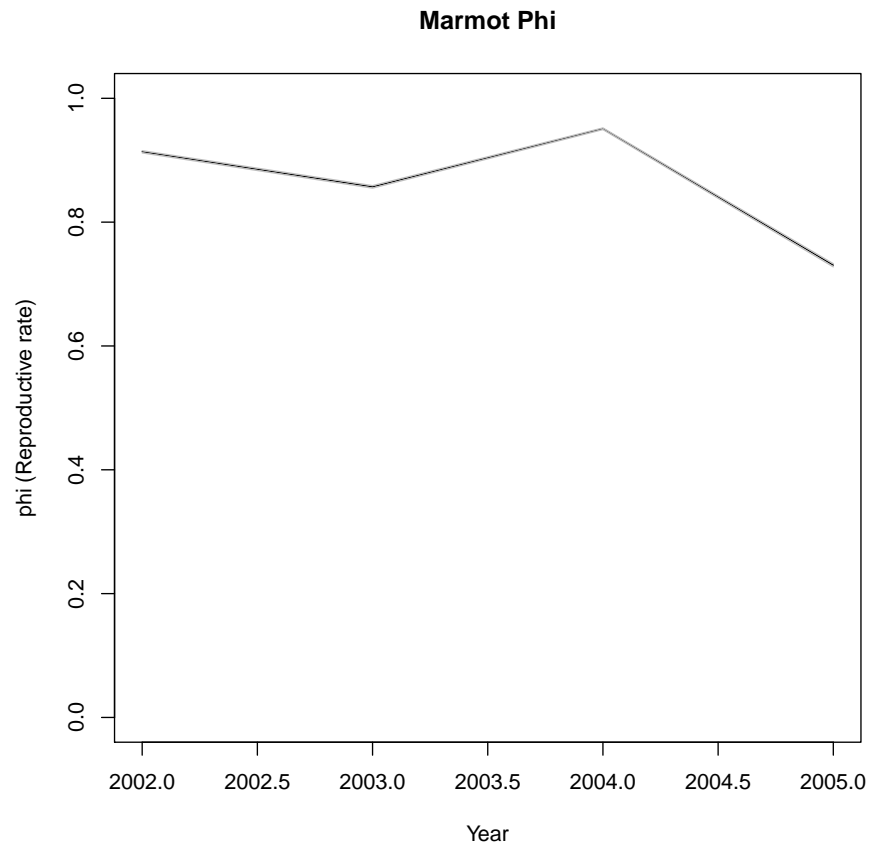


Figure 2.17: The reproductive rate ϕ at Marmot Island, reconstructed using the time series of the fishing index near Marmot Island and the June PDO. The estimated parameters β parameters are taken to be the mean of their posterior distributions. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

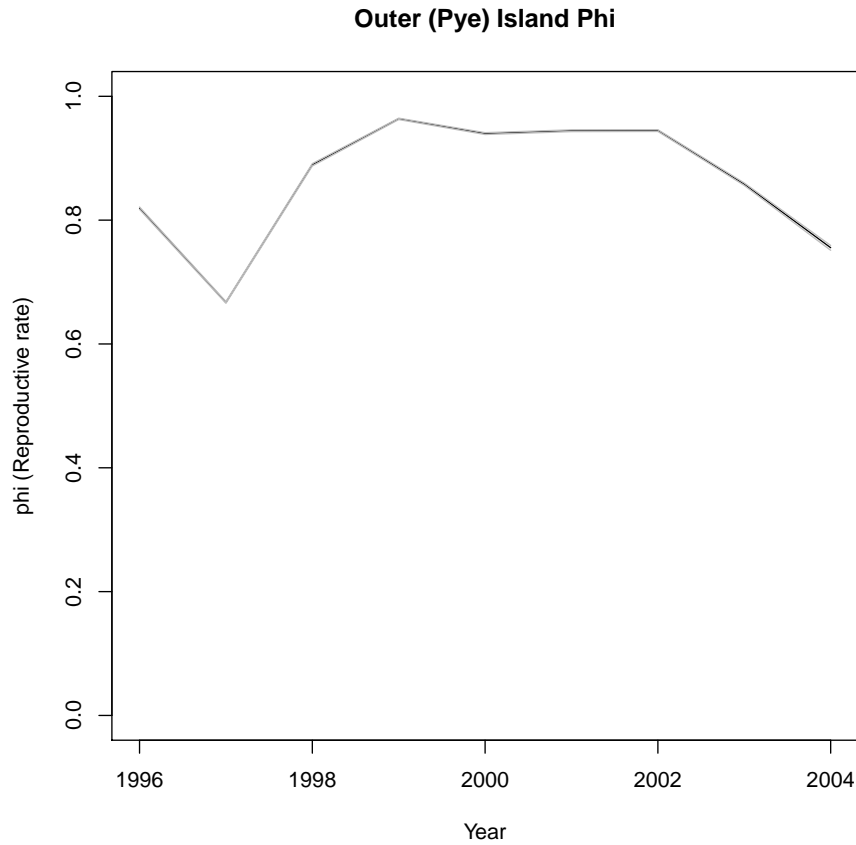


Figure 2.18: The reproductive rate ϕ at Outer (Pye) Island, reconstructed using the time series of the fishing index near Outer (Pye) Island and the June PDO. The estimated parameters β parameters are taken to be the mean of their posterior distributions. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

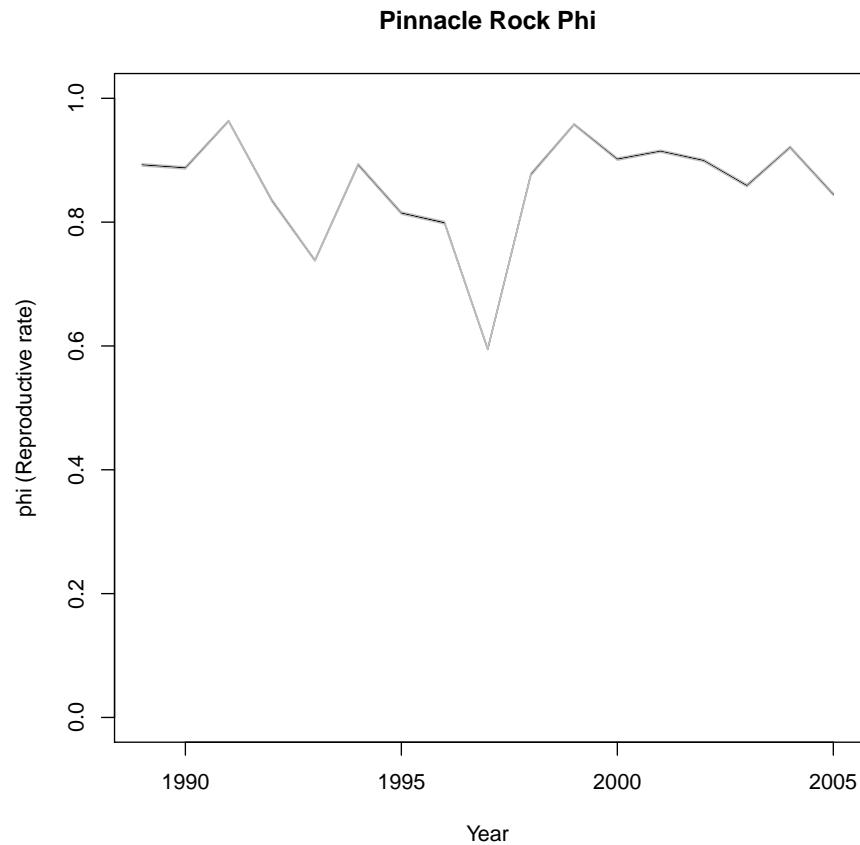


Figure 2.19: The reproductive rate ϕ at Pinnacle Rock, reconstructed using the time series of the fishing index near Pinnacle Rock and the June PDO. The estimated parameters β parameters are taken to be the mean of their posterior distributions. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

A correlation may also be driving this value higher, as is discussed below. The parameter $\beta_{\phi 0}$ controlling the baseline reproductive rate absent the influence of the PDO or fishing, is negatively correlated with the non pup survivorship baseline parameter $\beta_{\sigma 0}$. Since the adult survivorship is lower than is biologically realistic (as discussed below), this may artificially drive up the value of $\beta_{\phi 0}$, and in turn ϕ .

The results do show an impact of both the PDO and fishing on the reproductive rate. There is a slightly higher reproductive rate when the PDO is negative, while the PDO has the opposite effect of the pup survivorship (Table 2.4).

2.3.3 *Pup survivorship*

Two of the β parameters, $\beta_{\rho 0}$ and $\beta_{\rho 2}$, which have means substantially larger than the others (Table 2.4) are both related to ρ , suggesting that the June PDO has a strong effect on in the Steller sea lion pup survival. The two years with a strong negative June PDO also have a dramatic decline in pup survivorship, dropping nearly to zero at all sites from a value in other years which is close to one (Figures 2.20-2.25). Fishing has a much smaller impact on ρ than the PDO, although it still has a 95% Bayesian posterior confidence interval which does not include zero (Table 2.4). While these data can not speak to the initial cause of the decline, they suggest the role of the climate, as reflected in the June PDO, in preventing recovery.

The means of $\beta_{\rho 0}$ and $\beta_{\rho 2}$ are larger than other β parameters (Table 2.4), as well as having larger variances (Figures 44-46). This effect is to be expected from (2.5), since the logit transformation makes ρ relatively insensitive to changes in the predictors or parameters when ρ is near one or zero. The mean of $\beta_{\rho 1}$, controlling the effects of fishing on ρ , is small and also has a small variance (Figures 44-46). The 95% posterior interval of $\beta_{\rho 1}$ does not include zero (Table 2.4). The magnitude of the fishing effect

this represents, however, is small due to relative magnitudes of $\beta_{\rho 0}$ and $\beta_{\rho 2}$.

Transforming these estimates back into values of ρ using equation (2.5) reveals a high survivorship in most years, which also suffers dramatic, single year declines at all six sites (Figures 2.20-2.25). Pup survivorship is near one in most years, indicating high pup survivorship. Two years, correlated with a strongly negative June PDO, show a crash in pup survivorship (Figures 2.20-2.25). Every site with sufficient data shows a pup survivorship crash in the same years, 1991 and 1999, both of which had a strong negative June PDO. It is probable that these crashes have some influence on the failure of Steller sea lions to recover in the 1990s.

The posterior distributions for $\beta_{\rho 0}$ and $\beta_{\rho 2}$ have means (Table 2.4) which are far away from their respective prior distributions. Although the variances of these priors, 2 and 3 respectively (Table 2.3), were chosen to be larger than the expected magnitude of the parameters, both parameters converged to distributions somewhat outside of this expectation. This reinforces the strength of this result in the data. The convergence to a point well away from the prior is an indication the signal of these pup-survivorship failure events was sufficiently strong that it was sufficient to overcome the believed improbability of the result as represented in the prior.

The pup survivorship shows a marked pattern of single year crashes survivorship, strongly tied to the PDO. In 1991 and 1999, model estimates indicate large-scale deaths of pups born in 1990 or 1998. The mortalities are so overwhelming in magnitude, going from near one to near zero in a single year, that the pup survivorship failure is evident in the count data. Pup survivorship can be approximated, under the assumption of no non-pup mortality, as $M = \frac{A_t - A_{t-1}}{P_{t-1}}$, the size of the non-pup population change in year t over the number of pups from the previous year. While the size of the adult population change is also affected by adult mortality which varies

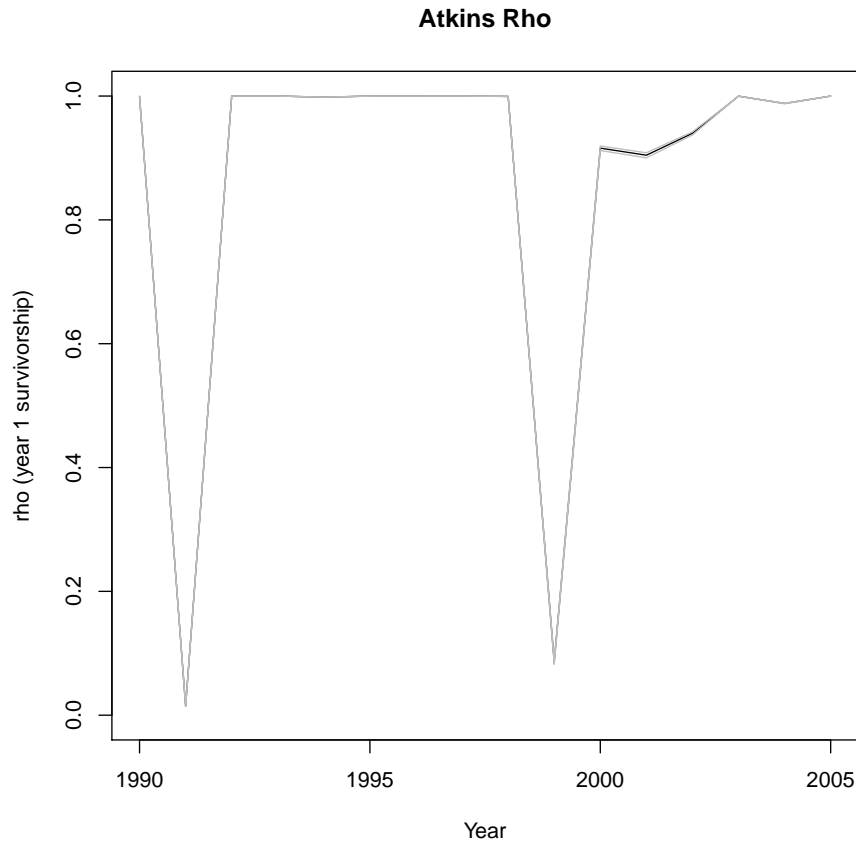


Figure 2.20: Reconstructed values of ρ , pup survivorship, at Atkins. The data indicate occasional, sudden crashes in pup survivorship, predicted by a strong negative June PDO. The overwhelming effect of the PDO, which is a region-wide phenomenon, on ρ parameters to be nearly identical at all the sites. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

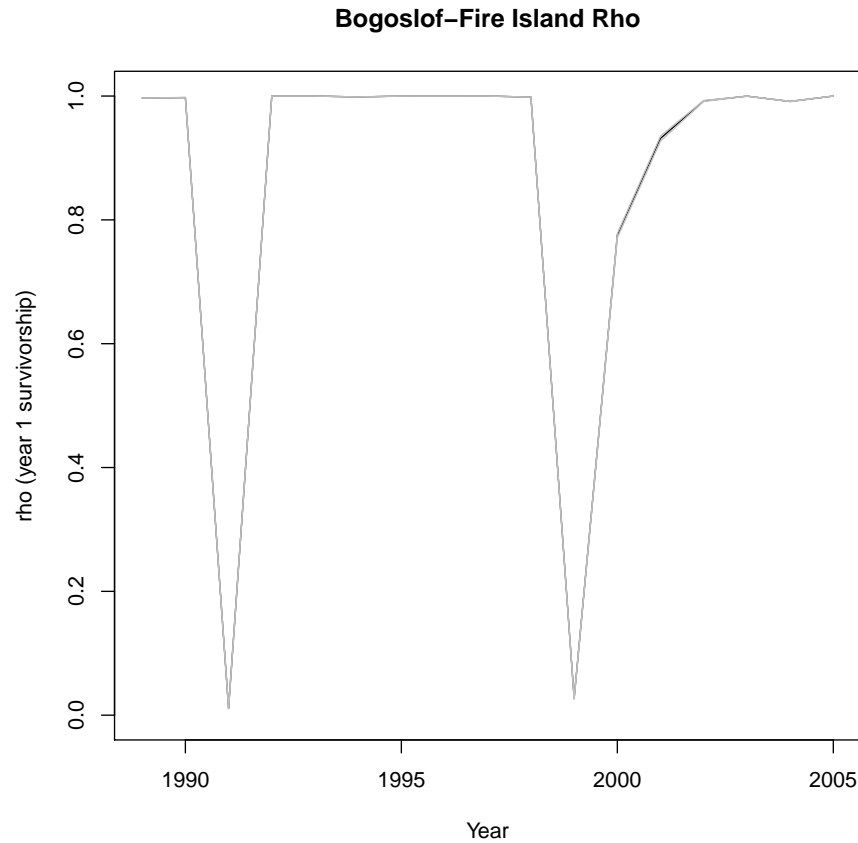


Figure 2.21: Reconstructed values of ρ , pup survivorship, at Bogoslof/Fire Island. The data indicate occasional, sudden crashes in pup survivorship, predicted by a strong negative June PDO. The overwhelming effect of the PDO, which is a region-wide phenomenon, on ρ parameters to be nearly identical at all the sites. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

