

Dealing with many correlated covariates in capture-recapture models

Olivier Gimenez¹, Christophe Barbraud²

¹CEFE UMR 5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, 1919 Route de Mende, 34293 Montpellier Cedex 5, France.

² CEBC UMR 7372, CNRS – Université de La Rochelle, 79360 Villiers en Bois, France.

Corresponding author: Olivier Gimenez (olivier.gimenez@cefe.cnrs.fr)

Word count: 2412

Summary: Capture-recapture models for estimating demographic parameters allow covariates to be incorporated to better understand population dynamics. However, high-dimensionality and multicollinearity can hamper estimation and inference. We propose a modeling framework to account for these two issues. Principal component analysis is used to reduce the number of predictors into uncorrelated synthetic new variables. Principal components are selected by sequentially assessing their statistical significance. We provide an example on seabird survival to illustrate our approach. Our method requires standard statistical tools, which permits an efficient and easy implementation using standard software.

Key words: Animal demography, Population dynamics, Principal-component capture-recapture model, Survival estimation.

Highlights:

- High-dimensionality and multicollinearity hamper model inference capture-recapture
- These issues are addressed with principal component capture-recapture (P2CR) models
- We provide an example on seabird survival to illustrate the P2CR method
- P2CR requires standard statistical tools and is implemented with standard software

INTRODUCTION

Survival is a key demographic parameter for conservation and management of plants and animals. Capture-recapture (CR) methods (e.g. Lebreton *et al.* 1992) are widely used for assessing the effect of explanatory variables on survival among other demographic parameters (Pollock 2002).

Generally however, complex situations arise where multiple covariates are required to capture patterns in survival. In such situations, one usually favors a multiple regression-like CR modeling framework that is however hampered by two issues: first, because it increases the number of parameters to be estimated, incorporating many covariates results in a loss of statistical power and a decrease in the precision of parameter estimates; second, correlation among the set of predictors – aka multicollinearity – may alter interpretation (see below).

To overcome these two issues, Grosbois *et al.* (2008) recommended to perform a principal component analysis (PCA) on the set of explanatory variables before fitting CR models. PCA is a multivariate technique that explains the variability of a set of variables in terms of a *reduced* set of *uncorrelated* linear combinations of such variables – aka principal components (PCs) – while maximizing the variance (Jolliffe 2002). Grosbois *et al.* (2008) then expressed survival as a function of the PCs that explained most of the variance in the set of original covariates, typically the first one or the first two ones.

However, the main drawback of this approach is that the PCs are selected based on covariates variation pattern alone, regardless of the response variable, and without guarantee that survival is most related to these PCs (Graham 2003). To deal with this issue in the context of logistic regression, Aguilera *et al.* (2006) proposed to test the significance of *all* PCs to decide which ones should be retained, instead of *a priori* relying on the PCs that explain most of the variation in the covariates.

In this paper, we implement the algorithm proposed by Aguilera *et al.* (2006) to deal with many possibly correlated covariates in CR models, a method we refer to as principal component capture-recapture (P2CR). We apply this new approach to a case study on survival of Snow petrels (*Pagodroma nivea*) that is possibly affected by climatic conditions. In this example, the issue of multicollinearity occurs, and summarizing the set of covariates in a subset of lower dimension is also crucial to get precise survival estimates. Overall, P2CR models can be fitted with statistical programs that perform PCA and CR data analysis. The data and R code are available from GitHub at <https://github.com/oliviergimenez/p2cr>.

METHODS

We used capture-recapture (CR) models to study open populations over K capture occasions to estimate the probability ϕ_i ($i = 1, \dots, K - 1$) that an individual survives to occasion $i + 1$ given that it is alive at time i , along with the probability p_j ($j = 2, \dots, K$) that an individual is recaptured at time j – aka as the Cormack-Jolly-Seber (CJS) model (Lebreton *et al.* 1992). Covariates were incorporated in survival probabilities using a linear-logistic function:

$$\text{logit}(\phi_i) = \log\left(\frac{\phi_i}{1-\phi_i}\right) = \alpha + \sum_{j=1}^p \beta_j X_{ij} \quad (1)$$

where α is the intercept parameter, X_{ij} is the value of covariate j ($j = 1, \dots, p$) in year i ($i = 1, \dots, K - 1$), and β_j is its associated slope parameter. Covariates were standardized to avoid numerical instabilities. To assess the significance of a covariate in CR models, we used the analysis of deviance (ANODEV; Skalski, Hoff & Smith 1993) that compares the amount of deviance explained by this covariate with the amount of deviance not explained by this covariate, the CR model with fully time-dependent survival serving as a reference. The ANODEV test statistic is given by:

$$\text{ANODEV} = \frac{\text{Dev}(X) - \text{Dev}(\text{constant})}{1} / \frac{\text{Dev}(\text{time}) - \text{Dev}(X)}{K - 1} \quad (2)$$

where $\text{Dev}(\text{constant})$, $\text{Dev}(X)$ and $\text{Dev}(\text{time})$ stand for the deviance of models with constant, covariate-dependent and time-dependent survival probabilities. To obtain the associated p-value, the value of the ANODEV is compared with the quantile of Fisher-Snedecor distribution with 1 and $K-1$ degrees of freedom.

To reduce the dimension of the set of covariates (X_1, \dots, X_p), we used PCA which aims at finding a small number of linear combinations of the original variables – the principal components (PCs) – while maximizing the variance in (X_1, \dots, X_p). Because the variables measurement units often differ, we performed the PCA on the correlation matrix. To select PCs, we used a forward model selection algorithm as proposed by Aguilera *et al.* (2006) for the logistic regression. The forward algorithm begins with no covariates in the model. Each PC is incorporated in simple linear regression-like CR models and the ANODEV p-value calculated. The PC that has the lowest p-value is added to the null model, say PC_k . Then the PCs that were not retained are incorporated along with PC_k in multiple regression-like CR models, and ANODEV p-values are calculated. In other words, we need to assess the effect of PC_j for $j \neq k$ in the presence of PC_k to decide whether PC_j should be retained. To do so, $\text{Dev}(\text{constant})$ and $\text{Dev}(X)$ are replaced by $\text{Dev}(\text{PC}_k)$ et $\text{Dev}(\text{PC}_k + \text{PC}_j)$ in Equation 2, where $\text{Dev}(\text{PC}_k + \text{PC}_j)$ is the deviance of the model with survival as a function of both principal components PC_k and PC_j . We repeat the process until no remaining PC is selected.

All models were fitted using the maximum-likelihood method using MARK (White & Burnham 1999) called with R (Laake 2013).

CASE STUDY

The Snow petrel is a medium sized Procellariiform species endemic to Antarctica that breeds in summer. Birds start to occupy breeding sites in early November, laying occurs in early December and chicks fledge in early March. This highly specialized species only forages within the pack-ice on crustaceans and fishes. Data on survival were obtained from a long-term CR study on Ile des Pétrels, Pointe Géologie Archipelago, Terre Adélie, Antarctica. We removed the first capture to limit heterogeneity among individuals, and worked with a total of 604 female capture histories from 1973 to 2002.

The following covariates were included to assess the effect of climatic conditions upon survival variation: sea ice extent (SIE; http://nsidc.org/data/seoice_index/); air temperature, which was obtained from the Météo France station at Dumont d'Urville, as a proxy for sea surface temperature; southern Oscillation Index (SOI) as a proxy for the overall climate condition (<https://crudata.uea.ac.uk/cru/data/soi/>). These environmental variables were averaged over seasonal time periods corresponding to the chick rearing period (January to March: summer period), the non-breeding period (April to June: autumn and July to September: winter), and the laying and incubation period of the same year (October to December: spring). In total, 9 covariates were included in the analysis: sea ice extent in summer (SIEsummer), in autumn (SIEautumn), in winter (SIEWinter), in spring (SIEspring), annual SOI, air temperature in summer (Tsummer), in autumn (Tauumn), in winter (Twinter) and in spring (Tspring).

RESULTS

The CJS model poorly fitted the data ($\chi^2 = 221.2$, $df = 127$, $p << 0.01$), and a closer inspection of the results revealed that the lack of fit was explained by a trap-dependence effect (Test2CT, $\chi^2 = 103.1$, $df = 27$, $p << 0.01$). Consequently, we distinguished two

recapture probabilities whether or not a recapture occurred the occasion before (Pradel 1993).

By first attempting to simplify the structure of recapture probabilities, we were led to consider an additive effect of time and a trap effect (Supplementary material). Estimates of recapture probabilities ranged from 0.14 (standard error [SE] = 0.07) to 0.79 (SE = 0.09) when no recapture occurred the occasion before and from 0.25 (SE = 0.18) to 0.89 (SE = 0.09) when a recapture occurred the occasion before (Supplementary material).

Because of multicollinearity, we were led to counterintuitive estimates of regression parameters in the CR model including all covariates (Supplementary material): the coefficient of SIE in autumn was estimated at 0.5 (SE = 0.24) and that of SIE in winter was estimated at -0.5 (SE = 0.21) while these two covariates were significantly positively correlated ($r = 0.67$, $p < 0.01$).

When we applied the P2CR approach, the algorithm selected two PCs, namely PC3 ($F_{1,27} = 7.34$, $p = 0.01$) at step 1 and PC4 ($F_{1,26} = 4.63$, $p = 0.04$) at step 2 (Supplementary material), but never did we pick PC1 as we would have done using a classical approach (Grosbois et al. 2008). PC3 was positively correlated to SIE in summer and negatively correlated to temperature in winter, while PC4 was positively correlated to temperature in spring and negatively correlated to SIE in summer (Supplementary material). Survival increased with increasing values of PC3 (Figure 1), with high values of SIE in summer and low values of temperature in winter (resp. low values of SIE in summer and high values of temperature in winter) corresponding to high (resp. low) survival.