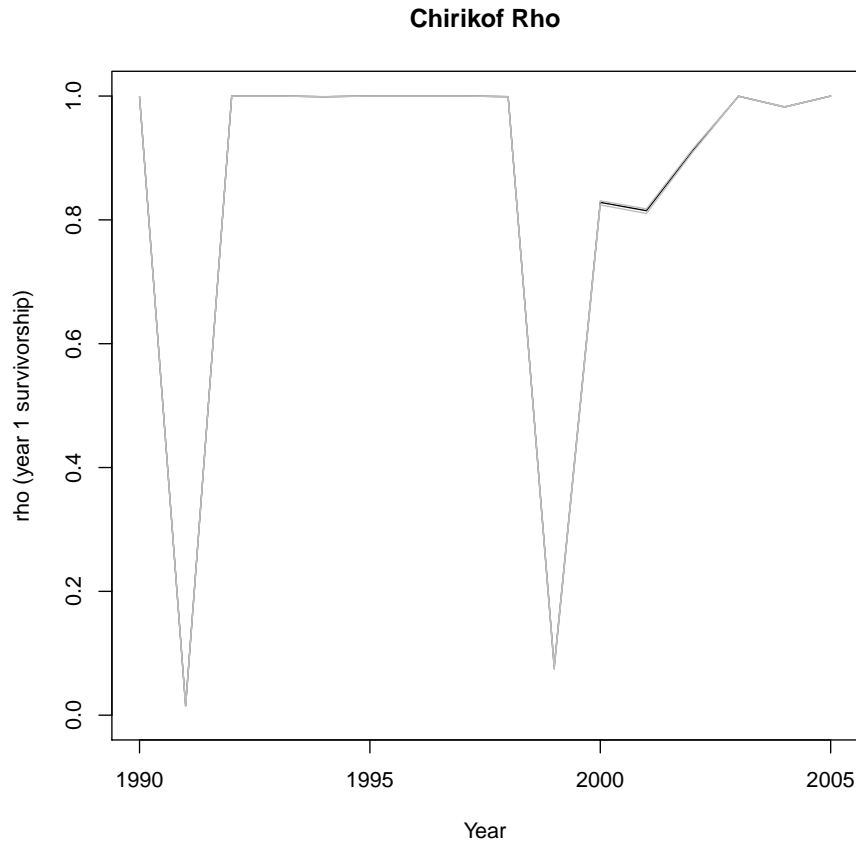


Figure 2.22: Reconstructed values of ρ , pup survivorship, at Chirikof. The data indicate occasional, sudden crashes in pup survivorship, predicted by a strong negative June PDO. The overwhelming effect of the PDO, which is a region-wide phenomenon, on ρ parameters to be nearly identical at all the sites. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

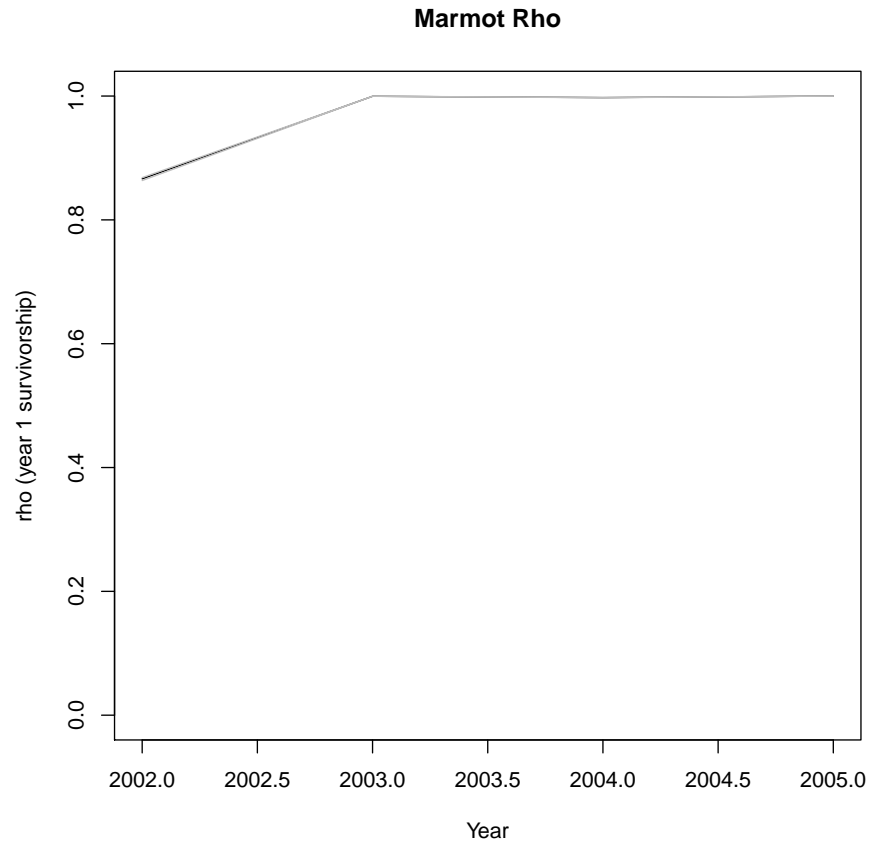


Figure 2.23: Reconstructed values of ρ , pup survivorship, at Marmot Island. The data indicate occasional, sudden crashes in pup survivorship, predicted by a strong negative June PDO. The overwhelming effect of the PDO, which is a region-wide phenomenon, on ρ parameters to be nearly identical at all the sites. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

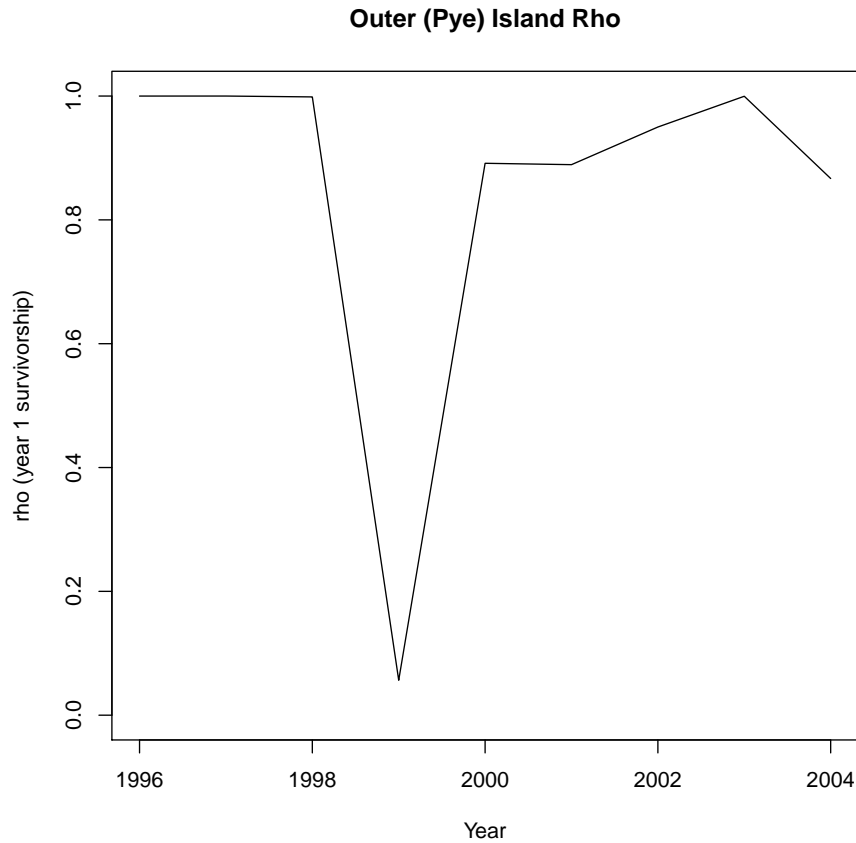


Figure 2.24: Reconstructed values of ρ , pup survivorship, at Outer (Pye) Island. The data indicate occasional, sudden crashes in pup survivorship, predicted by a strong negative June PDO. The overwhelming effect of the PDO, which is a region-wide phenomenon, on ρ parameters to be nearly identical at all the sites. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

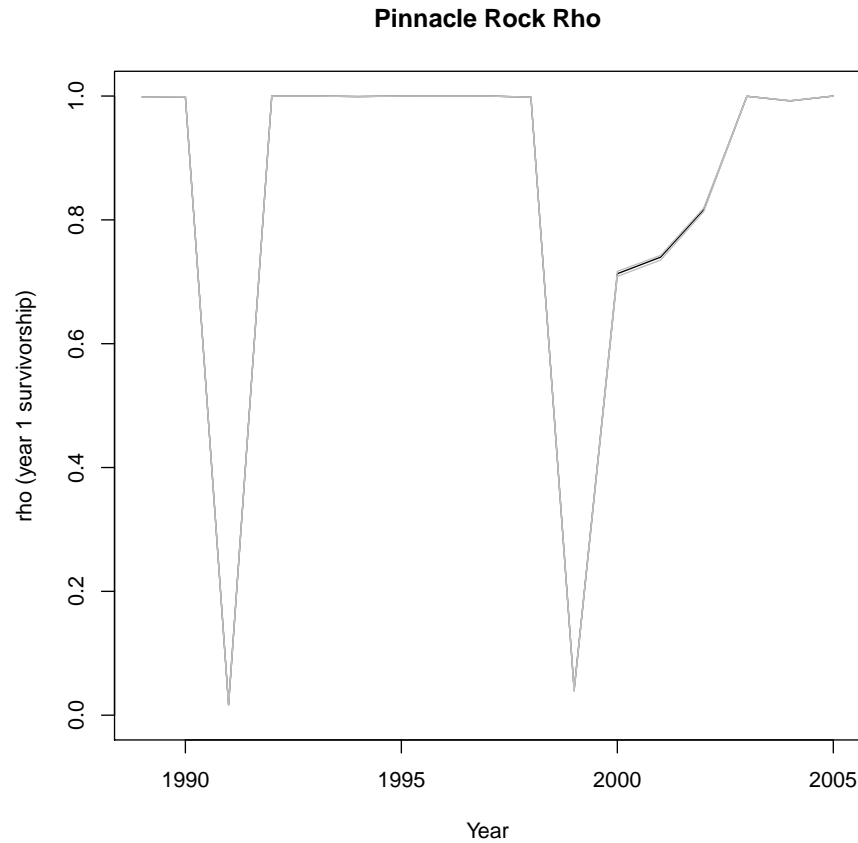


Figure 2.25: Reconstructed values of ρ , pup survivorship, at Pinnacle Rock. The data indicate occasional, sudden crashes in pup survivorship, predicted by a strong negative June PDO. The overwhelming effect of the PDO, which is a region-wide phenomenon, on ρ parameters to be nearly identical at all the sites. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

from year to year and is influenced by the June PDO as well, the size of the pup survivorship pulse is so strong, a complete failure of pup survival should be evident in these values.

To verify the pup survivorship crashes in the count data at the six sites of the model, every instance of a year with adequate data to calculate M from 1990 to 2005 was recorded. The years with a pup survivorship crash found in the model (Figures 2.20-2.25), 1991 and 1999, do have lower M values. The magnitude of the difference is striking; all of the years with sufficient data in which low pup survivorship would be expected have an M less than zero. The values of M between high and low survivorship years are plotted in figure 2.26. Although there are some years where M is low, which is not predicted in the model, these are generally higher than those in the low June PDO years. These deviations are taken to be noise reflecting an imperfect metric of pup survivorship. Even using M , a very crude estimate, these results independently confirm the pup survivorship crashes did indeed occur as fit in the model.

This ground truthing against the raw data strongly indicate the model fits are accurately portraying a real phenomenon. This has important implications for Steller sea lion conservation. These results are similar to the results of Holmes and York (2003), which found the pup survivorship changing through time, although these results indicate the pup survivorship is highly variable between years. The occasional pulses of failures of pup survivorship can both keep the Steller sea lions from recovery while observations on a rookery in any given year are likely to look perfectly normal.

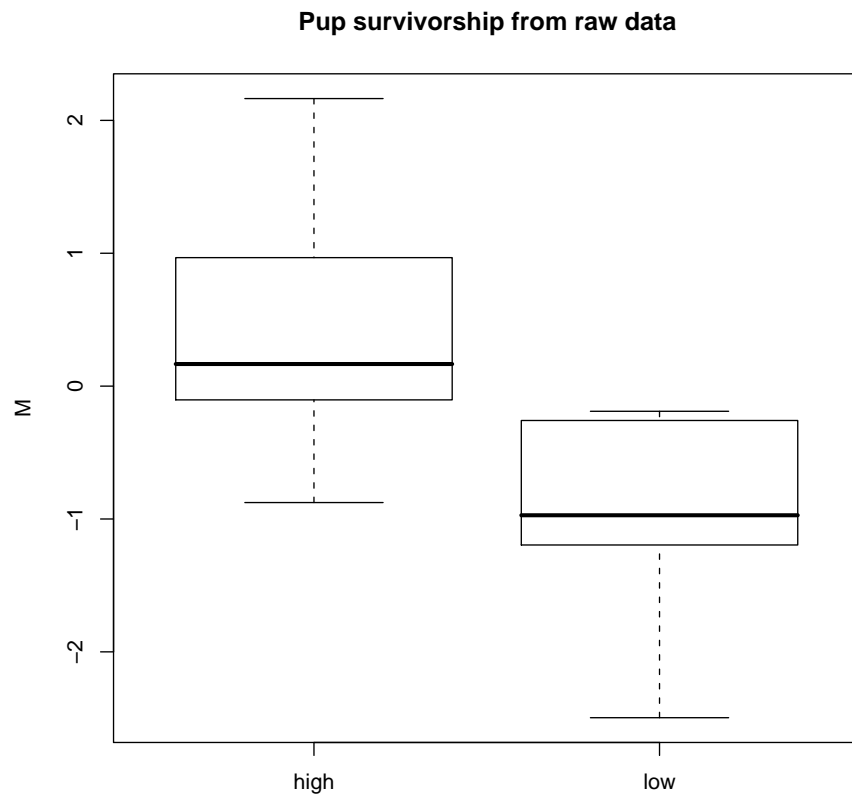


Figure 2.26: A proxy for pup survivorship, $M = \frac{A_t - A_{t-1}}{P_{t-1}}$, plotted in years where high pup survivorship is expected and years in which low survivorship is expected. The results show that the model fits of low survivorship in high June PDO years is reflected in the raw data.

2.3.4 *Non-pup survivorship*

The non-pup survivorship also varies widely from year to year (Figures 2.27-2.32), influenced by both fishing and the PDO as indicated by confidence intervals which do not include 0 (Table 2.4, Figures 50-52). The values are somewhat lower in many years than has been previously assumed (Wolf and Mangel, 2004), a factor which is likely to be in part responsible for the Steller sea lion failure to recover.

All of the estimated parameters are negative, indicating a drop in survivorship in high fishing index and June PDO years. The variance around these results are low (Figures 50-52), and the convergence to these results is strong (Figures 47-49). Reconstructing the values of σ_{it} indicate values lower than expected. Values drop as low as approximately 10% to highs of over 60% (Figures 2.27-2.32). These are all lower than 0.856, the value reported in Wolf and Mangel (2004) calculated from the values in the Leslie matrix reported in Holmes and York (2003).

2.3.5 *Auxiliary parameters*

In addition to estimating the nine β parameters which are used to examine the hypotheses, it was necessary to estimate a number of additional auxiliary parameters. Each of the six sites included in the model had a pup and adult initial population count estimated, for the year prior to the first year with data. A parameter C was also estimated to account for adult individuals at-sea at the time of the counting, which is the same at all sites.

The initial pup and adult counts at each site all converged to biologically realistic values (Table 2.5). In all six sites in the model the pup count converged to smaller values than the adult count. The ratio of pup to adult counts compares to the values found in actual data (Figure 2.33).

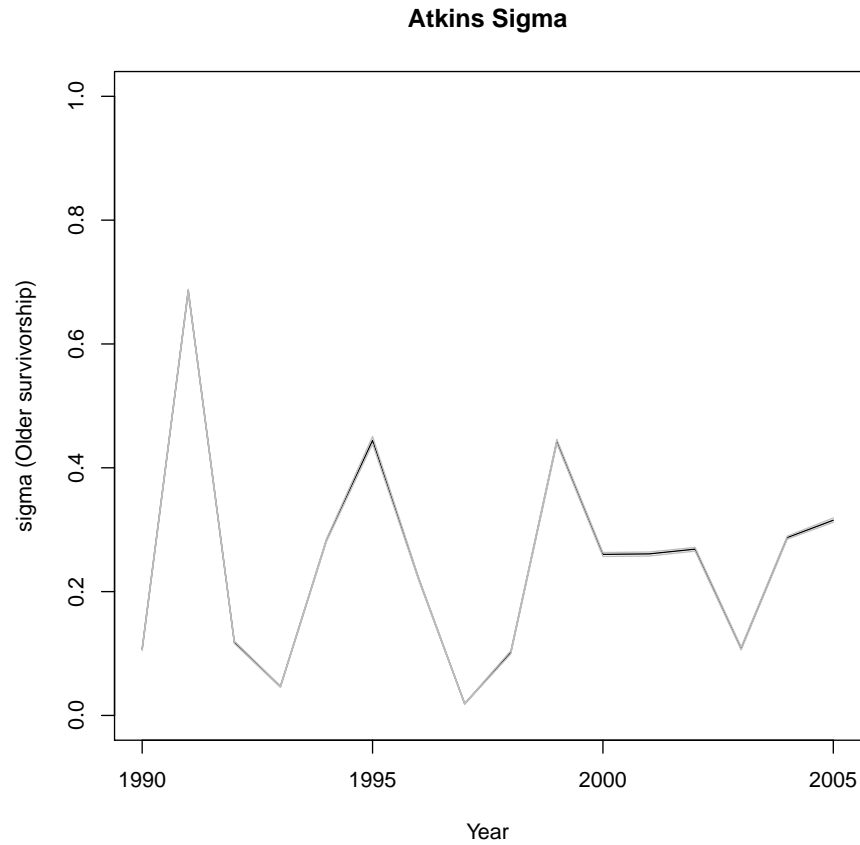


Figure 2.27: Reconstructed values of σ , the adult survivorship, at Atkins. These values are lower than have been reported elsewhere, and are strongly influenced by both the PDO and CPUE near sites. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

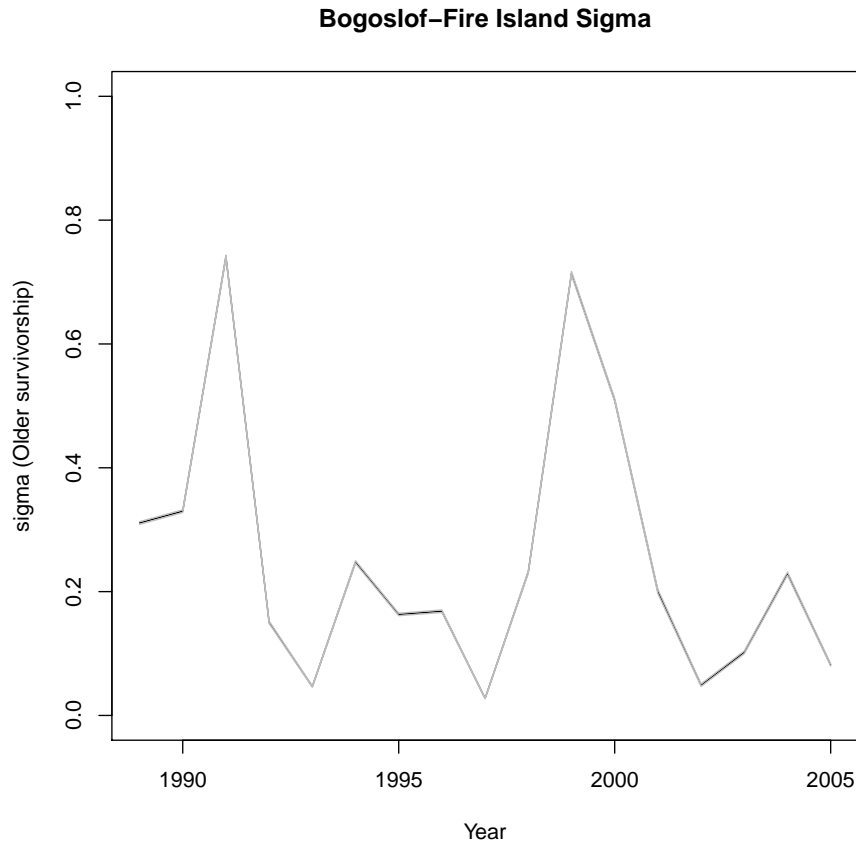


Figure 2.28: Reconstructed values of σ , the adult survivorship, at Bogoslof/Fire Island. These values are lower than have been reported elsewhere, and are strongly influenced by both the PDO and CPUE near sites. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

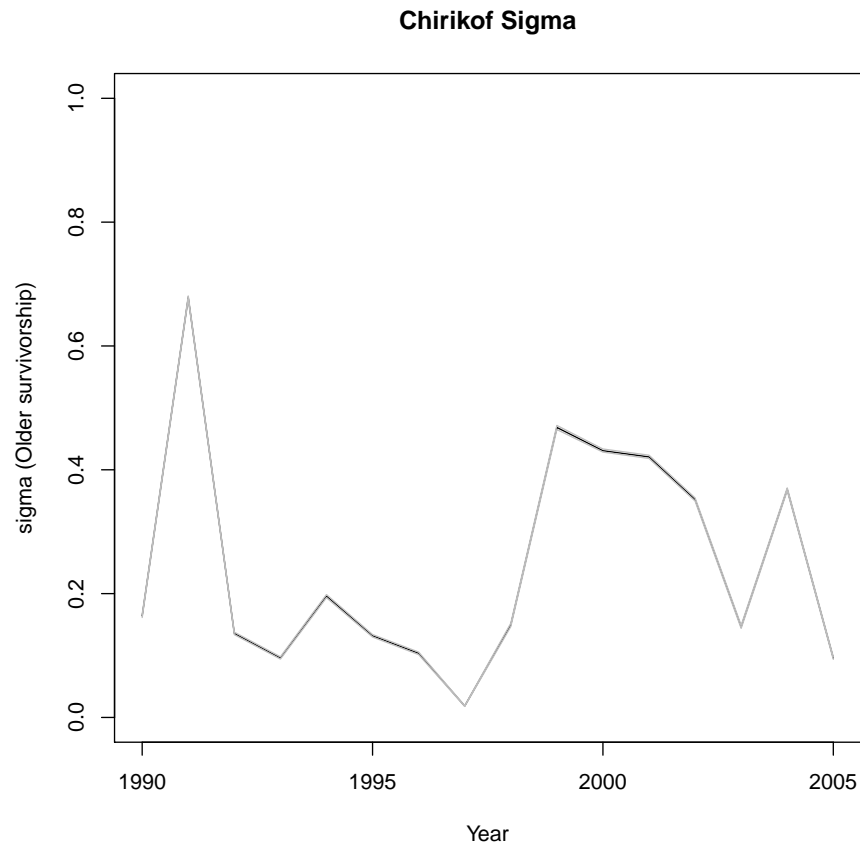


Figure 2.29: Reconstructed values of σ , the adult survivorship, at Chirikof. These values are lower than have been reported elsewhere, and are strongly influenced by both the PDO and CPUE near sites. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

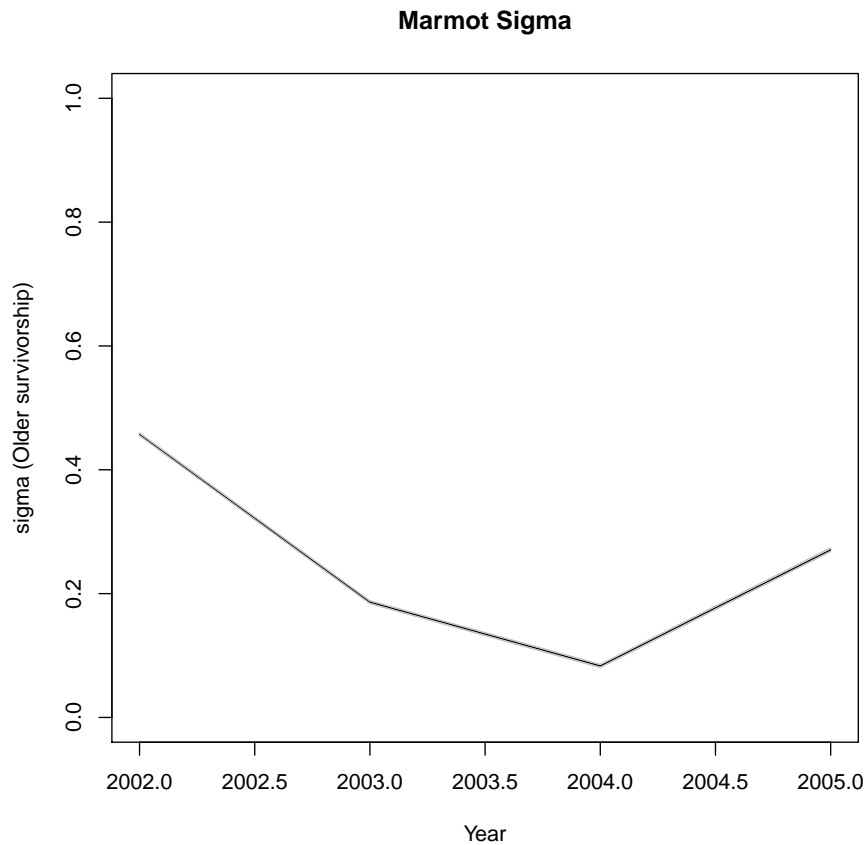


Figure 2.30: Reconstructed values of σ , the adult survivorship, at Marmot Island. These values are lower than have been reported elsewhere, and are strongly influenced by both the PDO and CPUE near sites. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

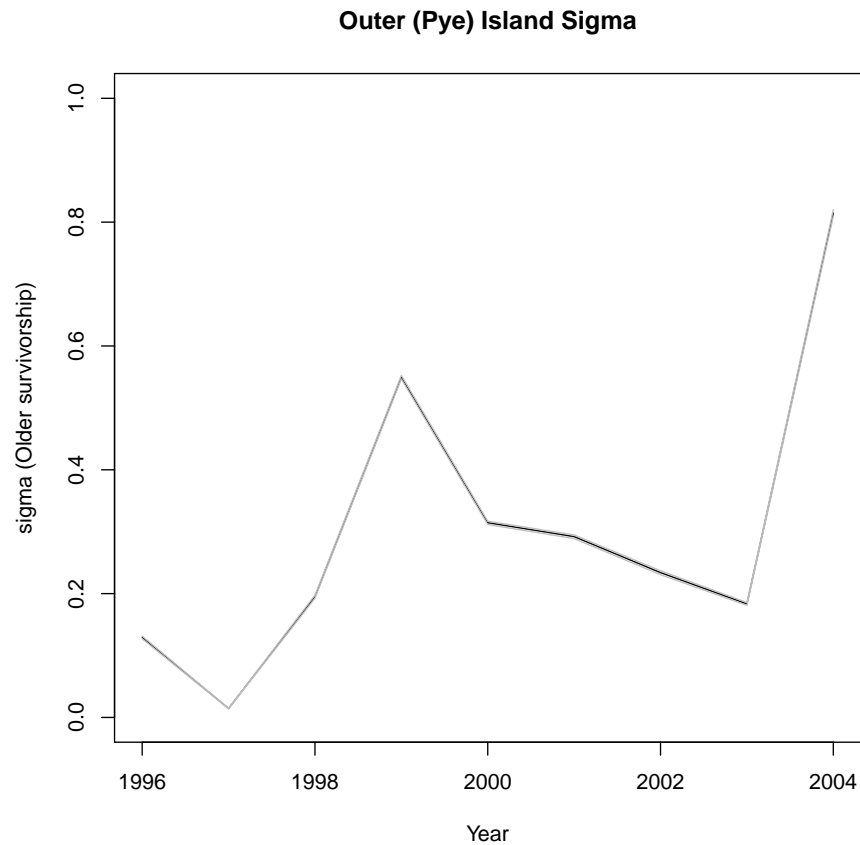


Figure 2.31: Reconstructed values of σ , the adult survivorship, at Outer (Pye) Island. These values are lower than have been reported elsewhere, and are strongly influenced by both the PDO and CPUE near sites. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

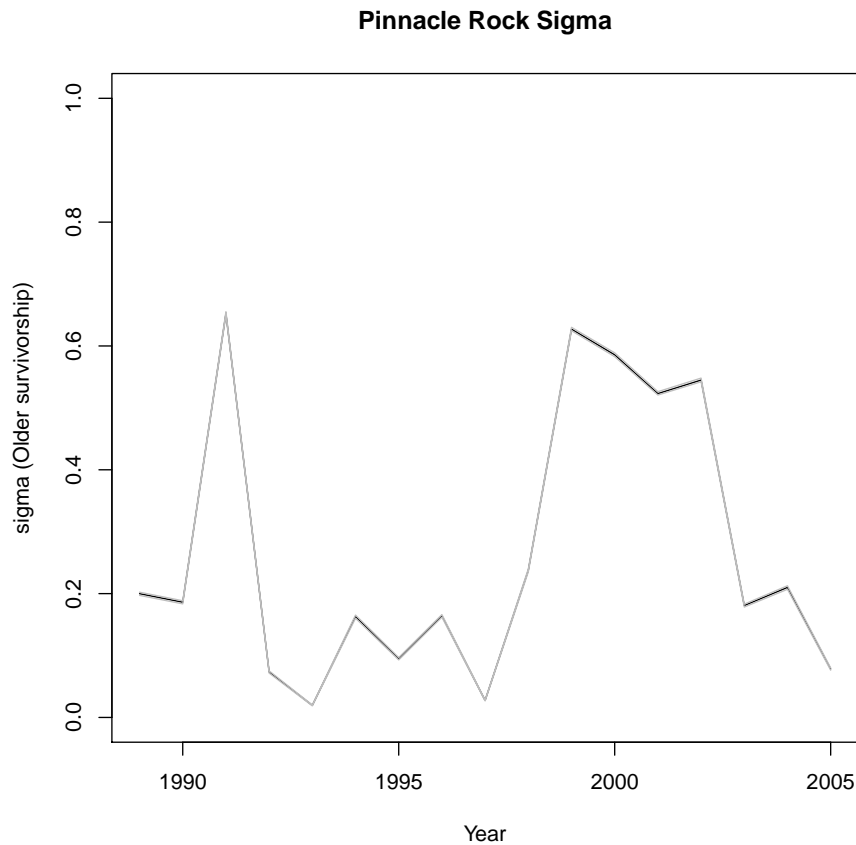


Figure 2.32: Reconstructed values of σ , the adult survivorship, at Pinnacle Rock. These values are lower than have been reported elsewhere, and are strongly influenced by both the PDO and CPUE near sites. A 95% credible interval (gray) is shown around the estimate (black), however the narrowness of the interval makes the two often visually indistinct.

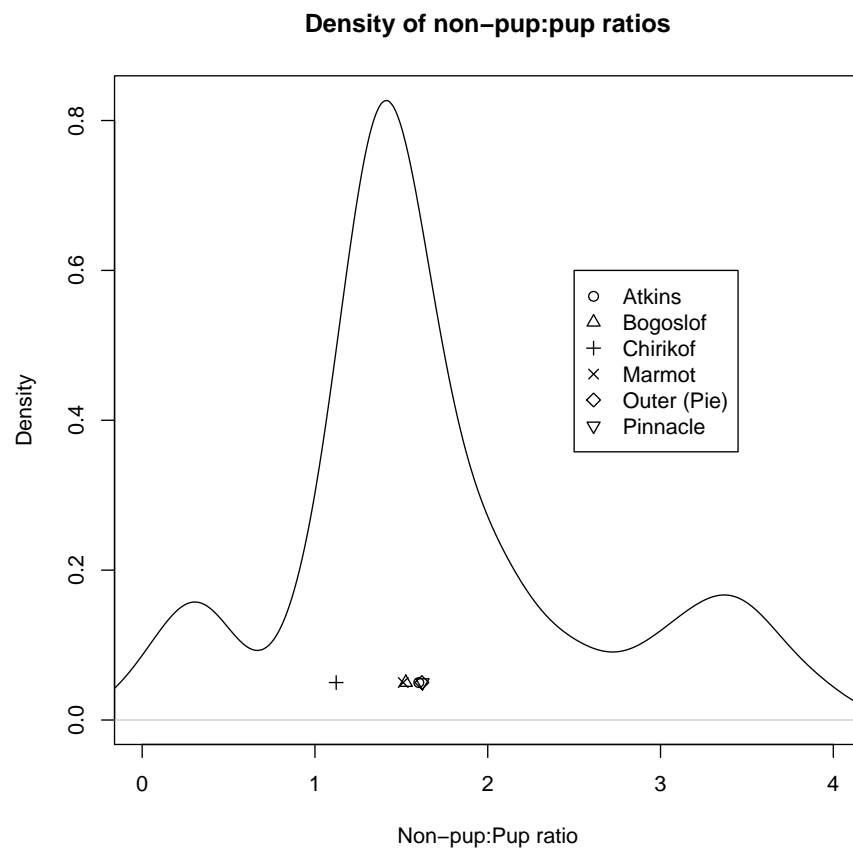


Figure 2.33: The distribution of the non-pup to pup ratios is over-plotted with vertical lines which are the model estimates for the non-pup to pup ratios at the six sites. These results show the estimated counts are in approximately the same ratio as the actual data.

Site	Mean	95% CI lower bound	95% CI upper bound
Atkins Pup	574.0221	572.1079	575.8600
Atkins Non-pup	520.3464	516.2313	524.4342
Bogoslof Pup	214.8064	212.0549	217.6478
Bogoslof Non-pup	520.3464	516.2313	524.4342
Chirikof Pup	461.3728	459.1651	463.7658
Chirikof Non-pup	681.2831	675.9429	686.7143
Marmot Pup	563.2526	558.8363	569.9650
Marmot Non-pup	401.7465	398.0452	405.0349
Outer (Pye) Island Pup	184.9132	182.8865	187.0649
Outer (Pye) Island Non-pup	180.2786	176.0075	183.7936
Pinnacle Rocks Pup	781.7321	777.0787	787.3075
Pinnacle Rocks Non-pup	1066.2848	1058.2215	1077.1425
C	1.237907	1.233503	1.241388

Table 2.5: The best Bayesian estimates of the auxiliary parameters, pup and adult counts at each of the six sites in the model and the at-sea inflation factor C .

The values of C , the inflation factor for under-counting, converged to approximately one (Table 2.5). This would seem to indicate there is no under-counting. While this seems unlikely, it is only slightly larger than one. A value of C very much larger than one would be unusual, since systematic over-counting seems unlikely.

2.3.6 Stationarity and convergence

The results from the model were thinned by taking only one in every 87,000 scans, after stationarity appeared to have been achieved, which was conservatively estimated to be the last 65% of the run. This also removed the burn-in period for the MCMC. The adequacy of the thinning was confirmed by examination of the autocorrelation plots (Figures 53 through 61). Although some autocorrelation did appear significant at various lags these may be spurious as they are not corrected for multiple comparisons.