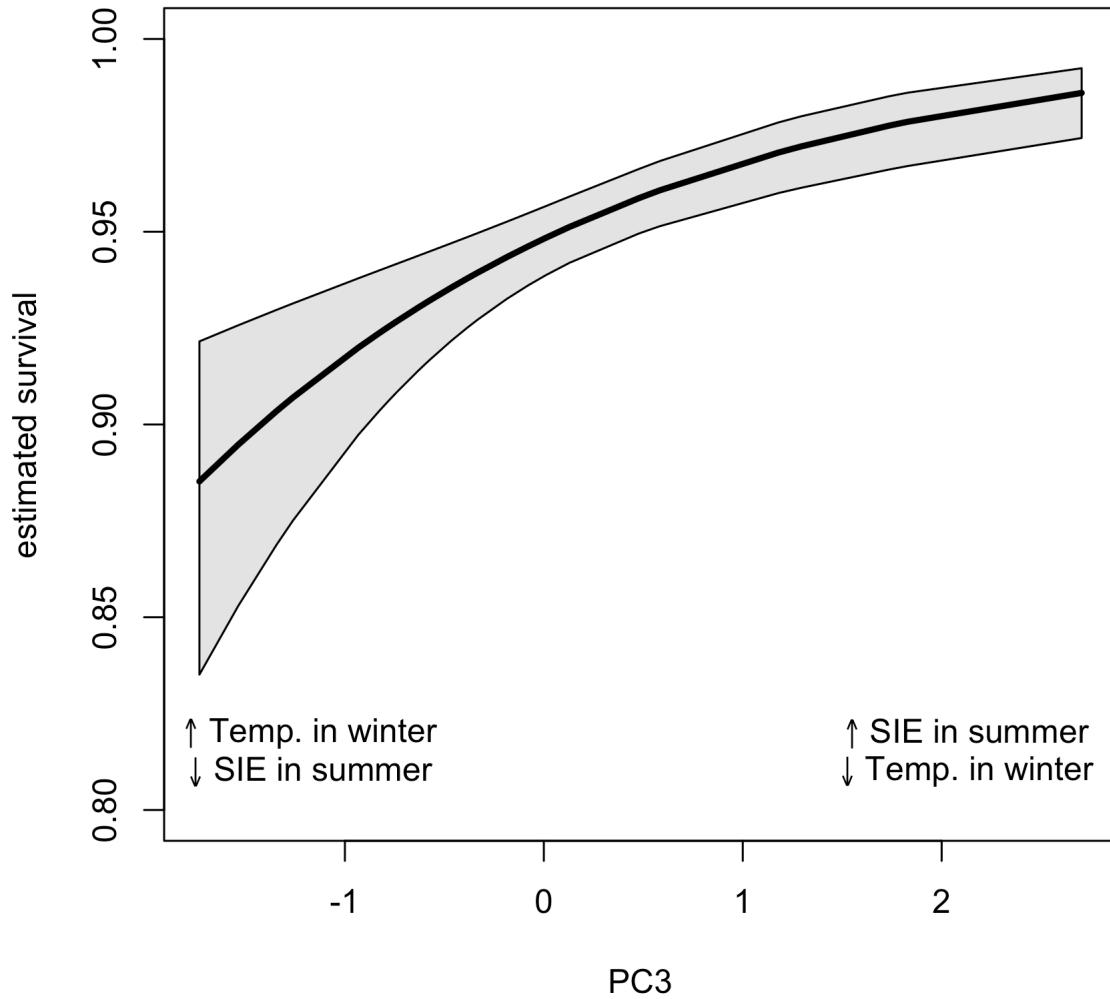


Figure 1: Survival of Snow petrel as a function of PC3.

Survival decreased with increasing values of PC4 (Figure 2), with high values of temperature in spring and low values of SIE in summer (resp. low values of temperature in spring and high values of SIE in summer) corresponding to low (resp. high) survival.

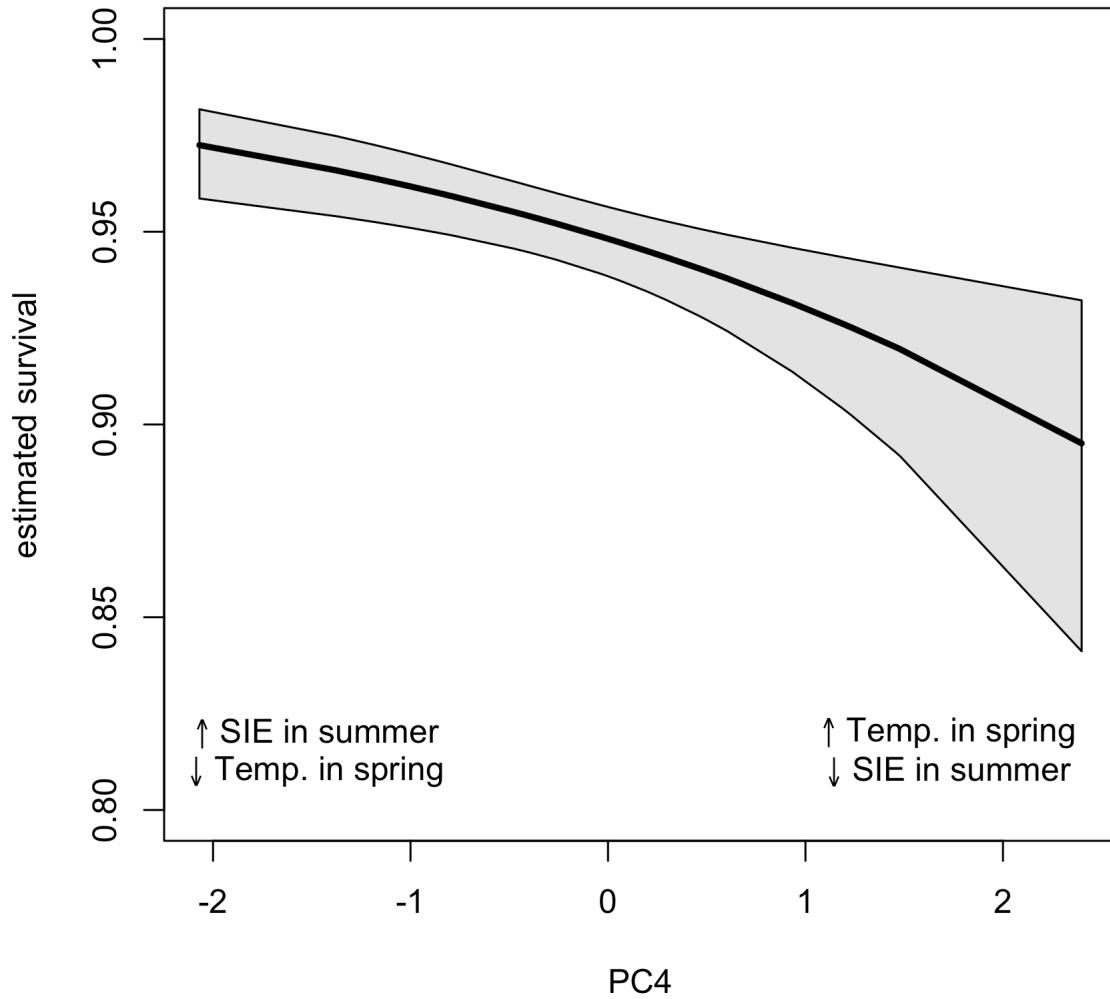


Figure 2: Survival of Snow petrel as a function of PC4.

The P2CR approach also led to more precise survival estimates when compared to the model incorporating all original covariates (Figure 3).

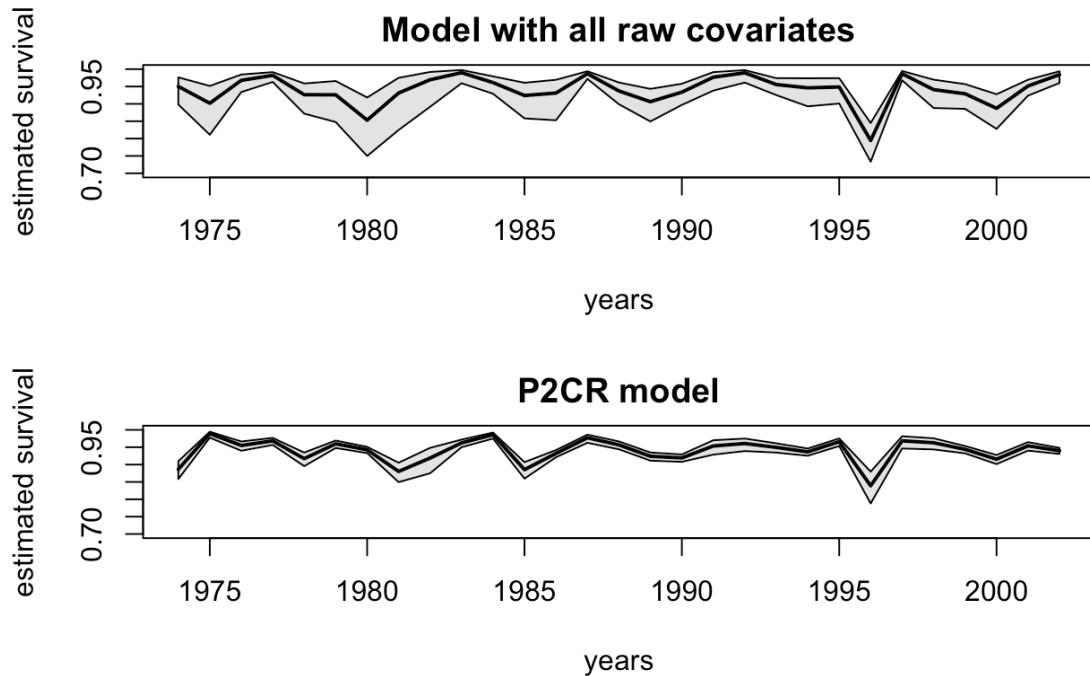


Figure 3: Survival of Snow petrel over time as estimated from the model with all original covariates (top panel) vs. the PC2R model (bottom panel).

DISCUSSION

Snow petrels and climatic conditions

In summer, snow petrels exclusively forage within the pack-ice tens to hundreds of kilometers from the colony where they catch sea ice-associated species, such as Antarctic silverfish (*Pleuragramma antarcticum*) and Euphausiids, to feed their chick (Ridoux & Offredo 1989). This is an energetically demanding period for breeding adults and, during years with reduced sea-ice extent, food resources may be less abundant and snow petrels may be forced to cover larger distances to find suitable foraging habitats, with potential survival costs. Assuming air temperature was a proxy of sea surface temperature variations, the negative effect of warmer temperatures on survival is coherent with general patterns found between sea surface temperature and demographic parameters in seabirds (Barbraud *et al.*

2012). In many marine ecosystems warmer temperatures are associated with decreased primary production and food resources for top predators. Although the low survival in 1996 corresponded to a year with reduced sea-ice extent in summer, the drop in survival was high and remains unexplained at the moment.

Principal component CR models

When multiple covariates have to be considered to estimate survival, both issues of dimensionality and multicollinearity can lead to biased estimates, inflated precision as well as lack of statistical power. In such a context, the P2CR modeling framework has proved particularly useful in our example, mainly because few PCs were selected which were easily interpretable. We acknowledge that PCs with little interpretability might have been picked up by our method. To make the interpretation easier, PCA results can be post-processed by rotating axes to improve correlations between raw variables and PCs like in the varimax method (Kaiser 1958). Recent developments in the field of multivariate analyses could also be useful, like methods to handle with missing values in PCA (Dray & Josse 2015).

In statistical ecology, one of our objectives is to try and explain variation in state variables such as abundance, survival and the distribution of species. Dimension-reduction methods are promising to deal with many correlated covariates for the analysis of CR or occupancy data.

ACKNOWLEDGEMENTS

We greatly acknowledge all of the wintering fieldworkers involved in the monitoring programs in Terre Adélie since 1962, and Dominique Besson for the management of the database. The study on petrels was supported by Expéditions Polaires Françaises, Institut

Paul Emile Victor (program IPEV 109, resp. H. Weimerskirch) and Terres Australes et Antarctiques Françaises.