Acceptance rates (Equation 2.8) in the model varied from about 15–30% over the

course of the run. The model was set to output an estimate (although not saved) of the acceptance rate for the previous 100 to 500 scans. These were tuned by repeatedly restarting the MCMC for a brief run after a burn-in period, to estimate the acceptance rate. The jump function is the primary factor in controlling the acceptance rate. If the jumps tend to be very large, they move away from the solution and tend to not be accepted. If the jumps are too small, they are frequently accepted however convergence is slow. Since the jump function is a multivariate normal (with a mean of the original parameters to be jumped from), the size of the jump is controlled by the correlation matrix. By multiplying the correlation matrix of the jump function by a tuning constant, the acceptance rate varied over this short test period. The tuning constant which gave an acceptance rate close to 0.23 was selected. Once selected, the tuning constant remained the same for the rest of the run. The burn in period was just over one million scans.

2.3.7 Correlation among parameters

The results of MCMC are not a collection of individual distributions but a joint distribution among all of the parameters. The parameters did show some correlations (Table 2.6). Beta parameters tend to be most strongly correlated with the other beta parameters which predict the same life history variables. There is also a strong negative correlation between parameters related to ϕ , the reproductive rate, and parameters related to σ , the non-pup survivorship (Table 2.6). The parameter $\beta_{\phi 0}$ shows a strong negative correlation with $\beta_{\sigma 0}$, which might account for the unusual values found for ϕ and σ .

	$\beta_{\phi 0}$	$\beta_{\phi 1}$	$\beta_{\phi 2}$	$\beta_{\rho 0}$	$\beta_{\rho 1}$	$\beta_{\rho 2}$	$\beta_{\sigma 0}$	$\beta_{\sigma 1}$	$\beta_{\sigma 2}$
$\beta_{\phi 0}$	1.000	0.263	-0.960	0.093	0.389	-0.211	-0.848	-0.255	-0.519
$\beta_{\phi 1}$	0.263	1.000	-0.232	-0.155	0.328	-0.295	-0.182	-0.269	-0.074
$\beta_{\phi 2}$	-0.960	-0.232	1.000	-0.080	-0.327	0.193	0.719	0.167	0.426
$\beta_{\rho 0}$	0.093	-0.155	-0.080	1.000	0.672	0.808	-0.274	-0.305	-0.343
$\beta_{\rho 1}$	0.389	0.328	-0.327	0.672	1.000	0.394	-0.515	-0.782	-0.706
$\beta_{\rho 2}$	-0.211	-0.295	0.193	0.808	0.394	1.000	0.198	-0.028	-0.196
$\beta_{\sigma 0}$	-0.848	-0.182	0.719	-0.274	-0.515	0.198	1.000	0.484	0.568
$\beta_{\sigma 1}$	-0.255	-0.269	0.167	-0.305	-0.782	-0.028	0.484	1.000	0.770
$\beta_{\sigma 2}$	-0.519	-0.074	0.426	-0.343	-0.706	-0.196	0.568	0.770	1.000

Table 2.6: The correlation among the β parameters' MCMC output, after thinning. There is strong correlation among the three parameters controlling specific life history parameters (i.e. ϕ , ρ , and σ). There is also strong correlation between some of the parameters controlling ϕ and those controlling σ , especially between $\beta_{\phi 0}$ and $\beta_{\sigma 0}$.

2.3.8 Observational error

One of the most evident results of the posterior predictive intervals is that many do not intersect the point they are predicting (Figures 2.2 through 2.12). The observational error function chosen, based on the same choice in Holmes et al. (2007), is normal. The variance of the observational error is fixed at 407, the value found in the anova to verify the validity of the comparability of count types (Table 2.1). Residuals of a sort can be calculated by taking the difference between the mean prediction for a pup or adult count and the actual observation at that same time and place. Under the model assumptions, these residuals should be approximately normally distributed, ideally with a variance as described. The residuals, however, show a large deviation from the normality assumption (Figure 2.34).

The quantile-quantile plot (Figure 2.34) shows a distribution of residuals which has heavier tails than a normal distribution. The excess kurtosis for these residuals is 2.16. The non-normality is confirmed by a Shapiro-Wilks test ($p = 0.0004045$). This

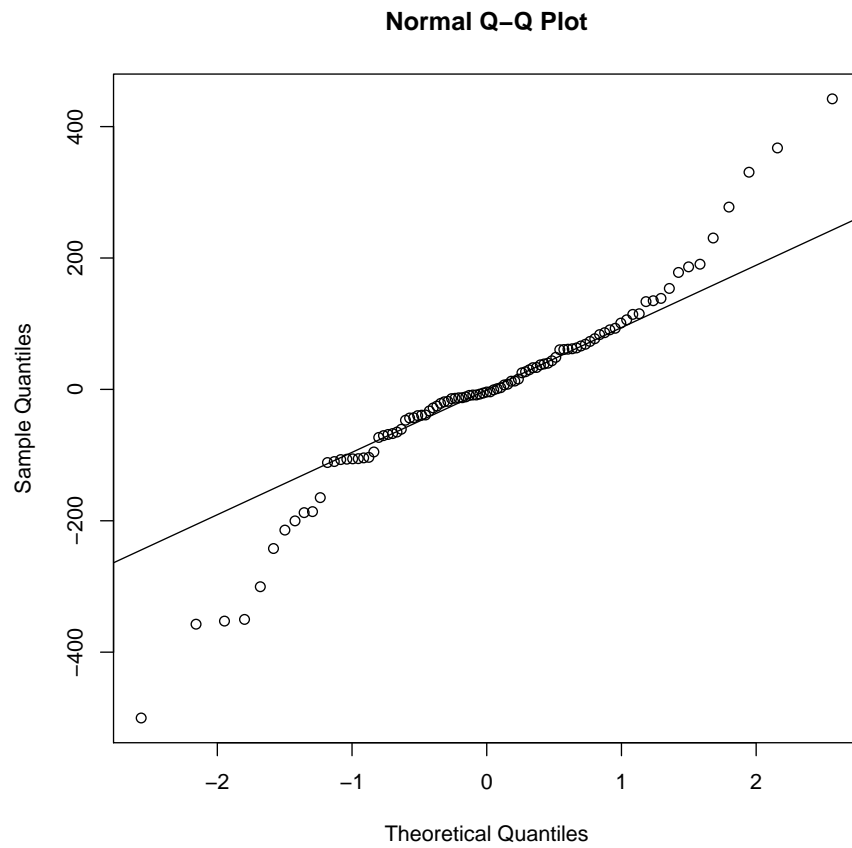


Figure 2.34: The quantile-quantile plot of the differences between the mean predicted count and actual count for both pups and adults at all sites. The plot shows a deviation from normality.

strongly indicates the error function in the model is simply incorrectly chosen.

Some of the sites also show a systematic bias in residuals, indicating the model over or underpredicts most or all of the observations at that site. Other than the first year pup and adult counts, there are no parameters that come from a specific site. Given that, there is no reason to expect that the residuals will have a mean of zero at any specific site. Moreover, since the predictions are made as a time series, unlike linear regression, there's no requirement that the mean residuals over all the sites will be zero. The mean of the residuals across all sites, including both pup and adult counts, is -3.649, while the variance is 20647.83. This indicates the model on average underpredicts the observations slightly.

2.4 Discussion

This work was motivated by the declines of the Steller sea lion, their subsequent failure to recover, and possible causes for the decline. Two hypothesized causes were examined. The results of this work indicate that pup survival was subject to periodic associated with climatic factors in the years 1991 and 1999. The results also indicate high variability in both reproductive rate and non-pup survivorship between sites and between years within the same site, caused by changing fishing and climate factors. There was some degree of influence of both PDO and fishing on all of the vital rate parameters. The strongest of these results was confirmed by a separate analysis of the data.

This work was influenced by several previous attempts to characterize the changes in life history parameters accompanying the decline of Steller sea lions. Holmes et al. (2007) looked at counts by age and sex at five rookeries in the western population. Their work involved finding maximum likelihood estimates of life history rate param-

eters over four time periods at five Steller sea lion rookeries in the western population. The rates were held constant during each of the four time periods in the period from 1976 to 2004. They found a declining birth rate and an adult survivorship which steeply declined in the initial crash of the Steller sea lion population, but which has been steadily increasing since. This built on earlier work, Holmes and York (2003), which found initial declines to be due to low juvenile survivorship, while later declines were due to low fecundity.

Pendleton et al. (2006) used mark-resight data at Marmot Island in the western population and Forrester Island in the eastern population to find survivorship-at-age during periods of decline and increase. Hot-branding techniques were used to individually mark a subset of animals. Although branding yields higher resolution results than Holmes et al. (2007), annual branding did not take place at the rookeries. Consequently the survivorships can only be estimated at particular times. Survivorship-at-age estimates are therefore not synchronous, since they must be made as the branded animals age. Their work shows that the declining population on Marmot Island had a lower juvenile survivorship than in the increasing population or the prior estimate from the 1970s when the Marmot Island population was assumed to be stable. Adult survivorship was also lower at Marmot Island than at Forrester, however no change was observed in the Marmot Island population adult female survivorship since the 1970s. The results seem to therefore appear to implicate juvenile survivorship as the cause of the failure to recover in the 1990s.

In contrast to Holmes et al. (2007) and Pendleton et al. (2006), the present project estimates life history parameters at a higher temporal and spatial resolution than either of these preceding projects. This project estimates life history parameters at every year and site combination. The results show fluctuation in the life history

parameters, varying from year to year. Fluctuations of this sort are not possible to be found in any other modeling exercise done to-date, due to their estimation of vital rate parameters on a multiple year intervals. Thus they lack resolution to detect the variability and correlations found in this project. The vital rate parameter estimates show impacts of both the PDO and fishing.

The comparison of the life history parameters between the present project and past work is complicated by the different age structures used in Holmes et al. (2007) and Pendleton et al. (2006). The model in this paper does not include a juvenile survivorship explicitly, however the changes in the pup survivorship found are consistent with the changes in juvenile survivorship found in the other models. The years covered in this project are later than the juvenile survivorship crash found in Holmes et al. (2007), and there were no years in the 1980s with as strongly negative June PDO as was responsible for the two crashes in the 1990s. There was a strong negative June PDO year in 1975, which was a year prior to any data used in their work. This suggests it is possible that different factors were responsible for the juvenile crash they discovered, or the juvenile crash in the early 1980s was primarily of non-pup individuals.

A further comparison of Pendleton et al. (2006) and the present project shows consistent results. Pendleton et al. (2006) studied Steller sea lion populations in years overlapping with the present project, finding a low juvenile survivorship in the late 1980s and early 1990s on Marmot Island. This time interval covers the low pup survivorship in 1991 found in this project. However Marmot Island pups were only branded in 1987 and 1988. Thus any indication of low pup survivorship in 1991 from the mark-resight data would have been in individuals turning 3 or 4 years old during the summer observation. It is possible that the pup crashes observed in the present

project (Figures 2.20-2.25), and directly observed in the data, did extend beyond pup survivorship to include juvenile age classes which are not modeled. The data used in this project are of insufficient resolution to verify that hypothesis, however. It is also possible that the re-sighting missed the 1991 pup crash entirely, if the pup crash detected in this project only applied to individuals entering their second year. The low juvenile survivorship detected by Pendleton et al. (2006) could be entirely found within the non-pup survivorship found in this model, and simply be lower than expected.

The correlation of pup crashes with the June PDO could potentially be misleading. While it is certain that the crashes in pup survivorship did occur, and mathematically they are associated with the low June PDO. The interpretation of these results is limited by the fact that there are only two years with low pup survivorship. It is possible that the association with the June PDO is purely coincidental, a result which is improbable but certainly not entirely ruled out by the results of this project. Had each each month's PDO been considered, and June selected for its good fit, there would be a problem of multiple comparisons. However since only the June PDO was used as a predictor in this model, and it was chosen for biological reasons, the problem of multiple comparisons which would otherwise make a coincidental association more probable is eliminated.

Although cause is often inaccessible from observational data, the correlation found here between climate as reflected in the June PDO and pup survivorship might be causative. There are few possible common causes for both the June PDO and pup survivorship crashes found. Ergo correlation, if it is not spurious as addressed above, is reasonably inferred to be causative.

2.4.1 Problems

Three substantial problem areas are highlighted by the model results. The reproductive rate is considerably higher than is biologically realistic, while simultaneously the non-pup survivorship is much lower. The posterior distributions had much smaller variances than should be found in such a dataset. Finally, the assumption of normality in observational errors is incorrect.

The non-pup survivorship found in this model was lower than anticipated, or is even biologically realistic. Although highly variable, non-pup survivorship rarely reaches values which would be consistent with values found in (Wolf and Mangel, 2004). Although Pendleton et al. (2006) did note low adult survivorship in declining populations, and Holmes et al. (2007) did find values in the time period prior to 2004 to be depressed below those of the 1970s, the values represented in those projects are well above those found in this one. There are two factors working together to lead to this result. The structure of the model used here does not differentiate between reproductive adults and non-reproductive sub-adults. This was a necessary simplification given the available data, however it would imply that individuals became reproductive at 2 years of age, rather than between 3 to 8 years, as is observed biologically (Pitcher and Calkins, 1981). Since individuals would no longer have to survive as long to reproduce in the model as they do in reality, the model can have a much lower non-pup survivorship while maintaining a viable population. A second factor is the strong negative correlation of parameters controlling adult survivorship with those controlling reproductive rate. This could indicate a compensatory effect between these parameters.

The reproductive rate appears to be influenced by the PDO and fishing. However the baseline reproductive rate, $\beta_{\phi 0}$ has a strong negative correlation with the baseline

non-pup survivorship, $\beta_{\sigma 0}$, one of the strongest negative correlation found in the results (Table 2.6). The reproductive rate is higher in many years at the sites than it could possibly be if there were a even sex ratio. It is possible that there was an under-counting of males, particularly juvenile males on the rookery sites, and the reproductive rate was in fact very high. This would contradict the findings of Holmes et al. (2007) and ignore the correlation with other non-pup survivorship. It is more probable that the high reproduction rate estimated in this effort resulted from the structure of this model.

This strong negative correlation between ϕ parameters and σ parameters may allow for a compensatory effect between reproduction and non-pup survival in the model. The periodic pup survivorship crashes and high variability in all of the vital rates have implications for the Steller sea lion recovery. Although the first year survivorship crashes can be observed in the original data, the unrealistic values of the adult survivorship and reproductive rate raise questions about the fits of those model parameters.

If correlation between parameters is indeed the cause of the results, this should have been evident in the posterior. Although the correlation is found, those parameters do not attain biologically realistic values in the posterior. The marginal posterior distributions of the β parameters consistently have very narrow variances, far more narrow than the prior variances. There are a number of possible causes for this, including programming error, non-global optima found by the MCMC, or some unusual interplay of model misspecification and the data. Although all of these possibilities have been investigated in some ways, no specific cause of the narrow posteriors has been identified.

The posterior predictive intervals (Figures 2.2 through 2.12), in many cases, do

not intersect the observations. The cause of this is likely to be in the mistaken assumption of normal observational error described above (Section 2.3.8). Since the observational errors are heavy-tailed (Figure 2.34), the normal error structure is not likely to account for all the observations very well no matter the variance.

Visual examination of the fit indicate predictions match the general trends of the data at all six sites. The assumption of normality does tend to over-emphasize the extreme data at the expense of data which are nearer to the estimates. Since the trend of the predictions tends to match the observations, the fit of the parameters is probably still a reasonable approximation. The best approach would be to determine a better-fitting error function and re-run the model using it. Although the fit might be improved by the use of a more accurate error function, there is nothing to suggest the the parameter fits made using the normal model are likely to change values enough to alter the interpretation of the model, but it does limit the confidence in the results.

The use of the first principle component of CPUE across species, specific to each site, has both benefits and drawbacks. It is clear from the results that fishing does predict some changes in the life history parameters, particularly in the reproductive rate and non-pup survivorship. The use of a principle component of fishing CPUE, however, while reducing the number of parameters estimated, also reduces the information gained from the results. Since the linear combination of CPUEs which was used at each of the sites to form the principle component was different at each site, there is little consistency as to what the fishing index represents at each site. While this has some advantage, since diet also varies by site, and thus a uniform predictor representing the “best diet” is not realistic, it has the disadvantage of not giving clear interpretations or predictions in cases of future fishing changes.

Clear results stemming from this model include the periodic crash in the pup sur-

vivorship rate, correlated with a strong negative PDO, high variability of life history parameters between years and sites, and the correlation of both the June PDO and fishing with all three life history parameters. These results add to those developed by others, and indicate directions for further research.

2.4.2 Other model runs

In addition to the model run reported here, two other models were run. A much larger run, consisting of 43 sites rather than 6, was attempted. It had a similar structure to the six site model, although it included both rookeries and haulouts. The second attempt was a run of the six site model, similar to the one discussed above. Both of these models were hampered by excessively narrow priors for the initial count parameters and unrealistically tight observational error. Errors importing data also excluded some years of data which were usable. These errors were both corrected in the model run reported above.

Despite running for several weeks, the 43 site did not converge. Although most of the parameters appeared stationary, and thus probably would have converged with additional scans, the run was discontinued after noting the problems with the priors and observational errors. Visual inspection of the β parameters indicated they trended towards values similar to those reported here. Although very little weight should be given to values derived from non-convergent MCMC chains, this is suggestive of a fairly robust result.