LITERATURE CITED

- Aguilera, A.M., Escabias, M. & Valderrama, M.J. (2006) Using principal components for estimating logistic regression with high-dimensional multicollinear data. *Computational Statistics and Data Analysis*, **50**, 1905–1924.
- Barbraud, C., Rolland, V., Jenouvrier, S., Nevoux, M., Delord, K. & Weimerskirch, H. (2012) Effects of climate change and fisheries bycatch on Southern Ocean seabirds: A review. *Marine Ecology Progress Series*, **454**, 285–307.
- Dray, S. & Josse, J. (2015) Principal component analysis with missing values: a comparative survey of methods. *Plant Ecology*, **216**, 657–667.
- Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology*, **84**, 2809–2815.
- Grosbois, V., Gimenez, O., Gaillard, J.M., Pradel, R., Barbraud, C., Clobert, J., Møller, A.P. & Weimerskirch, H. (2008) Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews*, **83**, 357–99.
- Jolliffe, I.T. (2002) Principal Component Analysis, Second Edition. Springer-Verlag, New York.
- Kaiser, H.F. (1958) The varimax criterion for analytic rotation in factor analysis. *Psychometrika*, **23**, 187–200.
- Laake, J.L. (2013) RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and

- testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs*, **62**, 67–118.
- Pollock, K.H. (2002) The use of auxiliary variables in capture-recapture modelling: an overview. *Journal of Applied Statistics*, **29**, 85–102.
- Ridoux, V. & Offredo, C. (1989) The diets of five summer breeding seabirds in Adélie Land, Antarctica. *Polar Biology*, **9**, 137–145.
- Skalski, J.R., Hoff, A. & Smith, S.G. (1993) Testing the significance of individual- and cohort-level covariates in animal survival studies. *Marked Individuals in the Study of Bird Population*, eds J.D. Lebreton & P.M. North, pp. 9–28. Birkhäuser Verlag, Basel.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, 120–139.

Supplementary material for 'Dealing with many correlated covariates in capture-recapture models' by Gimenez and Barbraud.

December 27, 2016

Introduction

We illustrate the principal component capture-recapture (P2CR) method for covariates selection in capture-recapture models using data on survival of Snow petrels in Pointe Géologie Archipelago, Terre Adélie, Antarctica. In total, the dataset consists of 604 female histories from 1973 to 2002. The objective is to investigate the effect of climatic conditions on adult survival.

Explore climatic covariates

First we explore the covariates sea ice extent in summer (SIE.Su), in autumn and winter (SIE.Au and SIE.Wi), in spring (SIE.Sp), annual southern oscillation index (SOI), air temperature in summer (T.Su), in autumn and winter (T.Au and T.Wi) and in spring (T.Sp).

Let us have a look to the correlations between these covariates:

```
cov <- read.table('cov-petrel.txt',header=T)
head(cov)

##   SIE.Su SIE.Au SIE.Wi SIE.Sp   SOI      T.Su      T.au      T.wi
## 1     0    341    478    348  0.96 -5.233333 -14.98333 -17.01667
## 2    189    300    600    341  1.33 -4.150000 -15.08333 -17.85000
## 3     26    270    337    230  0.06 -5.033333 -16.51667 -16.51667
## 4     81    256    348    337 -1.14 -4.300000 -13.76667 -15.86667
## 5     22    207    389    437 -0.29 -4.716667 -14.30000 -15.63333
## 6    111    215    307    437 -0.26 -5.116667 -15.06667 -16.15000
##
##   T.sp
## 1 -6.700000
## 2 -7.250000
## 3 -7.683333
## 4 -7.650000
## 5 -7.916667
## 6 -6.766667

round(cor(cov),2)

##           SIE.Su SIE.Au SIE.Wi SIE.Sp   SOI   T.Su   T.au   T.wi   T.sp
## SIE.Su  1.00 -0.05  0.01 -0.10  0.15  0.04 -0.02 -0.21  0.01
## SIE.Au -0.05  1.00  0.67  0.02  0.26 -0.30 -0.43 -0.23 -0.12
## SIE.Wi  0.01  0.67  1.00  0.21  0.22 -0.18 -0.24 -0.47  0.04
```

```

## SIE.Sp -0.10 0.02 0.21 1.00 -0.06 -0.11 0.19 -0.06 -0.18
## SOI 0.15 0.26 0.22 -0.06 1.00 -0.34 -0.37 0.13 0.14
## T.Su 0.04 -0.30 -0.18 -0.11 -0.34 1.00 0.47 0.27 -0.05
## T.au -0.02 -0.43 -0.24 0.19 -0.37 0.47 1.00 0.17 0.06
## T.wi -0.21 -0.23 -0.47 -0.06 0.13 0.27 0.17 1.00 0.00
## T.sp 0.01 -0.12 0.04 -0.18 0.14 -0.05 0.06 0.00 1.00

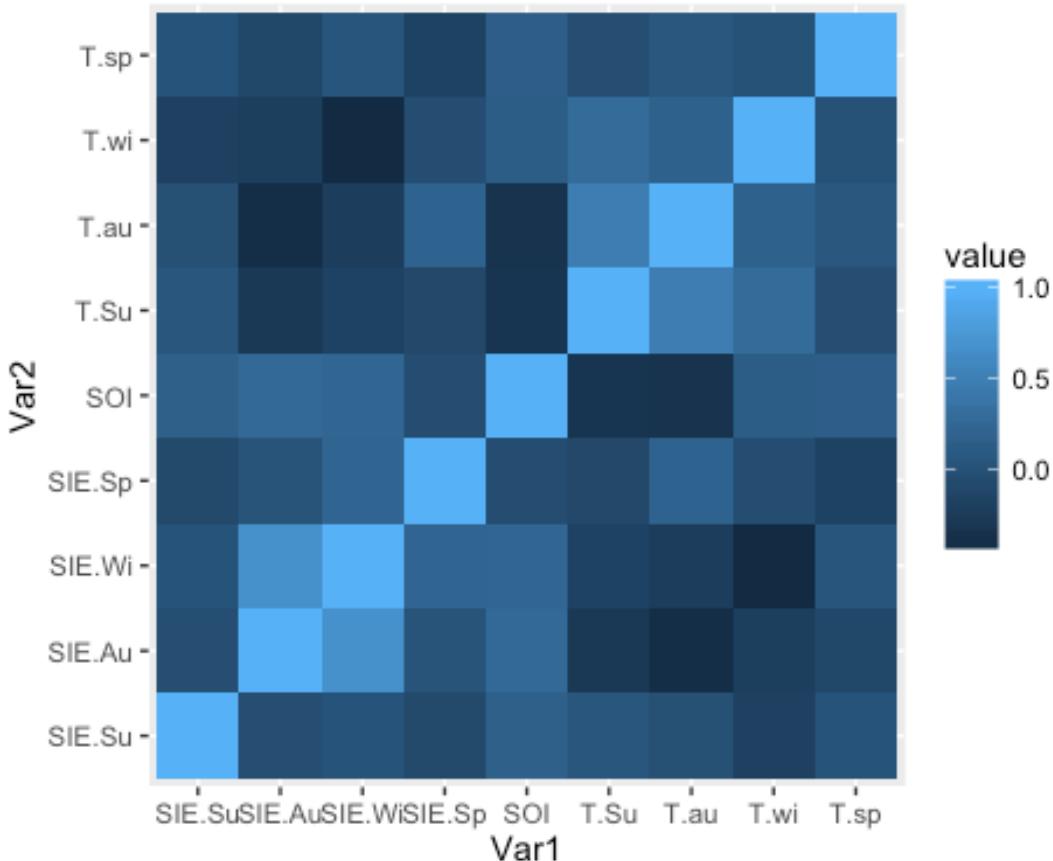
```

Visually, with a heatmap:

```

library(ggplot2)
library(reshape2)
qplot(x=Var1, y=Var2, data=melt(cor(cov)), fill=value, geom="tile")

```



What are the significant correlations?

```

library(psych)

##
## Attaching package: 'psych'

## The following objects are masked from 'package:ggplot2':
## 
##     %+%, alpha

corr.test(cov)

```

```

## Call:corr.test(x = cov)
## Correlation matrix
##           SIE.Su SIE.Au SIE.Wi SIE.Sp   SOI   T.Su   T.au   T.wi   T.sp
## SIE.Su    1.00 -0.05  0.01 -0.10  0.15  0.04 -0.02 -0.21  0.01
## SIE.Au   -0.05  1.00  0.67  0.02  0.26 -0.30 -0.43 -0.23 -0.12
## SIE.Wi    0.01  0.67  1.00  0.21  0.22 -0.18 -0.24 -0.47  0.04
## SIE.Sp   -0.10  0.02  0.21  1.00 -0.06 -0.11  0.19 -0.06 -0.18
## SOI       0.15  0.26  0.22 -0.06  1.00 -0.34 -0.37  0.13  0.14
## T.Su      0.04 -0.30 -0.18 -0.11 -0.34  1.00  0.47  0.27 -0.05
## T.au     -0.02 -0.43 -0.24  0.19 -0.37  0.47  1.00  0.17  0.06
## T.wi     -0.21 -0.23 -0.47 -0.06  0.13  0.27  0.17  1.00  0.00
## T.sp      0.01 -0.12  0.04 -0.18  0.14 -0.05  0.06  0.00  1.00
## Sample Size
## [1] 29
## Probability values (Entries above the diagonal are adjusted for multiple
## tests.)
##           SIE.Su SIE.Au SIE.Wi SIE.Sp   SOI   T.Su   T.au   T.wi   T.sp
## SIE.Su    0.00  1.00  1.00  1.00  1.00  1.00  1.00  1.00    1
## SIE.Au    0.79  0.00  0.00  1.00  1.00  1.00  0.64  1.00    1
## SIE.Wi    0.96  0.00  0.00  1.00  1.00  1.00  1.00  0.37    1
## SIE.Sp    0.59  0.90  0.28  0.00  1.00  1.00  1.00  1.00    1
## SOI       0.43  0.17  0.25  0.77  0.00  1.00  1.00  1.00    1
## T.Su      0.83  0.12  0.35  0.56  0.07  0.00  0.33  1.00    1
## T.au      0.92  0.02  0.20  0.32  0.05  0.01  0.00  1.00    1
## T.wi      0.28  0.23  0.01  0.76  0.52  0.15  0.37  0.00    1
## T.sp      0.97  0.53  0.84  0.34  0.47  0.80  0.77  0.99    0
##
## To see confidence intervals of the correlations, print with the
## short=FALSE option

print(corr.test(cov),short=FALSE)

## Call:corr.test(x = cov)
## Correlation matrix
##           SIE.Su SIE.Au SIE.Wi SIE.Sp   SOI   T.Su   T.au   T.wi   T.sp
## SIE.Su    1.00 -0.05  0.01 -0.10  0.15  0.04 -0.02 -0.21  0.01
## SIE.Au   -0.05  1.00  0.67  0.02  0.26 -0.30 -0.43 -0.23 -0.12
## SIE.Wi    0.01  0.67  1.00  0.21  0.22 -0.18 -0.24 -0.47  0.04
## SIE.Sp   -0.10  0.02  0.21  1.00 -0.06 -0.11  0.19 -0.06 -0.18
## SOI       0.15  0.26  0.22 -0.06  1.00 -0.34 -0.37  0.13  0.14
## T.Su      0.04 -0.30 -0.18 -0.11 -0.34  1.00  0.47  0.27 -0.05
## T.au     -0.02 -0.43 -0.24  0.19 -0.37  0.47  1.00  0.17  0.06
## T.wi     -0.21 -0.23 -0.47 -0.06  0.13  0.27  0.17  1.00  0.00
## T.sp      0.01 -0.12  0.04 -0.18  0.14 -0.05  0.06  0.00  1.00
## Sample Size
## [1] 29
## Probability values (Entries above the diagonal are adjusted for multiple
## tests.)
##           SIE.Su SIE.Au SIE.Wi SIE.Sp   SOI   T.Su   T.au   T.wi   T.sp
## SIE.Su    0.00  1.00  1.00  1.00  1.00  1.00  1.00  1.00    1