The same narrow priors and observational error terms were used in the six site model. Given the smaller number of parameters, this model did converge. The results of the run, despite the missing data and narrow priors, showed qualitatively similar results to the model results reported above. Only one of the β parameters, $\beta_{\rho 1}$ changed

sign. This result is consistent with a fairly robust model.

2.4.3 Future work

The shortcomings of this modeling effort indicate some ways in which this model could be improved in future work. The primary issue to determine is the source of the unrealistic parameters and the very low variance posteriors. These errors limit interpretation considerably. Additional work on improving the error structure is also warranted, possibly using a log-normal error or other non-normal forms for observational error. The model structure could also be modified to include the life history parameters as random effects at each site, rather than fixed across all sites. Extending the data used to fit the model is important to broadening the result. These data could come from a broader area of the western population, as was already considered, or include the eastern population as well. Each of these modifications could potentially improve the information derived from the data.

2.5 Conclusion

The decline of Steller sea lions and their failure to recover has been well studied. This project adds to this literature by considering the possibility that multiple factors may have been acting simultaneously to prevent population recovery. Although this project only addressed the data post 1989, the results demonstrate correlates of changes in the reproductive rate and survivorship with both the June PDO and the CPUE near Steller sea lion sites. This is consistent with the hypothesis that multiple factors are keeping the population depressed.

The reproductive rate is unusually high, while the non-pup survivorship is lower than expected. Both of these factors may be influenced by both the PDO and fishing.

The pup-to-adult survivorship showed a strong response to the June PDO (Table 2.4). The pup-to-adult survivorship shows the pattern of region-wide collapse in years with strong negative June PDO, while most years the survivorship is reasonably high. The posterior distributions of the β parameters are a cause for concern, since they show extremely low variance. The assumption of normal observational error also appears to have been violated.

Implications of these results for conservation and future work include a further investigation of the cause or causes of the occasional pup-survivorship declines, as well as research focused on identifying the specific causal pathways responsible for the PDO's impact on Steller sea lions. This project has also shown the effectiveness and drawbacks of this approach in determining fine temporal and spatial scale estimates of population parameters.

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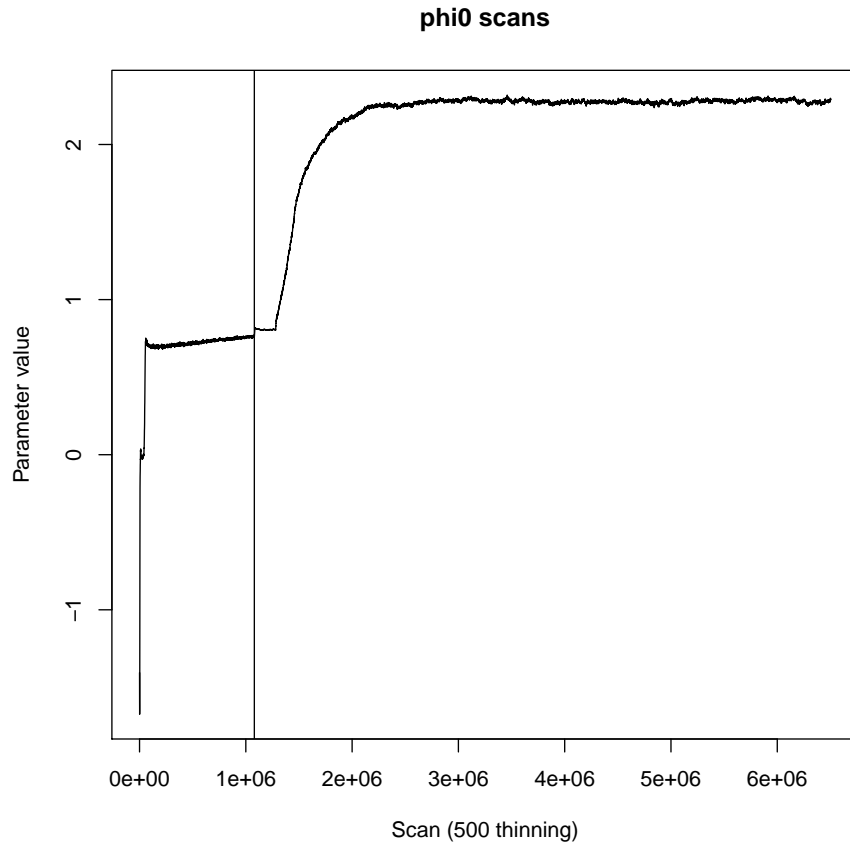


Figure 35: Scans of β_{ϕ_0} , controlling the value of ϕ , the reproductive rate, absent the effects of fishing or the PDO. A vertical line indicates the end of the burn-in phase.

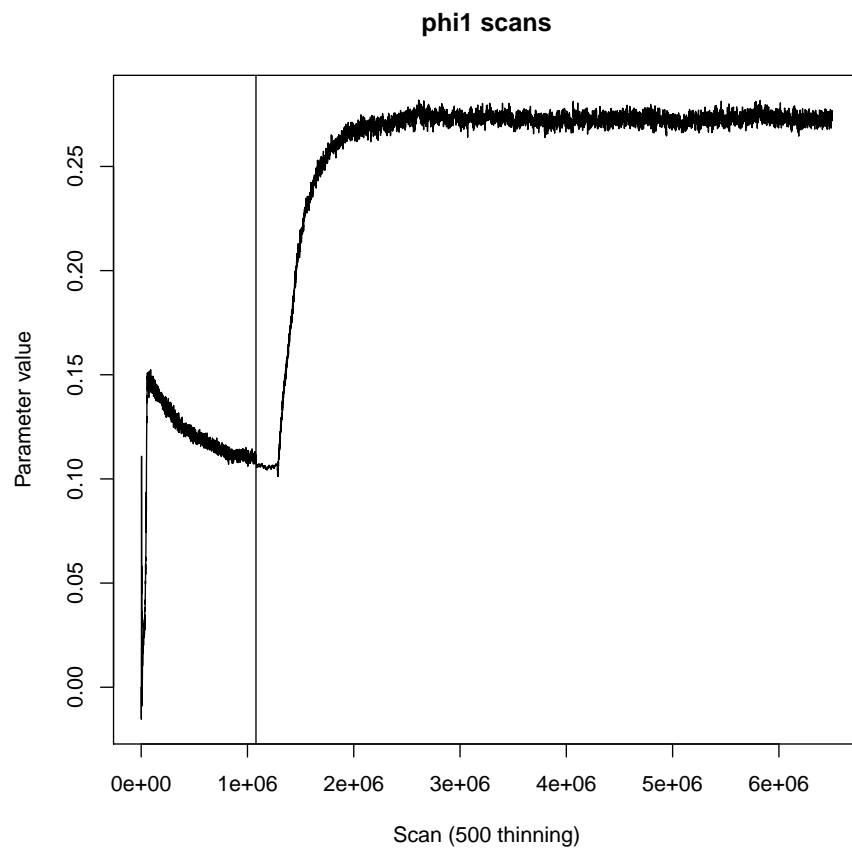


Figure 36: Scans of $\beta_{\phi 1}$, controlling the impact of fishing on the Steller sea lion reproductive rate. A vertical line indicates the end of the burn-in phase.

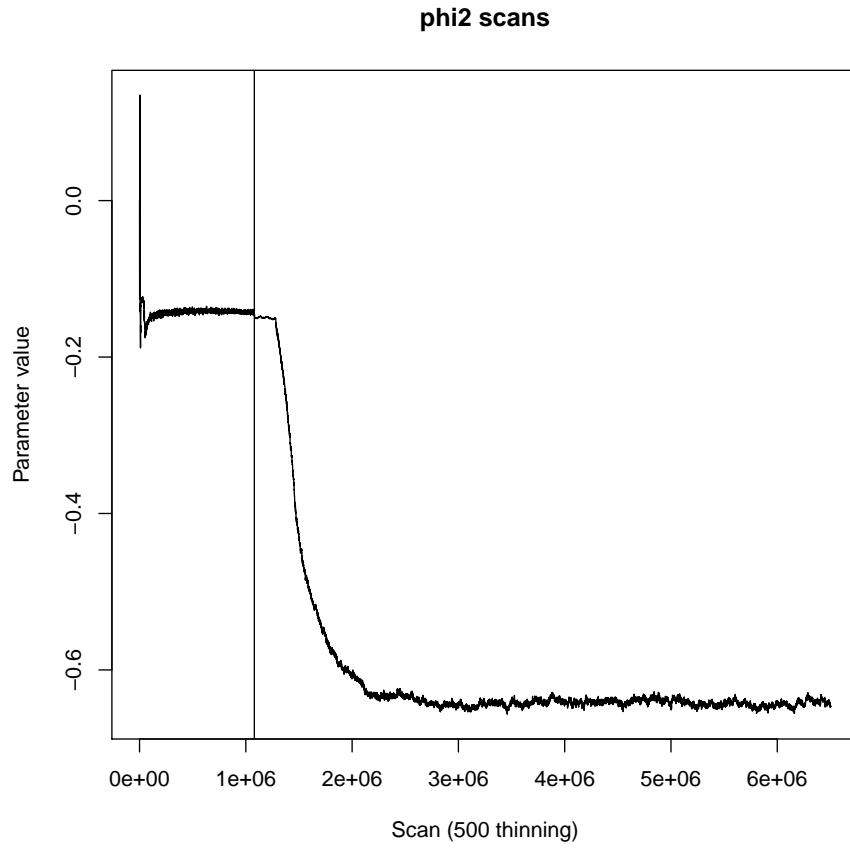


Figure 37: Scans of $\beta_{\phi 2}$, controlling the impact of the PDO on the Steller sea lion reproductive rate. A vertical line indicates the end of the burn-in phase.

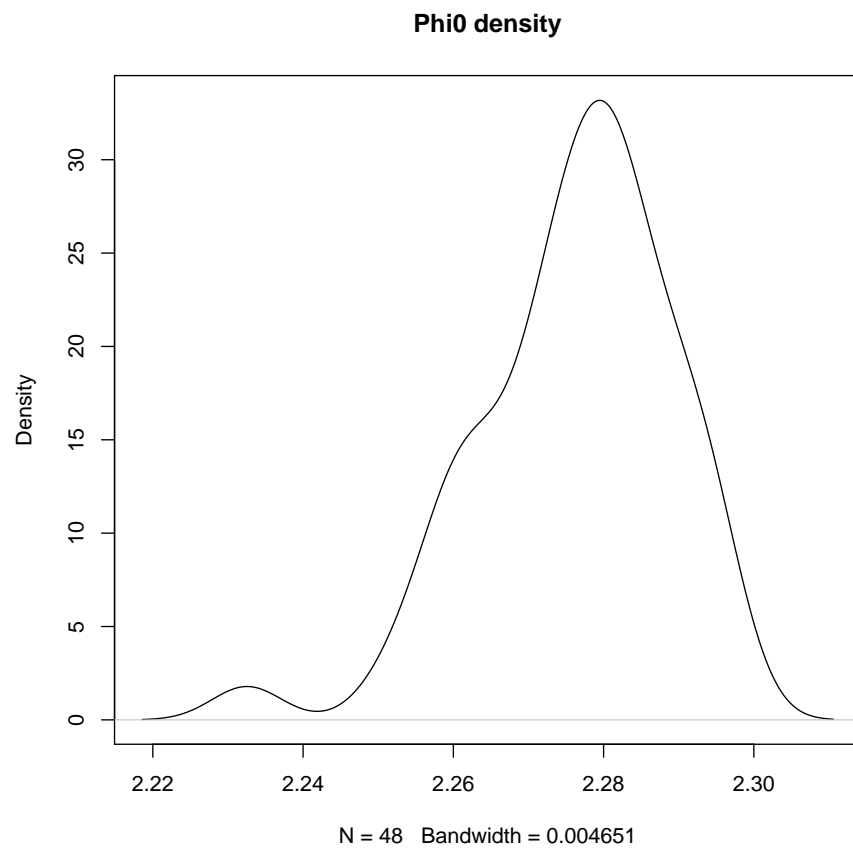


Figure 38: Posterior density of β_{ϕ_0} , showing the mean and low variance of the estimate.

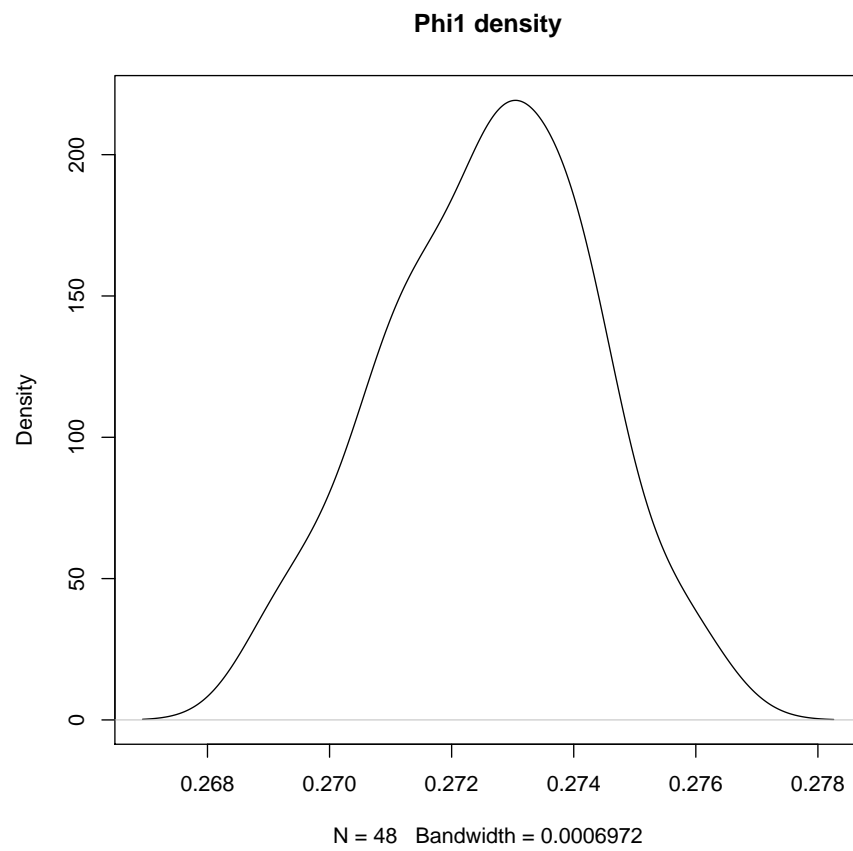


Figure 39: Posterior density of $\beta_{\phi 1}$, showing the mean and low variance of the estimate.

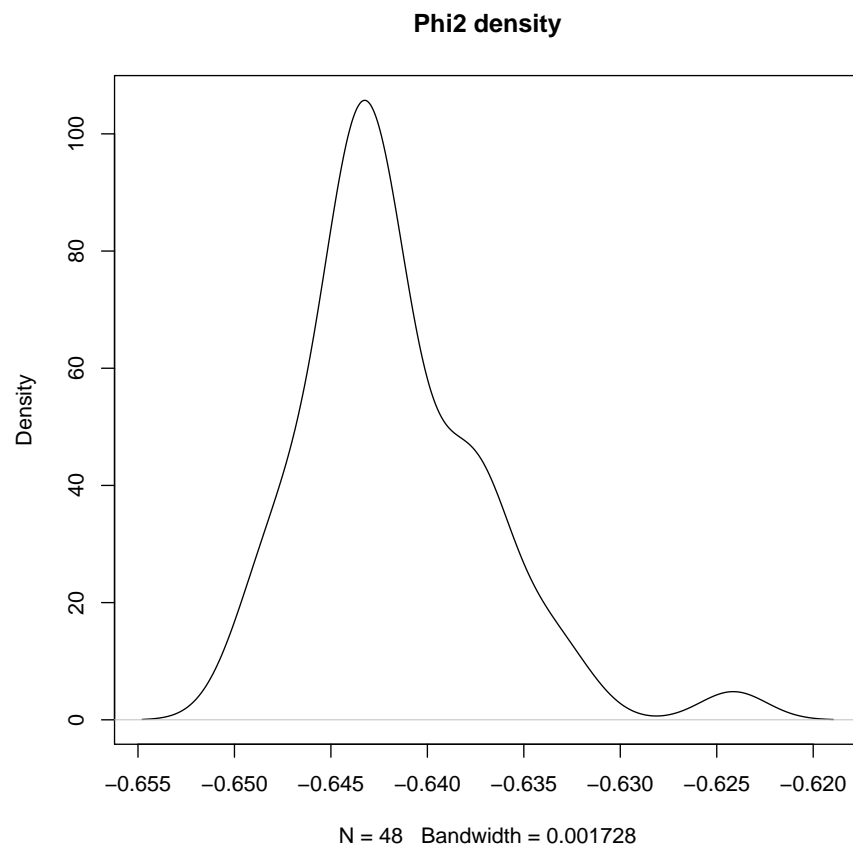


Figure 40: Posterior density of $\beta_{\phi 2}$, showing the mean and low variance of the estimate.

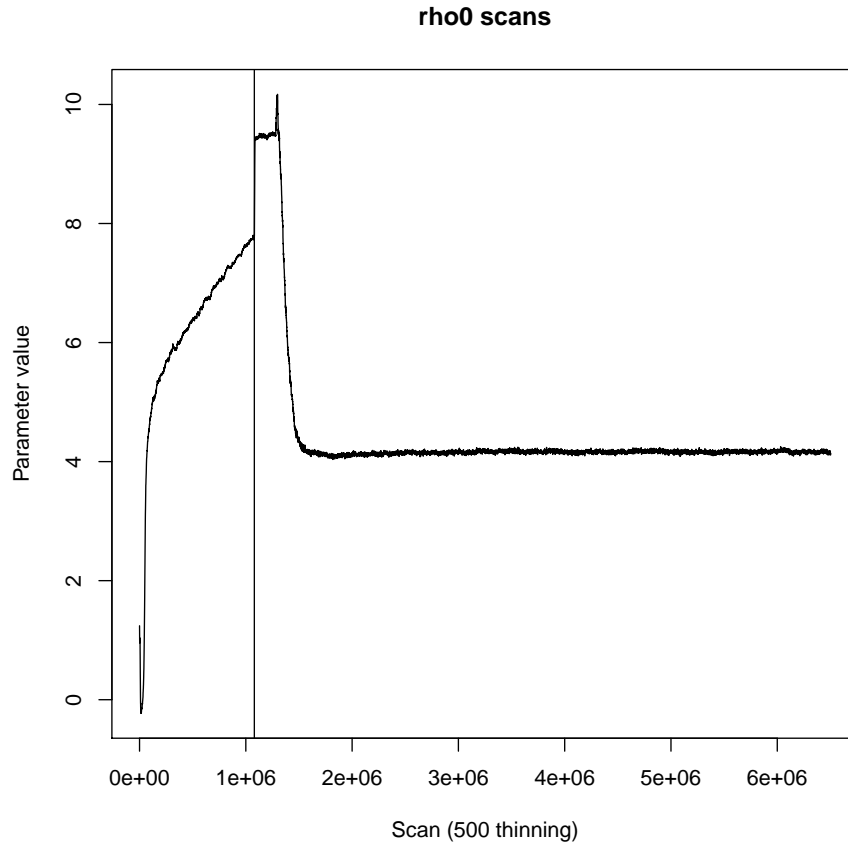


Figure 41: Scans of $\beta_{\rho 0}$, controlling the baseline of pup survivorship rate absent the PDO and fishing effects. The sudden change in behavior is due to a change in jump functions after an initial burn-in phase. For all parameters, only scans done after the burn-in phase are used for analysis. A vertical line indicates the end of the burn-in phase.

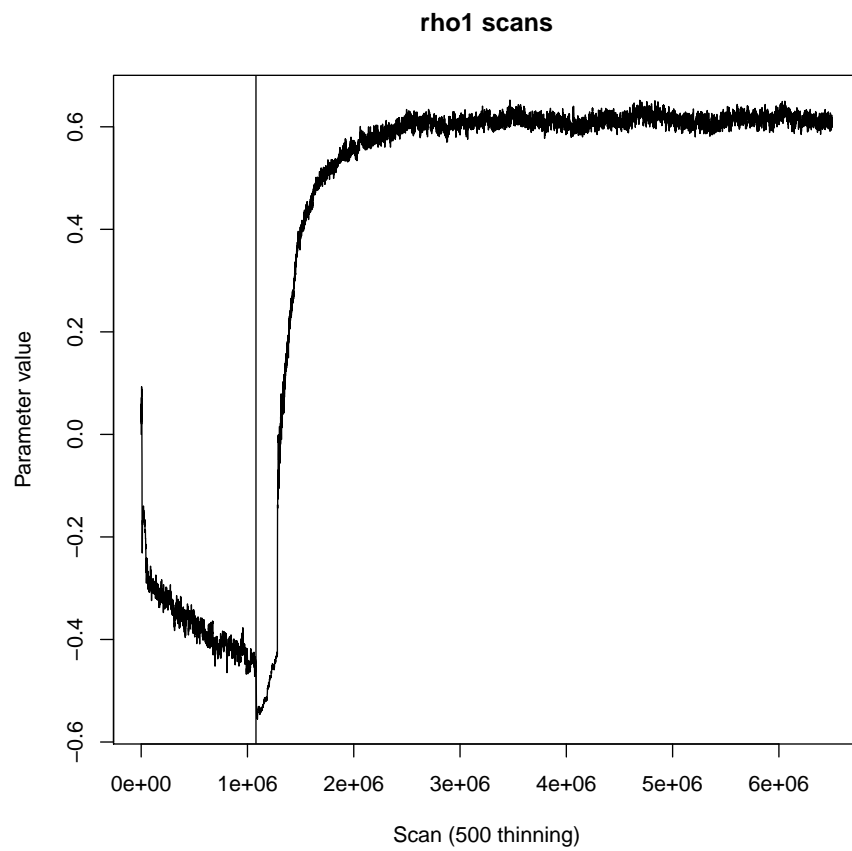


Figure 42: Scans of β_{ρ_1} , controlling the influence of the fishing on the pup survivorship. A vertical line indicates the end of the burn-in phase.

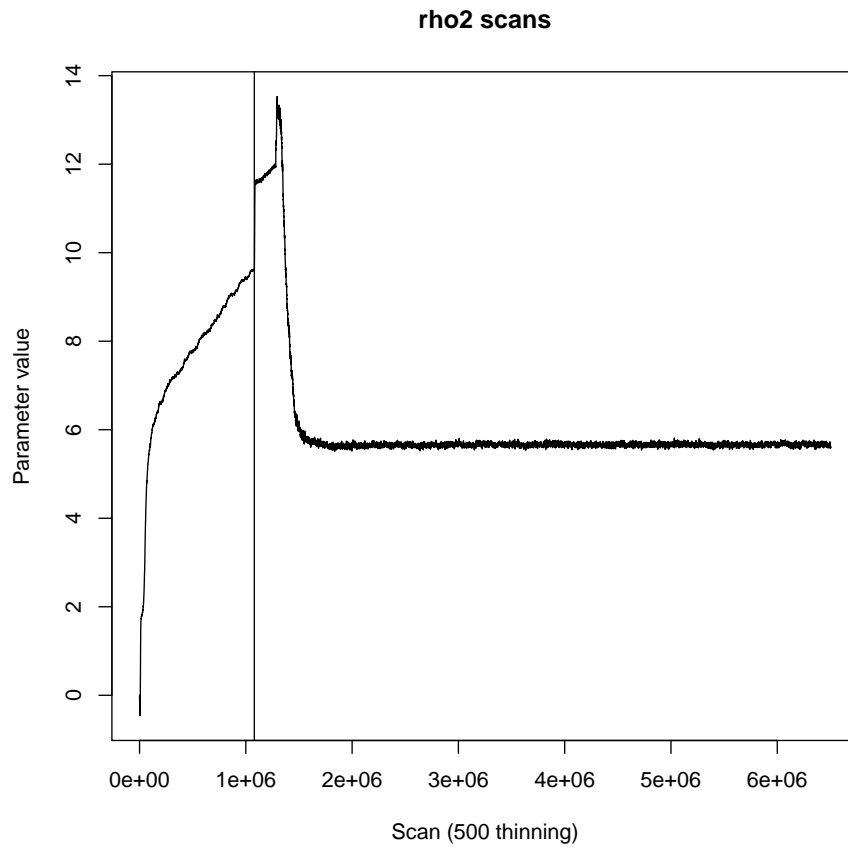


Figure 43: Scans of $\beta_{\rho 2}$, controlling the influence of the PDO on the pup survivorship. The sudden change in behavior is due to a change in jump functions after an initial burn-in phase. For all parameters, only scans done after the burn-in phase are used for analysis. A vertical line indicates the end of the burn-in phase.

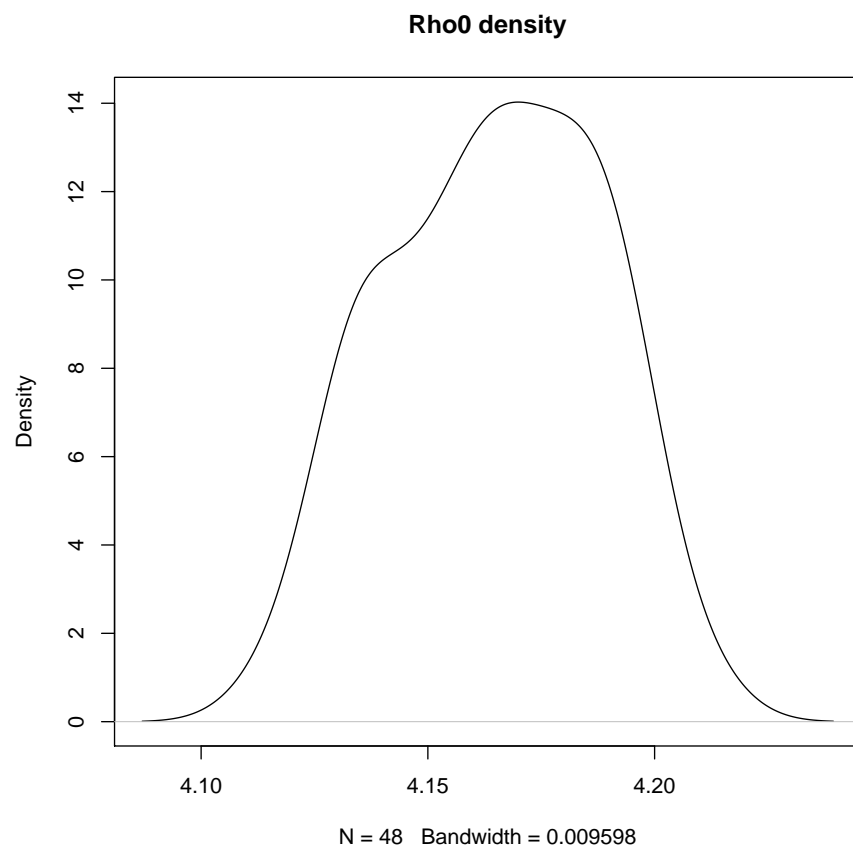


Figure 44: Posterior distribution of $\beta_{\rho 0}$, controlling which are the baseline value of ρ , absent the effects of the PDO or fishing

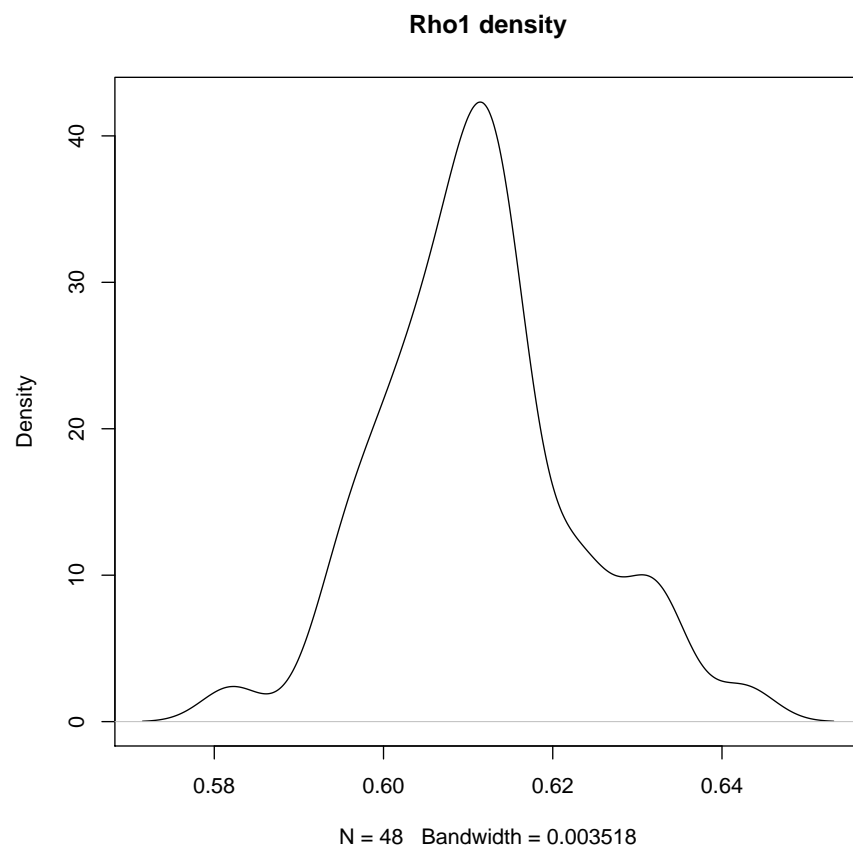


Figure 45: Posterior distribution of β_{ρ_1} , controlling the influence of fishing on the pup survivorship. Note that it is very near zero.

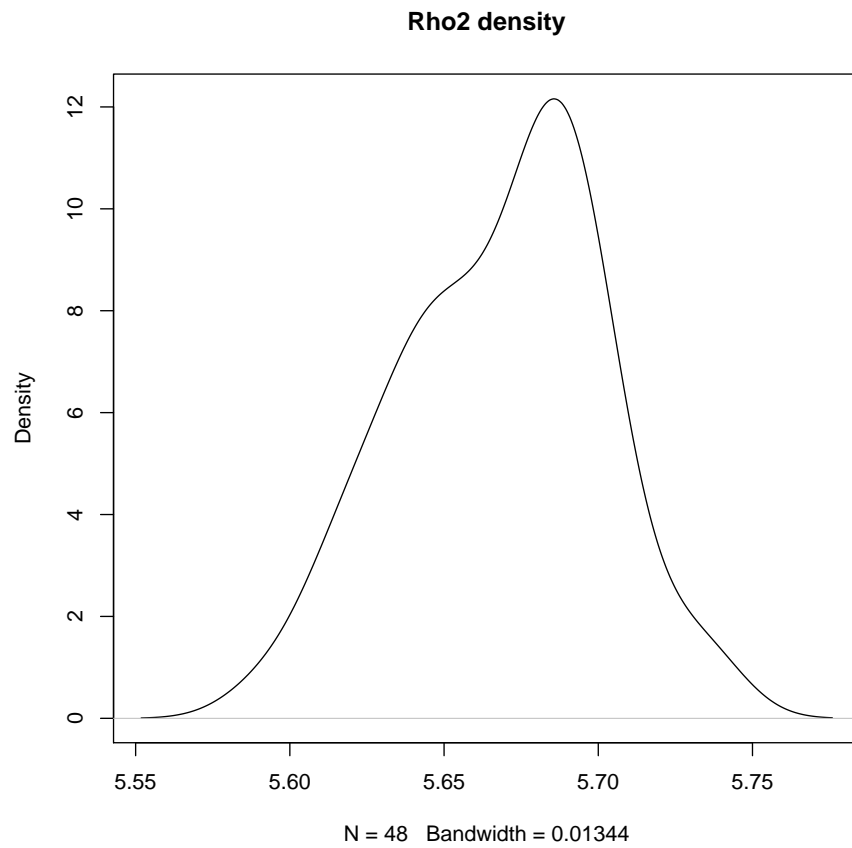


Figure 46: Posterior distribution of $\beta_{\rho 2}$, which controls the impact of the June PDO on pup survivorship. The very large value of found here indicates a crash of pup survivorship in years with a strong negative June PDO.

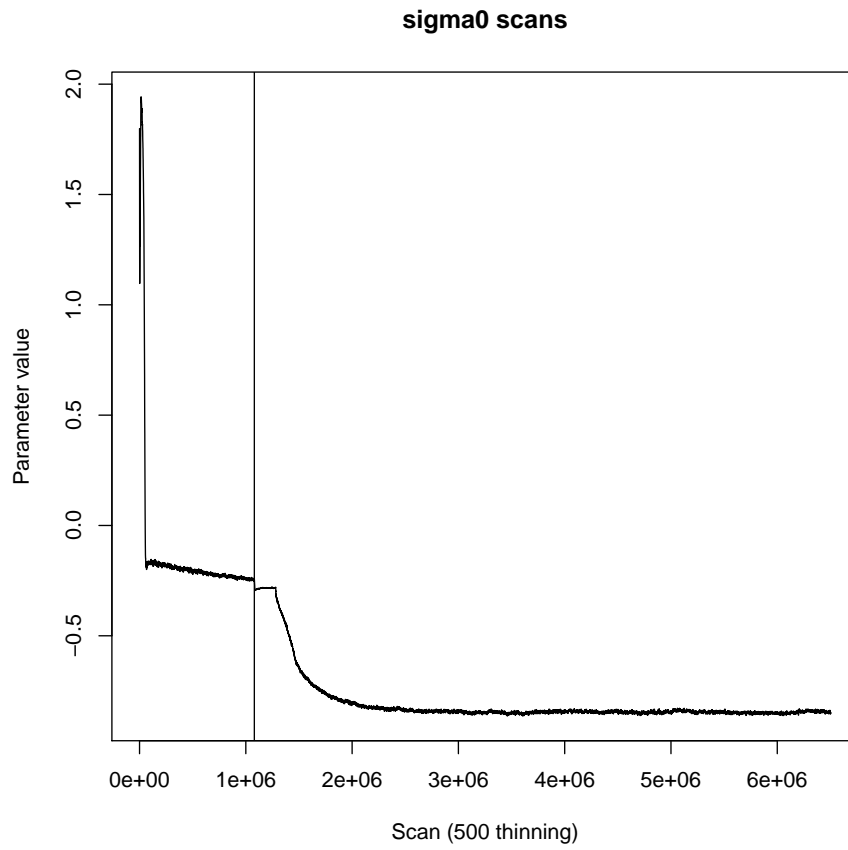


Figure 47: Scans of $\beta_{\sigma 0}$, controlling the baseline value of σ , the non-pup survivorship, absent the effects of the PDO or fishing. A vertical line indicates the end of the burn-in phase.