```

```

## SIE.Au  0.79  0.00  0.00  1.00 1.00 1.00 0.64 1.00  1
## SIE.Wi  0.96  0.00  0.00  1.00 1.00 1.00 1.00 0.37  1
## SIE.Sp  0.59  0.90  0.28  0.00 1.00 1.00 1.00 1.00  1
## SOI     0.43  0.17  0.25  0.77 0.00 1.00 1.00 1.00  1
## T.Su    0.83  0.12  0.35  0.56 0.07 0.00 0.33 1.00  1
## T.au    0.92  0.02  0.20  0.32 0.05 0.01 0.00 1.00  1
## T.wi    0.28  0.23  0.01  0.76 0.52 0.15 0.37 0.00  1
## T.sp    0.97  0.53  0.84  0.34 0.47 0.80 0.77 0.99  0
##
## To see confidence intervals of the correlations, print with the
## short=FALSE option
##
## Confidence intervals based upon normal theory. To get bootstrapped
## values, try cor.ci
##          lower      r upper      p
## SIE.Su-SIE.A -0.41 -0.05  0.32 0.79
## SIE.Su-SIE.W -0.36  0.01  0.38 0.96
## SIE.Su-SIE.Sp -0.45 -0.10  0.27 0.59
## SIE.Su-SOI   -0.23  0.15  0.49 0.43
## SIE.Su-T.Su  -0.33  0.04  0.40 0.83
## SIE.Su-T.au  -0.38 -0.02  0.35 0.92
## SIE.Su-T.wi  -0.53 -0.21  0.17 0.28
## SIE.Su-T.sp  -0.36  0.01  0.37 0.97
## SIE.A-SIE.W  0.40  0.67  0.83 0.00
## SIE.A-SIE.Sp -0.35  0.02  0.39 0.90
## SIE.A-SOI    -0.12  0.26  0.57 0.17
## SIE.A-T.Su   -0.60 -0.30  0.08 0.12
## SIE.A-T.au   -0.69 -0.43 -0.08 0.02
## SIE.A-T.wi   -0.55 -0.23  0.15 0.23
## SIE.A-T.sp   -0.47 -0.12  0.26 0.53
## SIE.W-SIE.Sp -0.17  0.21  0.53 0.28
## SIE.W-SOI    -0.16  0.22  0.54 0.25
## SIE.W-T.Su   -0.51 -0.18  0.20 0.35
## SIE.W-T.au   -0.56 -0.24  0.13 0.20
## SIE.W-T.wi   -0.71 -0.47 -0.12 0.01
## SIE.W-T.sp   -0.33  0.04  0.40 0.84
## SIE.Sp-SOI   -0.41 -0.06  0.32 0.77
## SIE.Sp-T.Su  -0.46 -0.11  0.26 0.56
## SIE.Sp-T.au  -0.19  0.19  0.52 0.32
## SIE.Sp-T.wi  -0.42 -0.06  0.31 0.76
## SIE.Sp-T.sp  -0.52 -0.18  0.20 0.34
## SOI-T.Su    -0.63 -0.34  0.03 0.07
## SOI-T.au    -0.65 -0.37  0.00 0.05
## SOI-T.wi    -0.25  0.13  0.47 0.52
## SOI-T.sp    -0.24  0.14  0.48 0.47
## T.Su-T.au   0.13  0.47  0.72 0.01
## T.Su-T.wi   -0.10  0.27  0.58 0.15
## T.Su-T.sp   -0.41 -0.05  0.32 0.80
## T.au-T.wi   -0.21  0.17  0.51 0.37

```

```
## T.au-T.sp      -0.32  0.06  0.41  0.77  
## T.wi-T.sp     -0.37  0.00  0.37  0.99
```

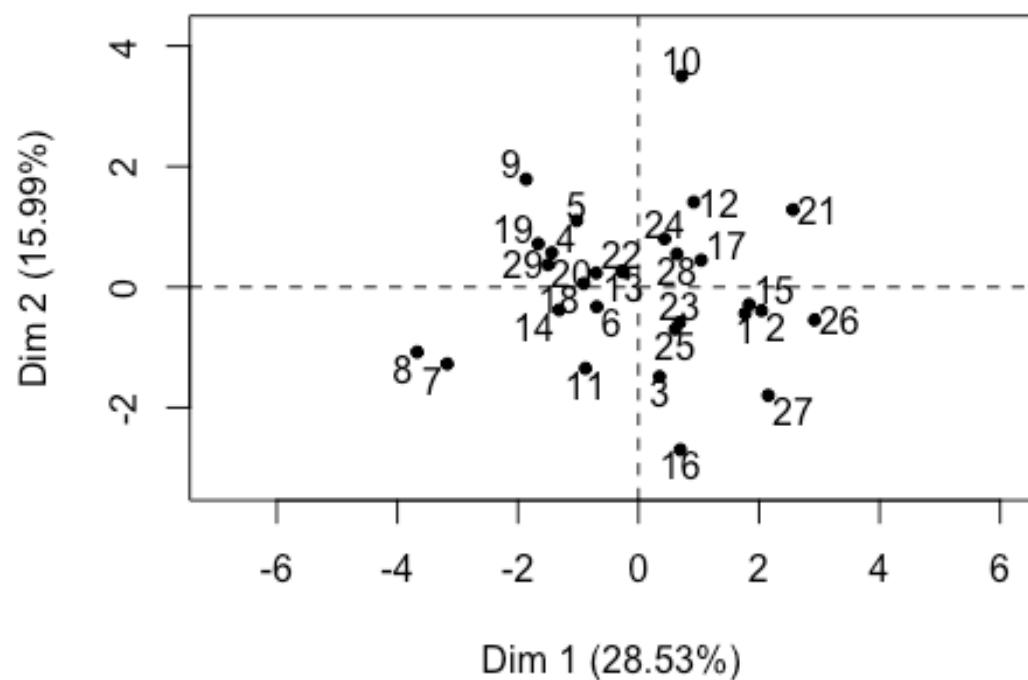
Seems like sea ice extent in autumn and winter are positively correlated, while sea ice extent in autumn and temperature in autumn are negatively correlated.

PCA on covariates

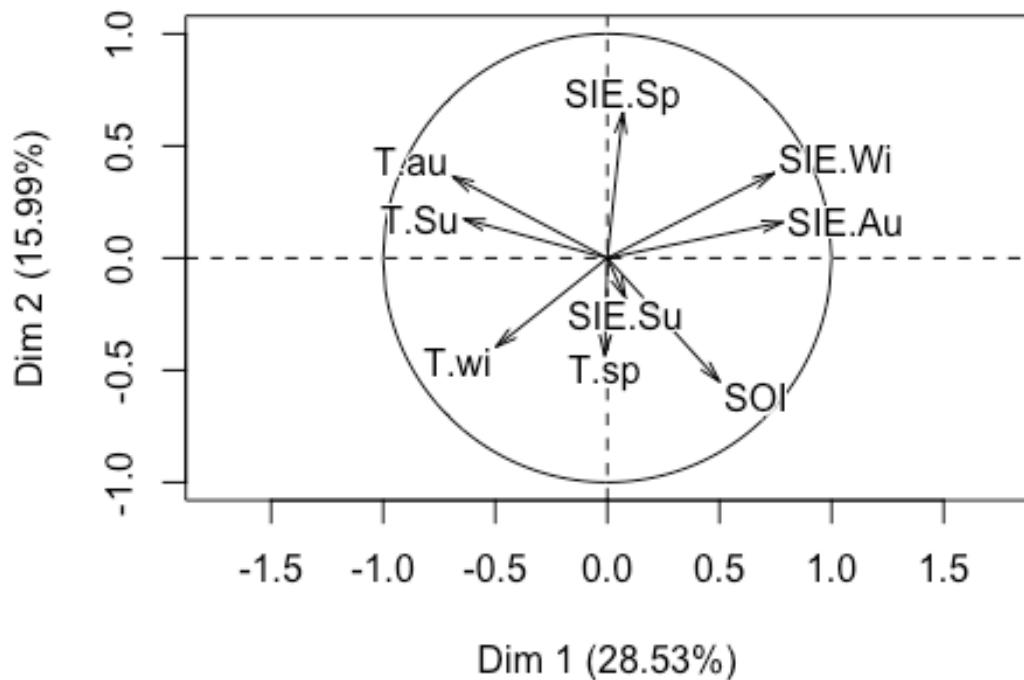
Let's perform a PCA on this set of covariates:

```
library(FactoMineR)  
res.pca = PCA(cov,scale.unit=T,graph=T,ncp=9)
```

Individuals factor map (PCA)



Variables factor map (PCA)



Find the covariates associated to each principal component:

```
dimdesc(res.pca,axes = 1:9)

## $Dim.1
## $Dim.1$quanti
##           correlation      p.value
## SIE.Au    0.7846343 4.703772e-07
## SIE.Wi    0.7444495 3.650675e-06
## SOI       0.5012694 5.604172e-03
## T.wi     -0.4966878 6.129402e-03
## T.Su     -0.6409107 1.798385e-04
## T.au     -0.6912833 3.291814e-05
##
## 
## $Dim.2
## $Dim.2$quanti
##           correlation      p.value
## SIE.Sp    0.6505897 0.000132906
## SIE.Wi    0.3787178 0.042773054
## T.wi     -0.3960426 0.033438570
## T.sp     -0.4367718 0.017836263
## SOI      -0.5519112 0.001910053
##
```

```

## $Dim.3
## $Dim.3$quanti
##      correlation      p.value
## SIE.Su    0.7413696 4.205825e-06
## T.wi     -0.5808892 9.527347e-04
##
## $Dim.4
## $Dim.4$quanti
##      correlation      p.value
## T.sp      0.8228262 4.300265e-08
## SIE.Su   -0.3946619 3.411627e-02
##
## $Dim.5
## $Dim.5$quanti
##      correlation      p.value
## SIE.Sp    0.6329789 0.0002286769
## SOI       0.4046400 0.0294590693
## SIE.Su    0.4020185 0.0306294870
##
## $Dim.6
## $Dim.6$quanti
##      correlation      p.value
## T.Su     0.5642562 0.001431237
## T.wi     0.3861381 0.038548955
##
## $Dim.8
## NULL

#plot(res.pca)

```

Percentage of variance explained:

```

res.pca$eig[,3]
## [1] 28.53227 44.52647 57.72122 68.86126 79.32825 89.27306 93.70949
## [8] 97.95676 100.00000

```

The loadings:

```

res.pca$var$cor

##           Dim.1      Dim.2      Dim.3      Dim.4      Dim.5
## SIE.Su  0.08057735 -0.1786150  0.7413696 -0.39466187  0.40201850
## SIE.Au  0.78463426  0.1601660 -0.1358873 -0.02360527 -0.28475060
## SIE.Wi  0.74444946  0.3787178  0.1390330  0.26085759 -0.10566944
## SIE.Sp  0.06940453  0.6505897 -0.2874635  0.14838490  0.63297890
## SOI    0.50126942 -0.5519112 -0.1726551  0.02166076  0.40463998