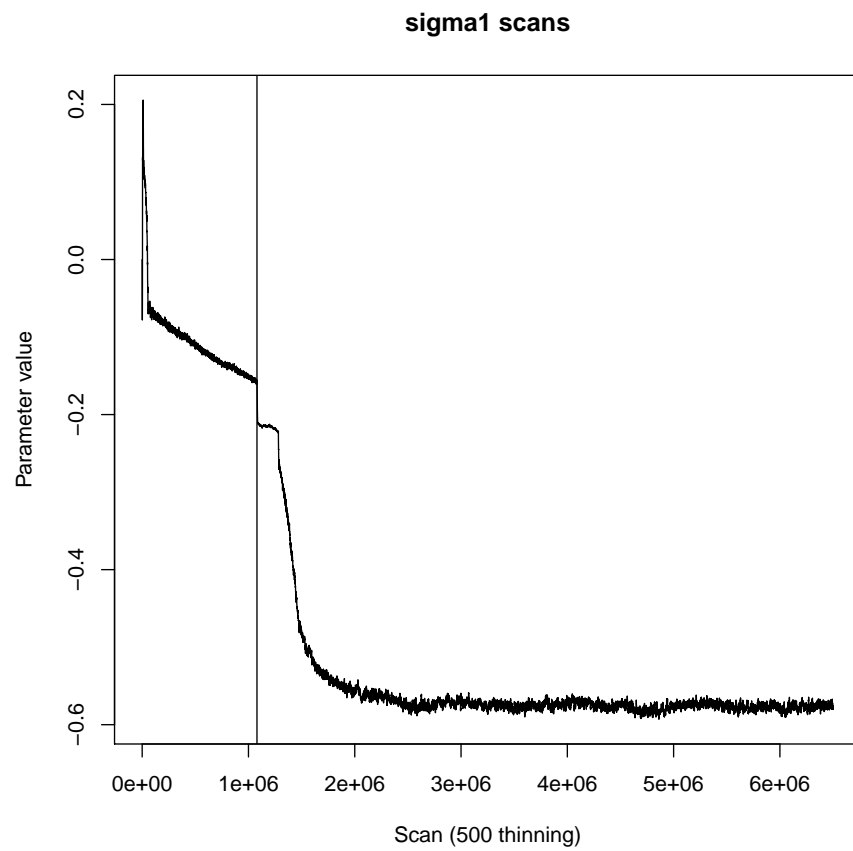


Figure 48: Scans of $\beta_{\sigma 1}$, controlling the impact of fishing on the Steller sea lion non-pup survival, σ . A vertical line indicates the end of the burn-in phase.

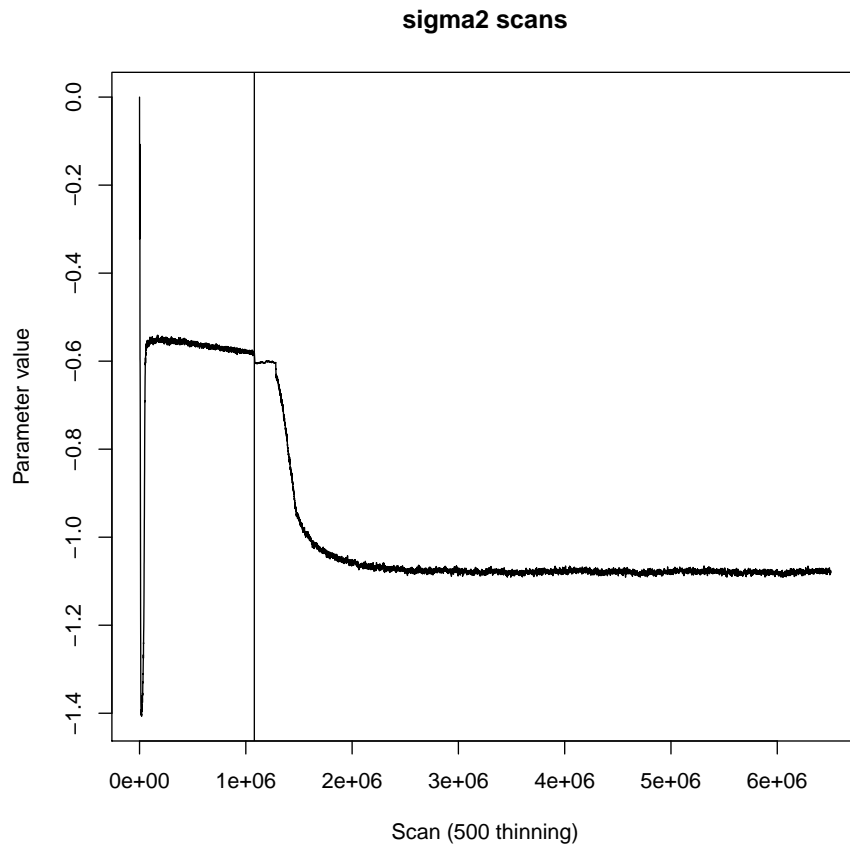


Figure 49: Scans of $\beta_{\sigma 2}$, controlling the impact of the PDO on the Steller sea lion non-pup survival, σ . A vertical line indicates the end of the burn-in phase.

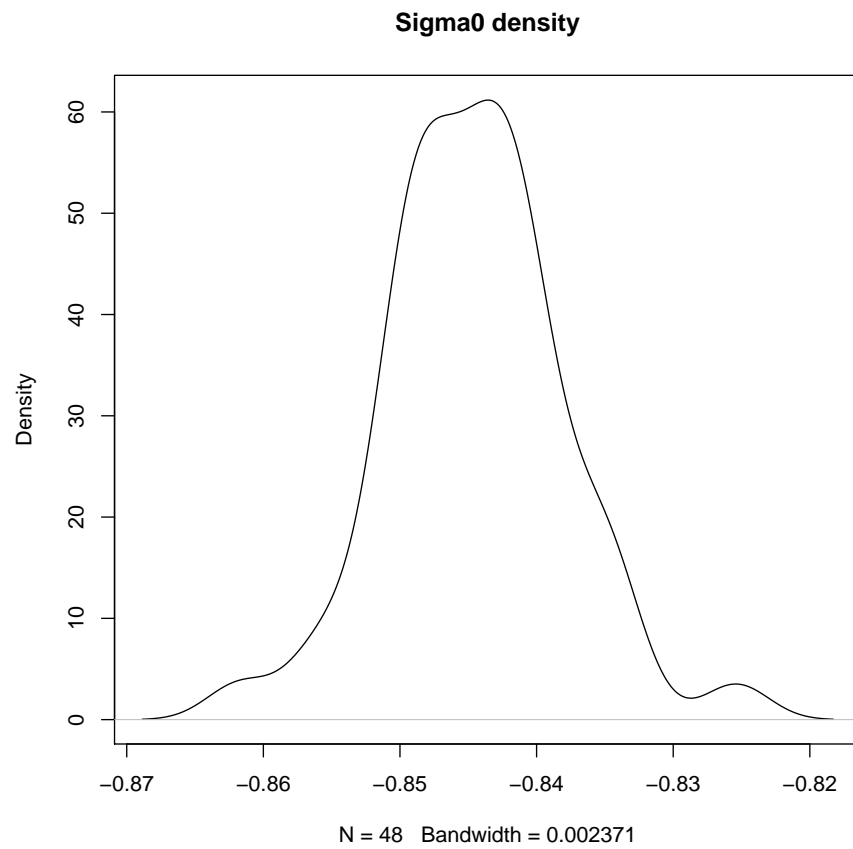


Figure 50: The posterior density of $\beta_{\sigma 0}$ parameter, which controls the baseline value of σ , absent the effects of fishing or the PDO.

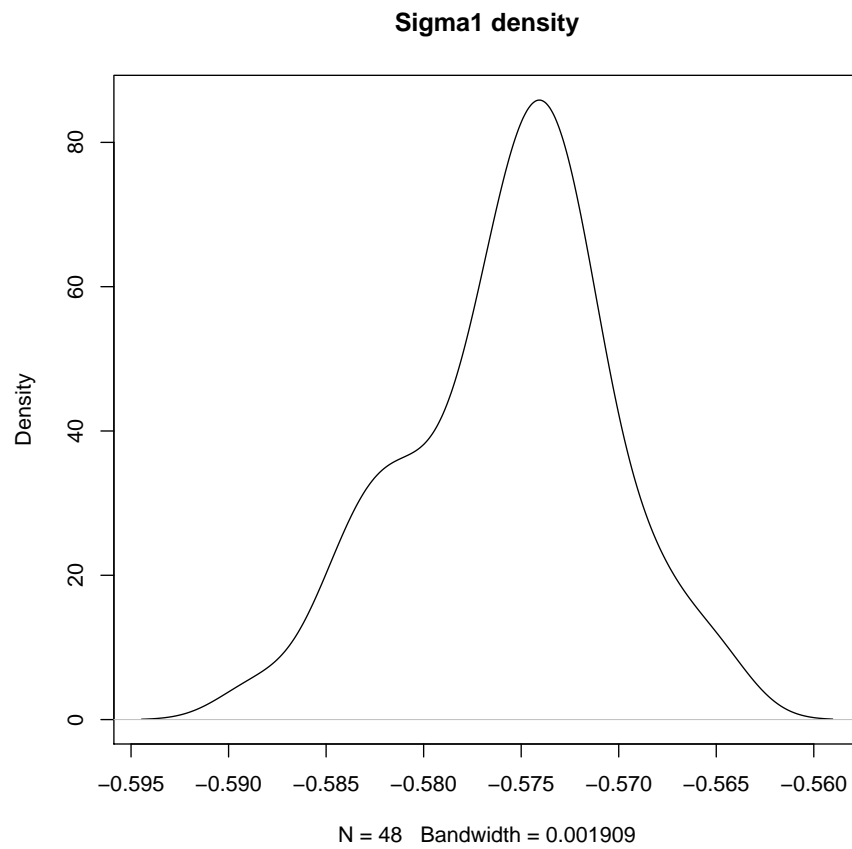


Figure 51: The posterior density of $\beta_{\sigma 1}$ parameter, which controls the impact of fishing on the value of σ , the non-pup survivorship.

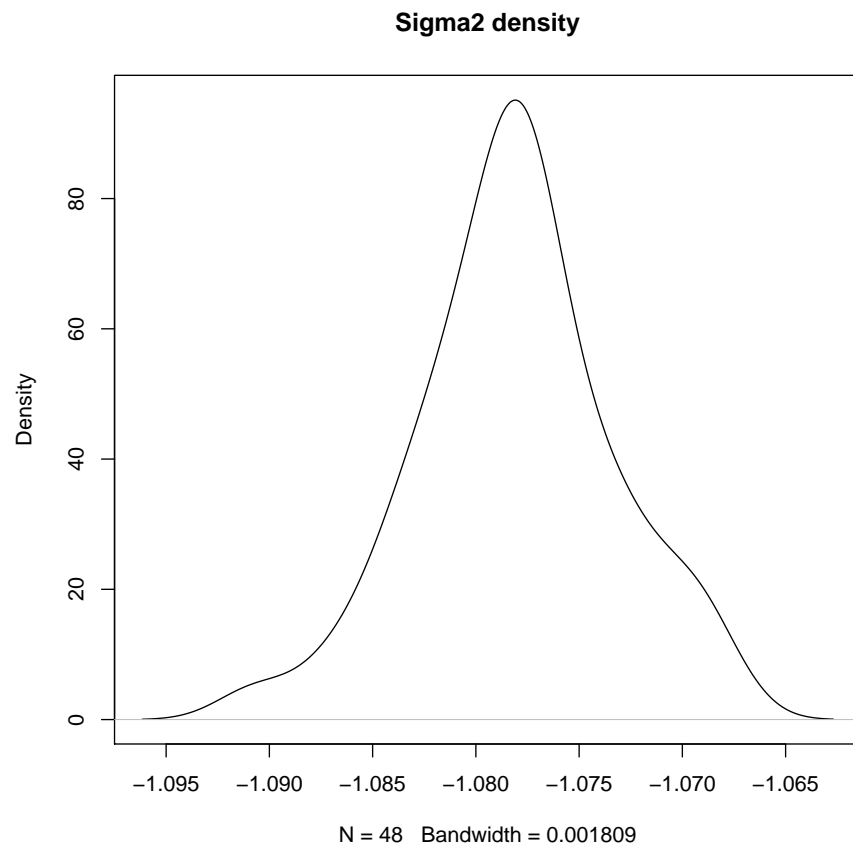


Figure 52: The posterior density of β_{σ_2} parameter, which controls the impact of the PDO on the value of σ , the non-pup survivorship.

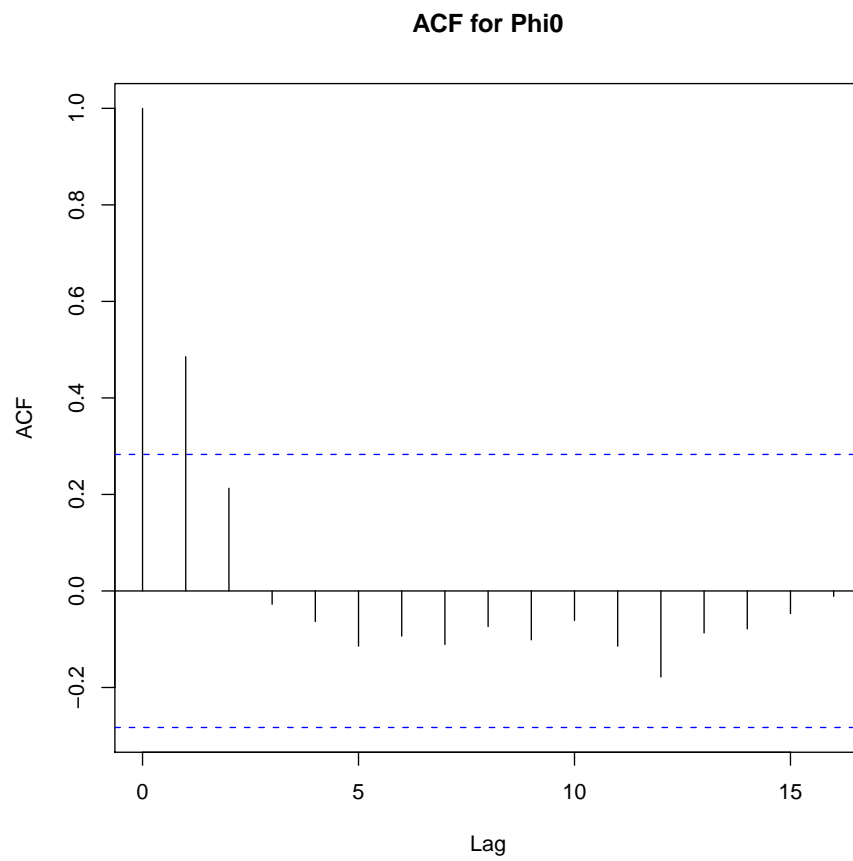


Figure 53: The autocorrelation function for the thinned β_{ϕ_0} parameter.

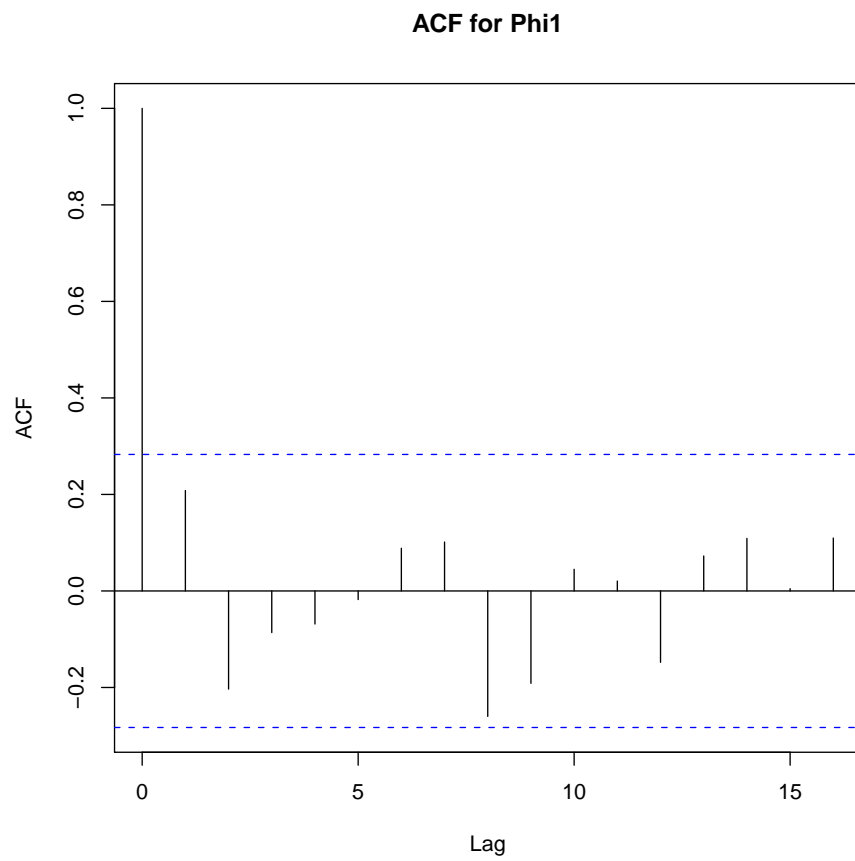


Figure 54: The autocorrelation function for the thinned $\beta_{\phi 1}$ parameter.