```

```

## T.Su   -0.64091072  0.1741091  0.1976988 -0.02932482 -0.29134793
## T.au   -0.69128327  0.3642634  0.1570772  0.27691731  0.17674456
## T.wi   -0.49668781 -0.3960426 -0.5808892 -0.03417841  0.08316850
## T.sp   -0.01138968 -0.4367718  0.2940550  0.82282616  0.02694411
##           Dim.6      Dim.7      Dim.8      Dim.9
## SIE.Su   0.20439145  0.16833601  0.15205046 -0.03696014
## SIE.Au   0.32726859  0.07959270  0.31757770  0.21046404
## SIE.Wi   0.33851943 -0.03721296 -0.08556715 -0.28376578
## SIE.Sp   0.00660304  0.22829056 -0.08806289  0.08176243
## SOI     0.34355549 -0.29450675 -0.19246270  0.09112650
## T.Su    0.56425618  0.10752351 -0.30114518  0.11600140
## T.au    0.20978102 -0.36666032  0.27977904  0.01097100
## T.wi    0.38613805  0.19899778  0.18999768 -0.16165470
## T.sp   -0.04458262  0.19690112  0.03311646  0.05485501

```

Re-project each covariate on each principal component:

```

pcs = res.pca$ind$coord
round(pcs,2)

##      Dim.1 Dim.2 Dim.3 Dim.4 Dim.5 Dim.6 Dim.7 Dim.8 Dim.9
## 1    1.77 -0.44 -0.78  1.45 -0.08  0.12 -0.97 -0.13  0.85
## 2    2.04 -0.39  2.70 -0.78  1.49  1.99 -0.44 -0.63 -0.21
## 3    0.35 -1.49 -0.46 -1.19 -1.33 -1.04 -0.78 -0.45  0.16
## 4   -1.44  0.57  0.48 -0.86 -0.07 -0.20 -0.01  0.59 -0.01
## 5   -1.03  1.10 -1.26 -0.40  1.18 -0.56 -0.37 -0.76 -0.33
## 6   -0.69 -0.33  0.59  0.08  2.17 -0.99  1.00 -0.10  0.37
## 7   -3.17 -1.28 -0.08  0.21  0.39  0.83  0.91 -0.79 -0.37
## 8   -3.67 -1.08 -1.54  0.46  1.39  0.75 -0.45  0.80  0.20
## 9   -1.87  1.79  0.56  2.40  0.67 -1.92 -0.76 -0.42 -0.51
## 10   0.72  3.50  0.01 -1.05  0.25  0.99 -0.45  0.57  0.30
## 11  -0.88 -1.35  1.83 -1.38  0.28  0.08  0.51 -0.52  0.43
## 12   0.92  1.41 -1.34  0.60  0.12  0.57  0.57 -1.13  0.63
## 13  -0.24  0.25 -0.19  0.61 -2.19  1.61 -0.49 -1.09 -0.63
## 14  -1.32 -0.38  1.73  0.04 -1.37 -0.51  0.10  0.65 -0.05
## 15   1.84 -0.29  0.57  0.29  1.08  0.43 -0.21  0.27  0.32
## 16   0.69 -2.70 -0.83 -0.01 -0.08 -1.06  0.02  0.14  0.20
## 17   1.04  0.45 -0.63  0.50  0.31  0.52  0.94  0.61  0.12
## 18  -0.91  0.06  1.18  1.48 -1.31  1.58  0.28  1.16  0.03
## 19  -1.66  0.72 -0.74 -2.07 -1.05 -0.19 -0.27  0.38  0.33
## 20  -0.70  0.23 -0.57 -0.99 -1.25 -0.31  0.93 -0.87 -0.01
## 21   2.56  1.28 -0.60 -0.26 -0.47 -1.17  1.54  0.61 -0.63
## 22  -0.28  0.27  0.13 -1.18  0.92 -0.31 -0.72  0.59 -1.06
## 23   0.68 -0.59 -1.73  1.23  0.13  1.37  0.41 -0.03 -0.33
## 24   0.43  0.80  1.79  1.19 -0.77 -1.32  0.27 -0.05  0.56
## 25   0.61 -0.70  1.29  0.93 -0.25 -0.66 -0.18 -0.29 -0.39
## 26   2.92 -0.55 -0.47 -0.47  0.15 -0.83 -0.75 -0.23 -0.15
## 27   2.15 -1.80 -0.93  0.19 -0.11  0.10 -0.05  0.95 -0.38
## 28   0.64  0.55 -0.39 -0.99  0.36  0.24  0.05 -0.17  0.05
## 29  -1.50  0.37 -0.33 -0.03 -0.52 -0.12 -0.61  0.33  0.52

```

Model fitting

We're gonna fit various capture-recapture models to the petrel data. We use [RMark](#) because everything can be done in R, and it's cool for reproducible research. But other pieces of software could be used too, like e.g. E-SURGE.

Before fitting capture-recapture models to the data, we check whether the standard Cormack-Jolly-Seber model is fitting the data well. We use the R package R2ucare.

```
library(R2ucare)
geese = read_inp("females_petrel.inp")
petrel.ch = geese$encounter_histories
freq = geese$sample_size
test3sr(petrel.ch, freq)

## $test3sr
##      stat      df    p_val sign_test
##    29.095  27.000    0.356    0.903
##
## $details
##   component  stat p_val signed_test test_perf
## 1           2 0.001 0.975     -0.032 Chi-square
## 2           3 0.249 0.618     -0.499 Fisher
## 3           4 0.213 0.644      0.462 Chi-square
## 4           5 0       1          0 Fisher
## 5           6 4.174 0.041     -2.043 Chi-square
## 6           7 0       1          0 Fisher
## 7           8 0       1          0 Fisher
## 8           9 0       0          0 None
## 9          10 1.13  0.288     -1.063 Chi-square
## 10         11 0       1          0 Fisher
## 11         12 1.766 0.184     -1.329 Fisher
## 12         13 1.19  0.275      1.091 Fisher
## 13         14 0       1          0 Fisher
## 14         15 1.224 0.269      1.106 Fisher
## 15         16 2.696 0.101     -1.642 Chi-square
## 16         17 0       1          0 Fisher
## 17         18 0       1          0 Fisher
## 18         19 3.695 0.055      1.922 Fisher
## 19         20 0       1          0 Fisher
## 20         21 1.885 0.17       1.373 Fisher
## 21         22 0.296 0.586      0.544 Fisher
## 22         23 0       0.984      0 Chi-square
## 23         24 0       1          0 Fisher
## 24         25 6.514 0.011      2.552 Fisher
## 25         26 0.749 0.387      0.865 Chi-square
## 26         27 0.102 0.749     -0.319 Chi-square
## 27         28 0       1          0 Fisher
## 28         29 3.211 0.073      1.792 Fisher
```

```

test3sm(petrel.ch, freq)

## $test3sm
##   stat      df  p_val
## 39.260 31.000  0.147
##
## $details
##   component   stat df p_val test_perf
## 1           2 0.756 1 0.384 Chi-square
## 2           3 4.883 1 0.027 Chi-square
## 3           4 0.172 2 0.918 Chi-square
## 4           5 0       1 1     Fisher
## 5           6 1.022 1 0.312 Chi-square
## 6           7 0.748 1 0.387 Chi-square
## 7           8 0       1 1     Fisher
## 8           9 0.294 1 0.588 Fisher
## 9          10 0.939 1 0.333 Chi-square
## 10         11 2.88  3 0.411 Chi-square
## 11         12 1.709 1 0.191 Chi-square
## 12         13 0.19  1 0.663 Chi-square
## 13         14 0       1 1     Fisher
## 14         15 5.705 1 0.017 Fisher
## 15         16 14.009 2 0.001 Chi-square
## 16         17 0.309 1 0.578 Chi-square
## 17         18 0.305 1 0.581 Chi-square
## 18         19 0       1 1     Fisher
## 19         20 1.337 1 0.248 Chi-square
## 20         21 0.547 1 0.46  Chi-square
## 21         22 0       1 1     Fisher
## 22         23 0       1 1     Fisher
## 23         24 1.867 1 0.172 Chi-square
## 24         25 0.657 1 0.417 Fisher
## 25         26 0.456 1 0.5  Chi-square
## 26         27 0.212 1 0.645 Chi-square
## 27         28 0.263 1 0.608 Fisher
## 28         29 0       0 0     None

test2ct(petrel.ch, freq)

## $test2ct
##   stat      df  p_val sign_test
## 103.115 27.000 0.000 -8.441
##
## $details
##   component dof   stat p_val signed_test test_perf
## 1           2 1 0.013 0.908      0.114 Chi-square
## 2           3 1 8.1 0.004     -2.846 Fisher
## 3           4 1 2.599 0.107     -1.612 Chi-square
## 4           5 1 1.207 0.272     -1.099 Chi-square
## 5           6 1 1.162 0.281     -1.078 Chi-square
## 6           7 1 0.499 0.48      -0.706 Chi-square

```

```

## 7      8   1  0.958 0.328      -0.979 Chi-square
## 8      9   1  0.977 0.323      -0.988 Chi-square
## 9     10   1  6.397 0.011      -2.529 Chi-square
## 10    11   1  2.674 0.102      -1.635 Chi-square
## 11    12   1  8.56  0.003      -2.926 Chi-square
## 12    13   1  0.056 0.814      -0.237 Chi-square
## 13    14   1  0.015 0.903       0.122 Chi-square
## 14    15   1  5.736 0.017      -2.395 Chi-square
## 15    16   1  5.291 0.021      -2.3   Chi-square
## 16    17   1  2.057 0.152      -1.434 Chi-square
## 17    18   1 10.988 0.001      -3.315 Chi-square
## 18    19   1  7.809 0.005      -2.794 Chi-square
## 19    20   1  0.149 0.699      -0.386 Chi-square
## 20    21   1  5.228 0.022      -2.286 Chi-square
## 21    22   1  9.259 0.002      -3.043 Chi-square
## 22    23   1  3.826  0.05      -1.956 Chi-square
## 23    24   1  9.147 0.002      -3.024 Chi-square
## 24    25   1      0   1          0   Chi-square
## 25    26   1  6.442 0.011      -2.538 Chi-square
## 26    27   1      0  0.984      0   Chi-square
## 27    28   1  3.966 0.046      -1.991 Chi-square

test2cl(petrel.ch, freq)

## $test2cl
##   stat      df  p_val
## 49.741 42.000  0.192
##
## $details
##   component dof  stat p_val test_perf
## 1            2   1      0   1 Fisher
## 2            3   1 1.077 0.299 Fisher
## 3            4   1  1.42 0.233 Chi-square
## 4            5   1 0.033 0.855 Chi-square
## 5            6   3 0.246  0.97 Chi-square
## 6            7   3 0.955 0.812 Chi-square
## 7            8   2 0.906 0.636 Chi-square
## 8            9   1 0.101  0.75 Chi-square
## 9           10   1 0.808 0.369 Chi-square
## 10          11   3 8.064 0.045 Chi-square
## 11          12   2 0.545 0.761 Chi-square
## 12          13   2 0.973 0.615 Chi-square
## 13          14   1 1.709 0.191 Chi-square
## 14          15   2 1.416 0.493 Chi-square
## 15          16   3 7.218 0.065 Chi-square
## 16          17   3  9.25 0.026 Chi-square
## 17          18   2 3.995 0.136 Chi-square
## 18          19   2 4.387 0.112 Chi-square
## 19          20   1 0.402 0.526 Chi-square
## 20          21   1 0.545  0.46 Chi-square