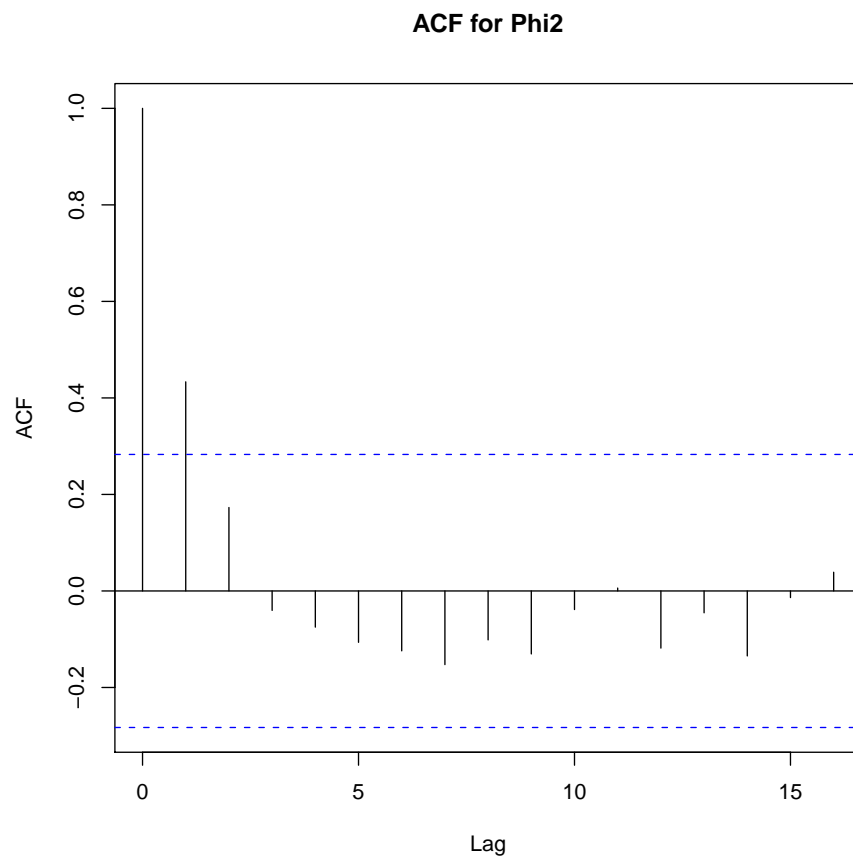


Figure 55: The autocorrelation function for the thinned β_{ϕ_2} parameter.

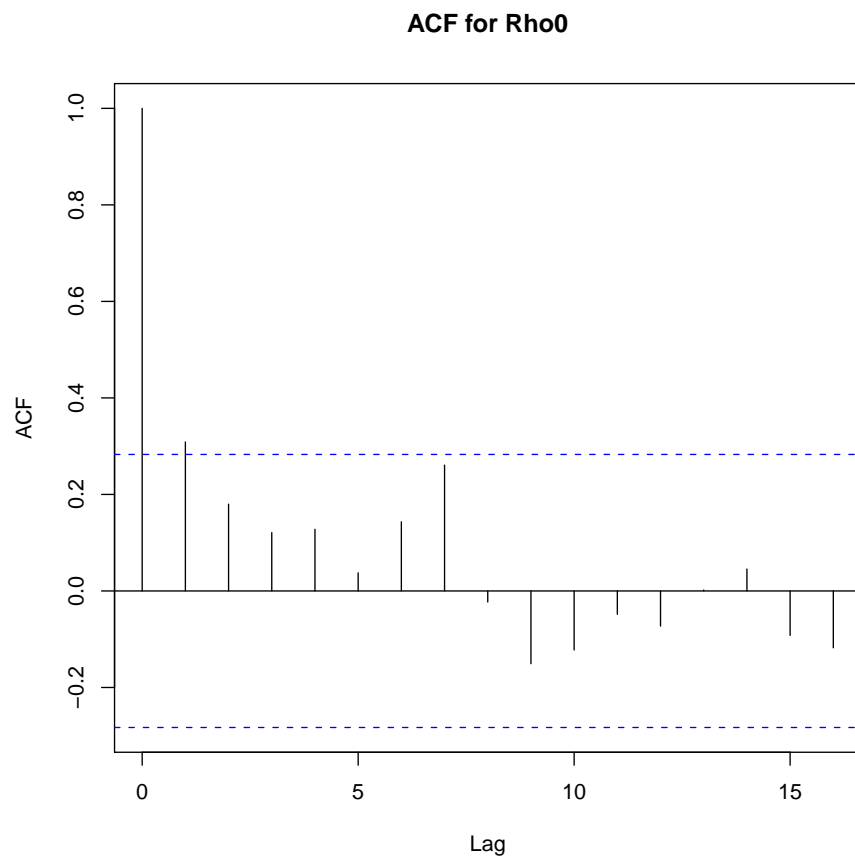


Figure 56: The autocorrelation function for the thinned β_{ρ_0} parameter.

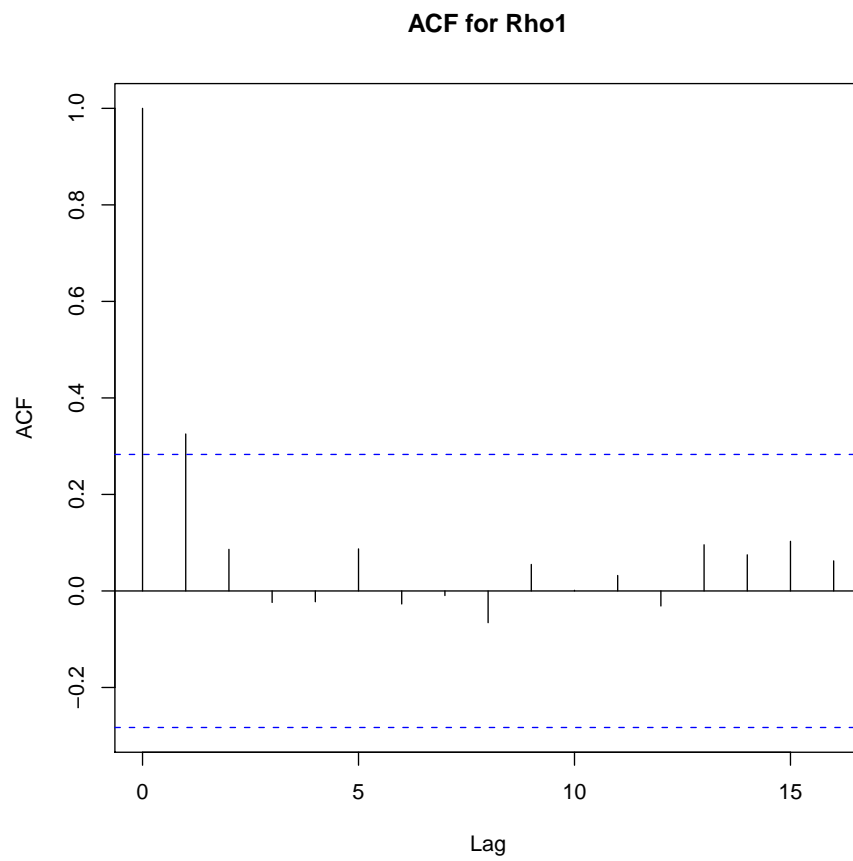


Figure 57: The autocorrelation function for the thinned $\beta_{\rho 1}$ parameter.

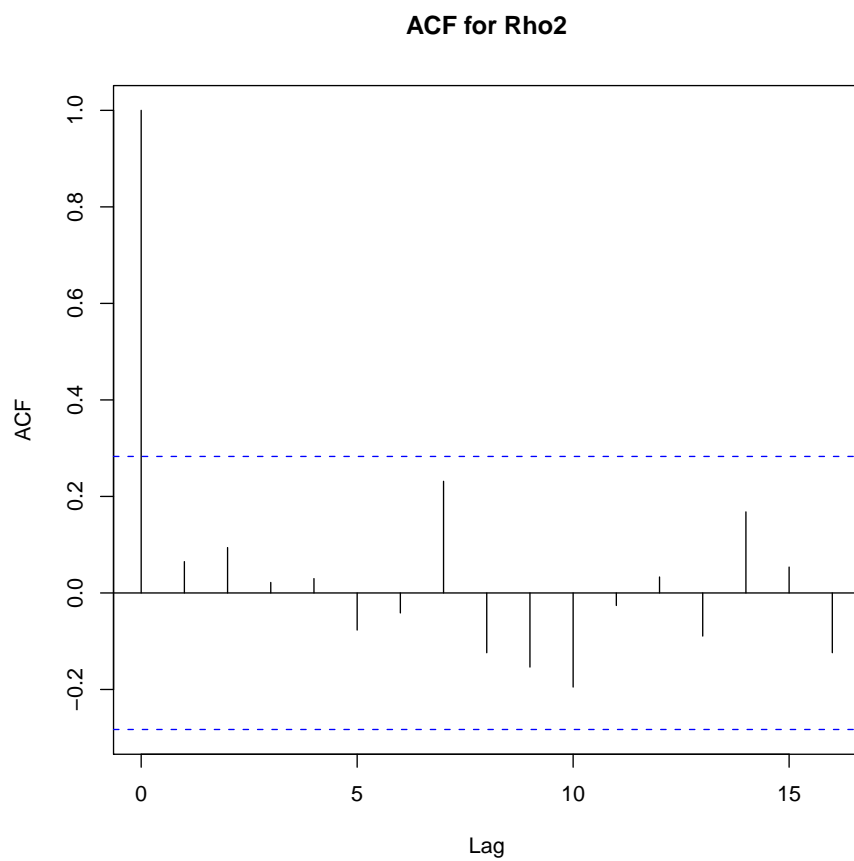


Figure 58: The autocorrelation function for the thinned β_{ρ_2} parameter.

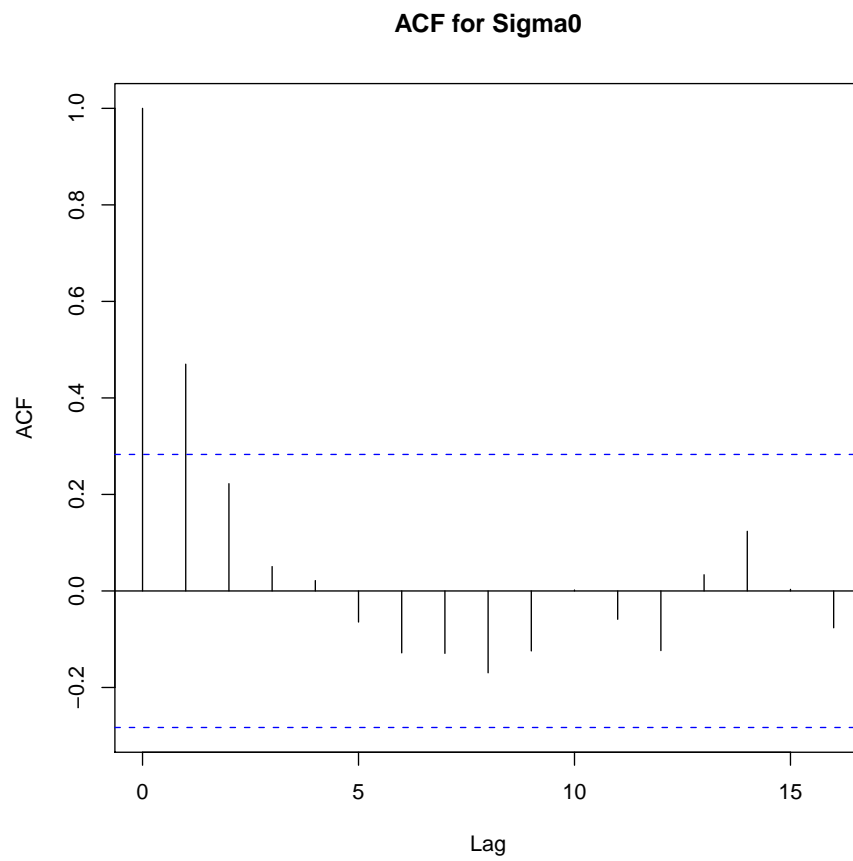


Figure 59: The autocorrelation function for the thinned β_{σ_0} parameter.

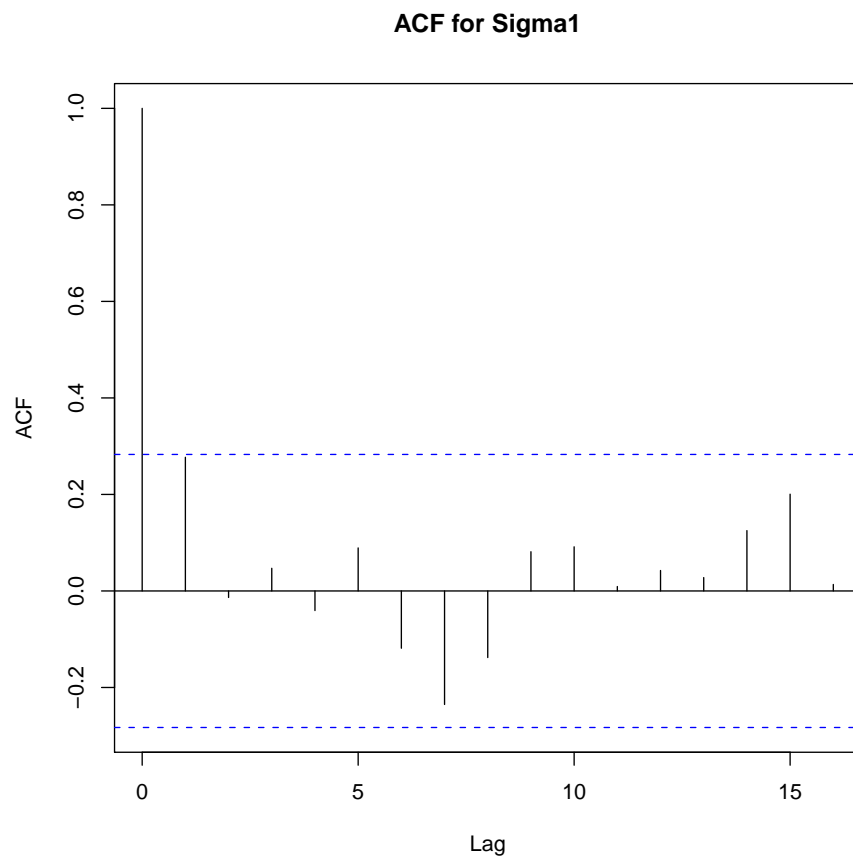


Figure 60: The autocorrelation function for the thinned $\beta_{\sigma 1}$ parameter.

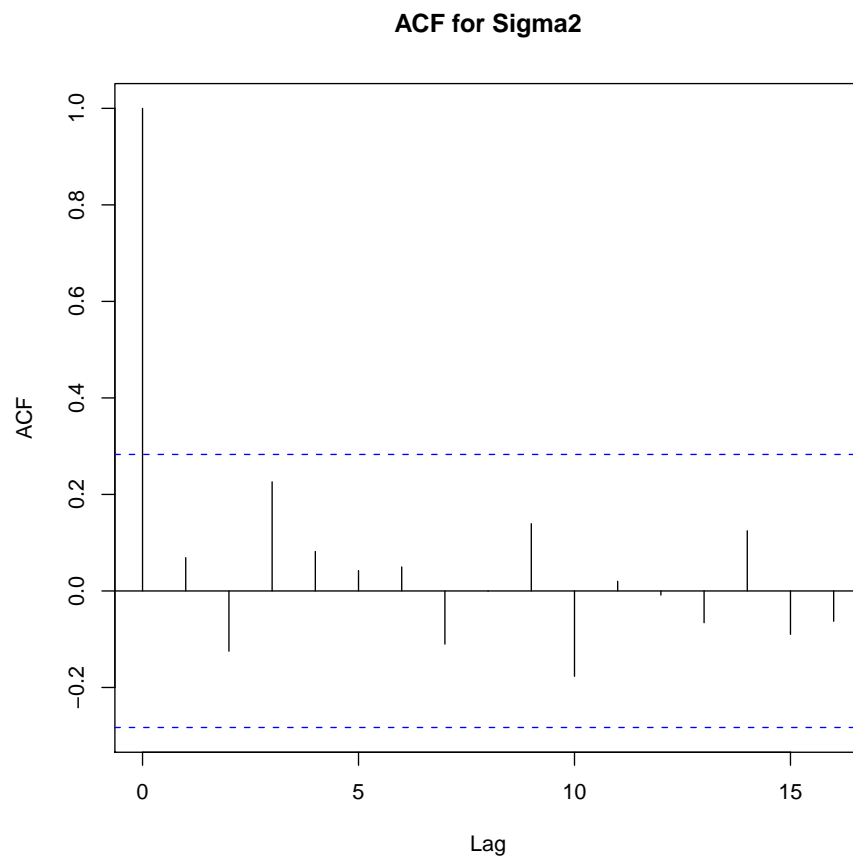


Figure 61: The autocorrelation function for the thinned β_{σ^2} parameter.