```

```

## 21      22   1 0.683 0.408 Chi-square
## 22      23   1 1.155 0.283 Chi-square
## 23      24   1 2.093 0.148 Fisher
## 24      25   1 0.229 0.633 Chi-square
## 25      26   1 1.319 0.251 Chi-square
## 26      27   1 0.212 0.645 Chi-square

overall_CJS(petrel.ch, freq)

##                               chi2 degree_of_freedom p_value
## Gof test for CJS model: 221.211                 127       0

```

It sounds like there is a strong trap-dependence effect. Let's deal with it and create an individual time-varying covariate for trap-dependence (see appendix C of the Gentle introduction to Mark):

```

# Let's read in the data:
library(RMark)

## This is RMark 2.2.0

petrel=convert.inp("females_petrel")
petrel.ch <- unlist(strsplit(petrel$ch, ""))
nocc <- nchar(petrel$ch[1])
petrel.td <- matrix(as.numeric(petrel.ch), ncol = nocc, byrow = TRUE)
petrel.td <- petrel.td[, 1:(nocc - 1)]
petrel.td <- as.data.frame(petrel.td)
begin.time <- 1974
names(petrel.td) <- paste('td', (begin.time + 1):(begin.time + nocc - 1), sep =
= ""))
#head(petrel.td) # dim 430 x 29
dim(petrel.td)

## [1] 430  29

petrel <- cbind(petrel, petrel.td)
#head(petrel)

```

Now process the data:

```
petrel.processed=process.data(petrel, model="CJS", begin.time=1974)
```

Create the default design matrix:

```

design.p=list(time.varying=c('td')) #td
design.parameters <- list(p=design.p)
petrel.ddl <- make.design.data(petrel.processed,parameters=design.parameters)

```

Standardize the covariates:

```

# standardize
moy = apply(cov,2,mean)
prec = apply(cov,2,sd)

```

```

moymat = matrix(rep(moy,nrow(cov)),ncol=ncol(cov),byrow=T)
precmat = matrix(rep(prec,nrow(cov)),ncol=ncol(cov),byrow=T)
covstar = (cov - moymat)/precmat
#apply(covstar,2,mean)
#apply(covstar,2,sd)
cov = covstar

```

Add raw covariates to the design matrix:

```

petrel.ddl$Phi$x1=0
petrel.ddl$Phi$x2=0
petrel.ddl$Phi$x3=0
petrel.ddl$Phi$x4=0
petrel.ddl$Phi$x5=0
petrel.ddl$Phi$x6=0
petrel.ddl$Phi$x7=0
petrel.ddl$Phi$x8=0
petrel.ddl$Phi$x9=0
ind=1
for (i in 1974:2002){
  petrel.ddl$Phi$x1[petrel.ddl$Phi$time==i]=cov[ind,1]
  petrel.ddl$Phi$x2[petrel.ddl$Phi$time==i]=cov[ind,2]
  petrel.ddl$Phi$x3[petrel.ddl$Phi$time==i]=cov[ind,3]
  petrel.ddl$Phi$x4[petrel.ddl$Phi$time==i]=cov[ind,4]
  petrel.ddl$Phi$x5[petrel.ddl$Phi$time==i]=cov[ind,5]
  petrel.ddl$Phi$x6[petrel.ddl$Phi$time==i]=cov[ind,6]
  petrel.ddl$Phi$x7[petrel.ddl$Phi$time==i]=cov[ind,7]
  petrel.ddl$Phi$x8[petrel.ddl$Phi$time==i]=cov[ind,8]
  petrel.ddl$Phi$x9[petrel.ddl$Phi$time==i]=cov[ind,9]
  ind=ind+1
}

```

Specify the effects on survival and detection probabilities:

```

# for survival probabilities
Phidot=list(formula=~1) # constant
Phitime=list(formula=~time) # time
PhiCov=list(formula=~x1+x2+x3+x4+x5+x6+x7+x8+x9) # all covariates
# Define range of models for detection probabilities
pdot=list(formula=~td) # constant, with trap-dependence
ptime=list(formula=~time+td) # additive effect of time and trap-dependence
(no interaction because of severe identifiability issues Gimenez et al. 2003)

```

Fit models:

```

# phi,p
phip =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phidot,p=pdot),output = FALSE,delete=T)
# phit,p
phitp =

```

```

mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phitime,p=dot),output = FALSE,delete=T)
# phi,pt
phipt =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phidot,p=ptime),output = FALSE,delete=T)
# phit,pt
phiptp =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phitime,p=ptime),output = FALSE,delete=T)

```

Compare models

```
collect.models()
```

	model	npar	AICc	DeltaAICc	weight	Deviance
## 4	Phi(~time)p(~time + td)	59	6535.213	0.00000	1.000000e+00	6414.843
## 2	Phi(~1)p(~time + td)	31	6580.016	44.80257	1.867433e-10	6517.358
## 3	Phi(~time)p(~td)	31	7035.196	499.98207	0.000000e+00	6972.538
## 1	Phi(~1)p(~td)	3	7141.081	605.86732	0.000000e+00	7135.073

Clearly, there is time variation in the detection process. Also, it's worth investigating further time variation in survival.

Now, let's fit a model with all covariates:

```

phixpt =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=PhiCov,p=ptime),output = FALSE,delete=T)

```

And have a look to the parameter estimates:

```
phixpt$results$beta
```

	estimate	se	lcl	ucl
## Phi:(Intercept)	3.0215060	0.1266494	2.7732732	3.2697387
## Phi:x1	-0.0214620	0.1238117	-0.2641330	0.2212090
## Phi:x2	0.5045047	0.2437983	0.0266601	0.9823493
## Phi:x3	-0.5050284	0.2135734	-0.9236323	-0.0864245
## Phi:x4	-0.1875423	0.1633858	-0.5077786	0.1326939
## Phi:x5	-0.3384231	0.1285901	-0.5904597	-0.0863865
## Phi:x6	0.0366714	0.1194053	-0.1973630	0.2707058
## Phi:x7	0.4200922	0.2218835	-0.0147995	0.8549838
## Phi:x8	-0.5388505	0.1450639	-0.8231758	-0.2545252
## Phi:x9	-0.1858380	0.1744092	-0.5276800	0.1560040
## p:(Intercept)	-0.2762016	0.3517732	-0.9656772	0.4132739
## p:time1976	1.4053160	0.5014804	0.4224145	2.3882176
## p:time1977	1.1939140	0.4353712	0.3405864	2.0472416
## p:time1978	-1.3620914	0.3973730	-2.1409425	-0.5832403
## p:time1979	0.8851054	0.4070028	0.0873800	1.6828308
## p:time1980	-1.3972451	0.4108840	-2.2025777	-0.5919125
## p:time1981	-0.8393193	0.4093394	-1.6416245	-0.0370140

```

## p:time1982      -1.4862613 0.4314627 -2.3319283 -0.6405944
## p:time1983      1.0600652 0.4127852  0.2510062  1.8691243
## p:time1984      0.4538497 0.3939467 -0.3182859  1.2259853
## p:time1985      -1.0119075 0.3845536 -1.7656325 -0.2581824
## p:time1986      0.0048380 0.3854982 -0.7507385  0.7604144
## p:time1987      -1.0459663 0.3889723 -1.8083521 -0.2835805
## p:time1988      0.5125816 0.3873434 -0.2466114  1.2717746
## p:time1989      1.1524630 0.4016116  0.3653043  1.9396217
## p:time1990      -0.3716715 0.3782079 -1.1129590  0.3696161
## p:time1991      0.6520627 0.3844183 -0.1013973  1.4055227
## p:time1992      0.6618918 0.3825929 -0.0879902  1.4117739
## p:time1993      0.6817241 0.3839534 -0.0708246  1.4342728
## p:time1994      0.0532029 0.3753291 -0.6824423  0.7888480
## p:time1995      0.7756565 0.3815531  0.0278125  1.5235005
## p:time1996      1.6025804 0.4091014  0.8007416  2.4044192
## p:time1997      1.4893106 0.4097755  0.6861506  2.2924706
## p:time1998      0.4982627 0.3783074 -0.2432197  1.2397452
## p:time1999      1.4753226 0.4081407  0.6753668  2.2752784
## p:time2000      0.5117819 0.3840192 -0.2408957  1.2644595
## p:time2001      -0.1193226 0.3820433 -0.8681275  0.6294823
## p:time2002      -0.0079864 0.3829045 -0.7584793  0.7425064
## p:time2003      0.2303222 0.3862746 -0.5267761  0.9874204
## p:td            0.7281693 0.0827992  0.5658830  0.8904557

```

The covariates are in that order: SIE.Su (x1), SIE.Au (x2), SIE.Wi (x3), SIE.Sp (x4), SOI (x5), T.Su (x6), T.au (x7), T.wi (x8) and T.sp (x9). Remember, from our preliminary exploration step above, we know that covariates 2 and 3 are highly positively correlated. However by inspecting the estimates here, these covariates seem to have an opposite effect on survival!

P2CR analysis

In this section, we show how to perform a P2CR analysis. First, we amend the design matrix we built before, and add the coordinates of the raw covariates on the principal components:

```

petrel.ddl$Phi$pc1=0
petrel.ddl$Phi$pc2=0
petrel.ddl$Phi$pc3=0
petrel.ddl$Phi$pc4=0
petrel.ddl$Phi$pc5=0
petrel.ddl$Phi$pc6=0
petrel.ddl$Phi$pc7=0
petrel.ddl$Phi$pc8=0
petrel.ddl$Phi$pc9=0
ind=1
for (i in 1974:2002){
  petrel.ddl$Phi$pc1[petrel.ddl$Phi$time==i]=pcs[ind,1]
  petrel.ddl$Phi$pc2[petrel.ddl$Phi$time==i]=pcs[ind,2]
  petrel.ddl$Phi$pc3[petrel.ddl$Phi$time==i]=pcs[ind,3]
  petrel.ddl$Phi$pc4[petrel.ddl$Phi$time==i]=pcs[ind,4]
  petrel.ddl$Phi$pc5[petrel.ddl$Phi$time==i]=pcs[ind,5]
}

```

```

petrel.ddl$Phi$pc6[petrel.ddl$Phi$time==i]=pcs[ind,6]
petrel.ddl$Phi$pc7[petrel.ddl$Phi$time==i]=pcs[ind,7]
petrel.ddl$Phi$pc8[petrel.ddl$Phi$time==i]=pcs[ind,8]
petrel.ddl$Phi$pc9[petrel.ddl$Phi$time==i]=pcs[ind,9]
ind=ind+1
}

```

In the first step of the P2CR analysis, we consider each PC separately:

```

Phipc1=list(formula=~pc1)
Phipc2=list(formula=~pc2)
Phipc3=list(formula=~pc3)
Phipc4=list(formula=~pc4)
Phipc5=list(formula=~pc5)
Phipc6=list(formula=~pc6)
Phipc7=list(formula=~pc7)
Phipc8=list(formula=~pc8)
Phipc9=list(formula=~pc9)
phipc1 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc1,p=pftime),ou
tput = FALSE,delete=T)
phipc2 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc2,p=pftime),ou
tput = FALSE,delete=T)
phipc3 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc3,p=pftime),ou
tput = FALSE,delete=T)
phipc4 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc4,p=pftime),ou
tput = FALSE,delete=T)
phipc5 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc5,p=pftime),ou
tput = FALSE,delete=T)
phipc6 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc6,p=pftime),ou
tput = FALSE,delete=T)
phipc7 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc7,p=pftime),ou
tput = FALSE,delete=T)
phipc8 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc8,p=pftime),ou
tput = FALSE,delete=T)
phipc9 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc9,p=pftime),ou
tput = FALSE,delete=T)

```

We now use ANODEV to test the significance of these PCs:

```

# get info on model with time-dependent survival
devtime = phiptpt$results$lnl
npartime = phiptpt$results$npar

```

```

# get info on model with constant survival
devct = phipt$results$lnl
nparct = phipt$results$npar

# test each PC:
stat = rep(NA,9)
df1 = rep(NA,9)
df2 = rep(NA,9)
for (i in 1:9){
  name = paste('phipc',i,sep="")
  devco = get(name)$results$lnl
  nparco = get(name)$results$npar
  num = (devct - devco)/(nparco-nparct)
  den = (devco - devtime)/(npartime-nparco)
  stat[i] <- num/den
  df1[i] <- nparco-nparct
  df2[i] <- npartime-nparco
}
# calculate p-value
pval = 1-pf(stat,df1,df2)
stat

## [1] 0.4561618 2.0348053 7.3439558 3.0089184 3.0594652 2.4351876 0.1359247
## [8] 0.3111153 0.7808127

df1

## [1] 1 1 1 1 1 1 1 1 1

df2

## [1] 27 27 27 27 27 27 27 27 27

pval

## [1] 0.50516694 0.16519557 0.01154684 0.09421181 0.09162924 0.13028569
## [7] 0.71524166 0.58159232 0.38469346

```

We can reject the null hypothesis that PC3 has no effect on survival.

In step 2 of the P2CR, we keep PC3 and test the significance of the other PCs:

```

Phipc1=list(formula=~pc1+pc3)
Phipc2=list(formula=~pc2+pc3)
Phipc3=list(formula=~pc4+pc3)
Phipc4=list(formula=~pc5+pc3)
Phipc5=list(formula=~pc6+pc3)
Phipc6=list(formula=~pc7+pc3)
Phipc7=list(formula=~pc8+pc3)
Phipc8=list(formula=~pc9+pc3)
phipc11 =

```

```

mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc1,p=pftime),ou
tput = FALSE,delete=T)
phipc21 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc2,p=pftime),ou
tput = FALSE,delete=T)
phipc31 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc3,p=pftime),ou
tput = FALSE,delete=T)
phipc41 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc4,p=pftime),ou
tput = FALSE,delete=T)
phipc51 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc5,p=pftime),ou
tput = FALSE,delete=T)
phipc61 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc6,p=pftime),ou
tput = FALSE,delete=T)
phipc71 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc7,p=pftime),ou
tput = FALSE,delete=T)
phipc81 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc8,p=pftime),ou
tput = FALSE,delete=T)

stat = rep(NA,8)
df1 = rep(NA,8)
df2 = rep(NA,8)
for (i in 1:8){
  name = paste('phipc',3,sep="")
  devct = get(name)$results$lnl
  nparct = get(name)$results$npar
  namex = paste('phipc',paste(i,'1',sep=""),sep="")
  devco = get(namex)$results$lnl
  nparco = get(namex)$results$npar
  num = (devct - devco)/(nparco-nparct)
  den = (devco - devtime)/(npartime-nparco)
  stat[i] <- num/den
  df1[i] <- nparco-nparct
  df2[i] <- npartime-nparco
}

pval = 1-pf(stat,df1,df2)
stat

## [1] 0.115032061 2.935263243 4.629627302 2.517956493 3.502807470
0.275952354
## [7] 0.006486012 0.723243675

df1

```

```

## [1] 1 1 1 1 1 1 1 1 1
df2

## [1] 26 26 26 26 26 26 26 26 26
pval

## [1] 0.73721058 0.09856598 0.04088835 0.12464492 0.07255722 0.60381802
## [7] 0.93642787 0.40284611

```

Now PC4 is significant according the ANODEV (remember that PC3 was removed from the list).

In step 3 of the P2CR analysis, we reiterate the process, that is we test the significance of the other PCs in presence of PC3 and PC4:

```

Phipc1=list(formula=~pc1+pc3+pc4)
Phipc2=list(formula=~pc2+pc3+pc4)
Phipc3=list(formula=~pc5+pc3+pc4)
Phipc4=list(formula=~pc6+pc3+pc4)
Phipc5=list(formula=~pc7+pc3+pc4)
Phipc6=list(formula=~pc8+pc3+pc4)
Phipc7=list(formula=~pc9+pc3+pc4)
phipc12 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc1,p=pftime),ou
tput = FALSE,delete=T)
phipc22 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc2,p=pftime),ou
tput = FALSE,delete=T)
phipc32 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc3,p=pftime),ou
tput = FALSE,delete=T)
phipc42 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc4,p=pftime),ou
tput = FALSE,delete=T)
phipc52 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc5,p=pftime),ou
tput = FALSE,delete=T)
phipc62 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc6,p=pftime),ou
tput = FALSE,delete=T)
phipc72 =
mark(petrel.processed,petrel.ddl,model.parameters=list(Phi=Phipc7,p=pftime),ou
tput = FALSE,delete=T)

```

What does the ANODEV tell us?

```

stat = rep(NA,7)
df1 = rep(NA,7)
df2 = rep(NA,7)
for (i in 1:7){

```

```

name = paste('phipc',31,sep="")
devct = get(name)$results$lnl
nparct = get(name)$results$npar
namex = paste('phipc',paste(i,'2',sep=""),sep="")
devco = get(namex)$results$lnl
nparco = get(namex)$results$npar
num = (devct - devco)/(nparco-nparct)
den = (devco - devtime)/(npartime-nparco)
stat[i] <- num/den
df1[i] <- nparco-nparct
df2[i] <- npartime-nparco

}

pval = 1-pf(stat,df1,df2)
stat

## [1] 0.074403780 1.878326793 1.383423294 0.547418815 0.235266864
0.002265893
## [7] 1.282105461

df1

## [1] 1 1 1 1 1 1 1

df2

## [1] 25 25 25 25 25 25 25

pval

## [1] 0.7872701 0.1827058 0.2505979 0.4662660 0.6318690 0.9624122 0.2682518

```

No more significant PC, the algorithm stops here.

Post-process results

We will make two plots, one with time-varying survival estimates, and another one to illustrate the relationship between survival and the selected PCs.

First, a figure displaying the time variation in survival according to a model with all raw covariates and the PC2R model:

```

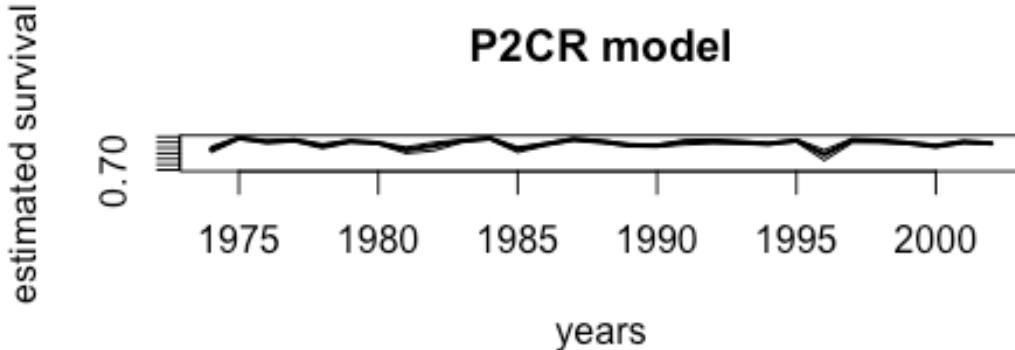
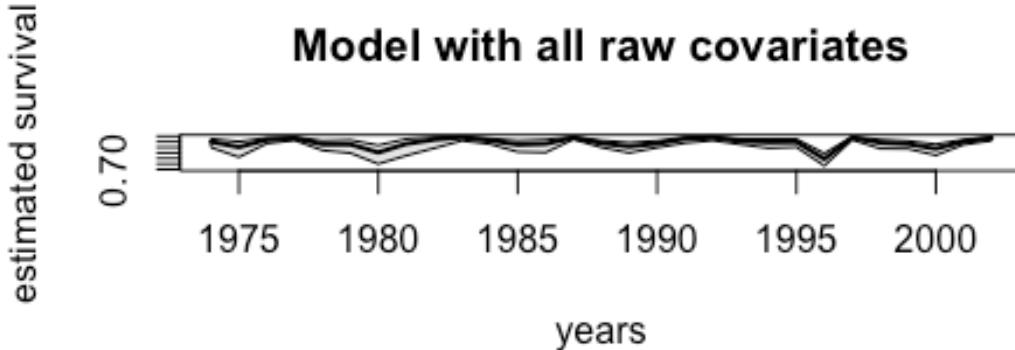
#phit_mle <- phitpt$results$real[1:29,]
phicov_mle <- phixpt$results$real[1:29,]
phipca_mle <- phipc31$results$real[1:29,]
# Make a 6x6 inch image at 300dpi
#ppi <- 300
#png("time_survival_allcov.png", width=6*ppi, height=6*ppi, res=ppi)
par(mfrow=c(2,1))
plot(1974:2002,phicov_mle[,1],lwd=2,col='black',type='n',ylim=c(0.7,1),xlab='years',ylab='estimated survival',main='Model with all raw covariates')

```

```

polygon(x=c(1974:2002, rev(1974:2002)),y=c(phicov_mle[,3],
rev(phicov_mle[,4])),col='grey90')
lines(1974:2002,phicov_mle[,1],lwd=2,col='black')
#dev.off()
#png("time_survival_p2cr.png", width=6*ppi, height=6*ppi, res=ppi)
plot(1974:2002,phipca_mle[,1],lwd=2,col='black',type='n',ylim=c(0.7,1),xlab='
years',ylab='estimated survival',main='P2CR model')
polygon(x=c(1974:2002, rev(1974:2002)),y=c(phipca_mle[,3],
rev(phipca_mle[,4])),col='grey90')
lines(1974:2002,phipca_mle[,1],lwd=2,col='black')

```



```
#dev.off()
```

Second, a figure displaying the relationship between survival and the PCs selected by the P2CR analysis.

Get the coefficient estimates for each PC and the intercept:

```

phipc31$results$beta[1:3,]

##                   estimate          se          lcl          ucl
## Phi:(Intercept) 2.9065522 0.0930351  2.7242034  3.0889011
## Phi:pc4         -0.3179564 0.0937600 -0.5017259 -0.1341868
## Phi:pc3         0.4987761 0.1117003  0.2798436  0.7177086

```

Get estimates of recapture probabilities:

```
# recapture given no recapture before
lp1=phipc31$results$beta$estimate[4] + phipc31$results$beta$estimate[5:32]
p1 = 1/(1+exp(-lp1))
p1

## [1] 0.6849746 0.6950760 0.1598929 0.6532750 0.1491627 0.2186214 0.1380855
## [8] 0.6799233 0.5559293 0.2101191 0.4365717 0.2081893 0.5650886 0.7013967
## [15] 0.3322997 0.5843022 0.5899870 0.6135584 0.4454385 0.6270107 0.7892102
## [22] 0.7614159 0.5662430 0.7626795 0.5415127 0.3768231 0.4066767 0.4896963

# recapture given recapture before
lp2=phipc31$results$beta$estimate[4]+phipc31$results$beta$estimate[5:32]+phip
c31$results$beta$estimate[33]
p2 = 1/(1+exp(-lp2))
p2

## [1] 0.8225429 0.8293322 0.2886228 0.8006576 0.2720513 0.3736066 0.2545787
## [8] 0.8191149 0.7274257 0.3618683 0.6228953 0.3591785 0.7347356 0.8335364
## [15] 0.5147810 0.7497732 0.7541472 0.7719294 0.6313063 0.7818290 0.8886588
## [22] 0.8718483 0.7356503 0.8726249 0.7157297 0.5631334 0.5936855 0.6716644

# get min/max for p1 with SEs
ind.min = which.min(p1) # index min p1
ind.max = which.max(p1) # index max p1
varlp1 = phipc31$results$beta$se[4]^2 + phipc31$results$beta$se[5:32]^2 # var
of p1 on logit scale
lp1mi = lp1[ind.min]
varlp1mi = varlp1[ind.min]
library(msm)
sep1mi = deltaMethod(~ 1/(1+exp(-x1)), lp1mi, varlp1mi)
min(p1)

## [1] 0.1380855

sep1mi

## [1] 0.06613978

lp1ma = lp1[ind.max]
varlp1ma = varlp1[ind.max]
sep1ma = deltaMethod(~ 1/(1+exp(-x1)), lp1ma, varlp1ma)
max(p1)

## [1] 0.7892102

sep1ma

## [1] 0.08957517

# get min/max for p2 with SEs
ind.min = which.min(p2) # index min p2
```

```

ind.max = which.max(p2) # index max p2
varlp2 = phipc31$results$beta$se[4]^2 + phipc31$results$beta$se[5:32]^2 +
phipc31$results$beta$estimate[33]^2# var of p2 on logit scale
lp2mi = lp2[ind.min]
varlp2mi = varlp2[ind.min]
sep2mi = deltamethod(~ 1/(1+exp(-x1)), lp2mi, varlp2mi)
min(p2)

## [1] 0.2545787

sep2mi

## [1] 0.1781984

lp2ma = lp2[ind.max]
varlp2ma = varlp2[ind.max]
sep2ma = deltamethod(~ 1/(1+exp(-x1)), lp2ma, varlp2ma)
max(p2)

## [1] 0.8886588

sep2ma

## [1] 0.0919113

```

Get confidence intervals using the delta-method:

```

library(msm)
PC3 = pcs[,3]
PC4 = pcs[,4]
phi_SE3 = matrix(0, nrow = 29, ncol = 1)
estmean3 <- c(2.9065503,0.4987728)
estvar3 <- diag(c(0.0930351,0.1117004)^2)
phi_SE4 = matrix(0, nrow = 29, ncol = 1)
estmean4 <- c(2.9065503,-0.3179579)
estvar4 <- diag(c(0.0930351,0.0937603)^2)
for (i in 1:29){
  temp3 <- PC3[i]
  temp4 <- PC4[i]
  phi_SE3[i,] <- deltamethod(~ x1+x2*temp3, estmean3, estvar3)
  phi_SE4[i,] <- deltamethod(~ x1+x2*temp4, estmean4, estvar4)
}

ilogitphi3 <- estmean3[1] + estmean3[2] * PC3
ilogitphi3lb <- ilogitphi3 - 1.96 * as.vector(phi_SE3)
ilogitphi3ub <- ilogitphi3 + 1.96 * as.vector(phi_SE3)
phi3lb <- 1/(1+exp(-(ilogitphi3lb)))
phi3ub <- 1/(1+exp(-(ilogitphi3ub)))
phi3 <- 1/(1+exp(-(ilogitphi3)))

ilogitphi4 <- estmean4[1] + estmean4[2] * PC4
ilogitphi4lb <- ilogitphi4 - 1.96 * as.vector(phi_SE4)

```

```

ilogitphi4ub <- ilogitphi4 + 1.96 * as.vector(phi_SE4)
phi4lb <- 1/(1+exp(-(ilogitphi4lb)))
phi4ub <- 1/(1+exp(-(ilogitphi4ub)))
phi4 <- 1/(1+exp(-(ilogitphi4)))

```

Before plotting the survival as a function of the PC values, we need to find out about the raw covariates that were used to build these PCs:

```

dimdesc(res.pca,axes = c(3:4))

## $Dim.3
## $Dim.3$quanti
##           correlation      p.value
## SIE.Su    0.7413696 4.205825e-06
## T.wi     -0.5808892 9.527347e-04
##
## 
## $Dim.4
## $Dim.4$quanti
##           correlation      p.value
## T.sp      0.8228262 4.300265e-08
## SIE.Su   -0.3946619 3.411627e-02

```

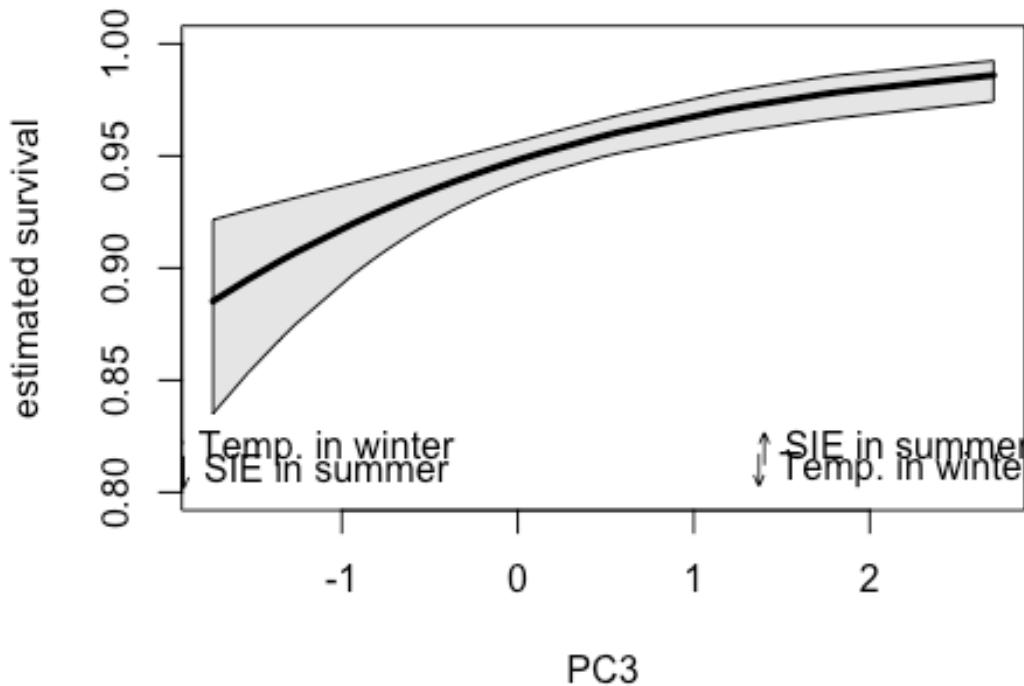
High (resp. low) values of PC3 mean high (resp. low) values of SIE in summer and low (resp. high) values of temperature in winter. High (resp. low) values of PC4 mean high (resp. low) values of temperature in spring and low (resp. high) values of SIE in summer.

Now we can plot the survival - PC relationships, and add the interpretation of the PCs:

```

# Make a 6x6 inch image at 300dpi
#ppi <- 300
#png("pc3_survival.png", width=6*ppi, height=6*ppi, res=ppi)
ord<-order(PC3)
plot(PC3[ord],phi3[ord],lwd=3,col='black',type='n',xlab='PC3',ylab='estimated
survival',main='',ylim=c(0.8,1))
polygon(x=c(PC3[ord], rev(PC3[ord])),y=c(phi3lb[ord],
rev(phi3ub[ord])),col='grey90')
lines(PC3[ord],phi3[ord],lwd=3,col='black')
text(-1.2,0.82,expression('' %up% 'Temp. in winter'),cex=1)
text(-1.2,0.81,expression('' %down% 'SIE in summer'),cex=1)
text(2.1,0.82,expression('' %up% 'SIE in summer'),cex=1)
text(2.1,0.81,expression('' %down% 'Temp. in winter'),cex=1)

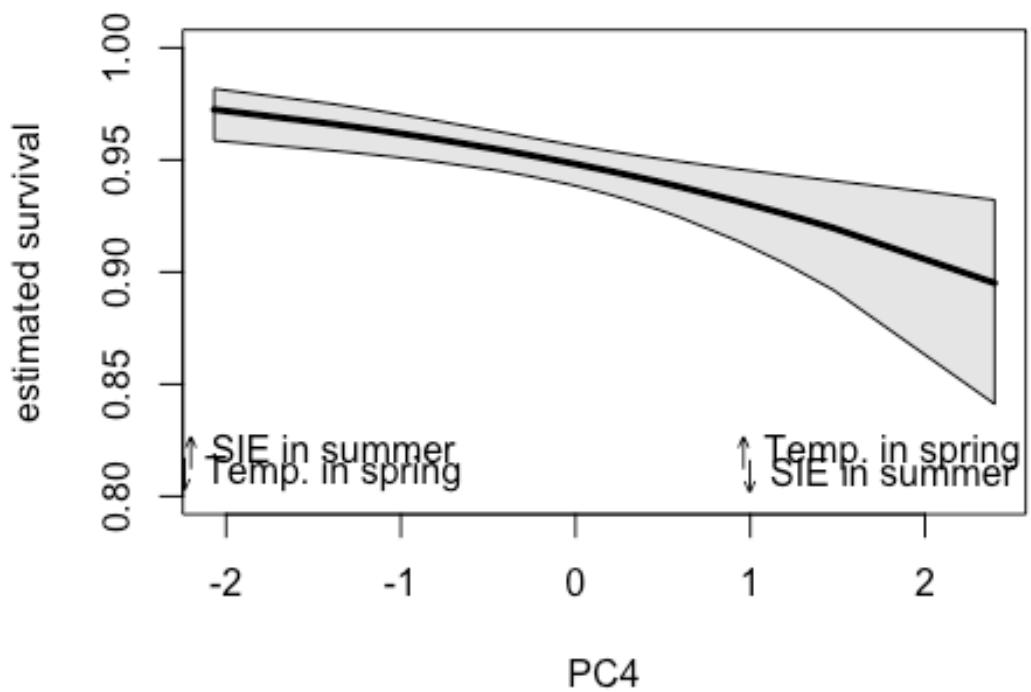
```



```

ord<-order(PC4)
#dev.off()
#png("pc4_survival.png", width=6*ppi, height=6*ppi, res=ppi)
plot(PC4[ord],phi4[ord],lwd=3,col='black',type='n',xlab='PC4',ylab='estimated
survival',main='',ylim=c(0.8,1))
polygon(x=c(PC4[ord], rev(PC4[ord])),y=c(phi4lb[ord],
rev(phi4ub[ord])),col='grey90')
lines(PC4[ord],phi4[ord],lwd=3,col='black')
text(-1.5,0.82,expression('' %up% 'SIE in summer'),cex=1)
text(-1.5,0.81,expression('' %down% 'Temp. in spring'),cex=1)
text(1.7,0.82,expression('' %up% 'Temp. in spring'),cex=1)
text(1.7,0.81,expression('' %down% 'SIE in summer'),cex=1)

```



#dev.off()