Migration ranks for bowhead whales (*Balaena mysticetus*) at Barrow in spring

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ABSTRACT

In a series of aerial photographic surveys of bowhead whales migrating past Barrow in Alaska in the spring, 40 individuals were captured in more than one year. To study individual-specific persistency in migratory pattern, the relative ranks of the captures of these whales among all captures that year were analysed. Controlling for body length and the presence of calves, the correlation of relative ranks in individuals captured multiple times was found not to be significantly different from zero (p-value=0.78).

KEYWORDS: BOWHEAD WHALE; MARK-RECAPTURE; MIGRATION; MODELLING; PHOTO-ID; SURVEY – AERIAL; BERING SEA; BEAUFORT SEA; CHUKCHI SEA; NORTHERN HEMISPHERE

INTRODUCTION

Bowhead whales in the Bering-Chukchi-Beaufort Seas migrate in the spring north and eastwards past Barrow, Alaska, but to what degree does an individual keep its temporal rank in the migration from year to year? This question is interesting from a behavioural point of view. Behaviour is of interest in itself, and is also of concern for abundance estimation and other studies. Schweder *et al.* (2009) used results from the present paper when estimating abundance and demographic parameters from aerial photographic surveys of bowhead whales.

The spring migration happens during or shortly after the mating season, so bowhead whales have an opportunity for genetic interchange across most of the population if there is little temporal stratification in the ranking of whales through the migration. The question above is therefore also of interest when investigating possible structure in the bowhead whale population in the Bering-Chukchi-Beaufort Seas.

The calendar time of the migratory season varies from year to year (Rugh *et al*., 2008). The calendar day of capture is therefore not directly useful, and the relative rank of a capture within the captures made in the respective year was used. Provided the surveys were timed similarly relative to the migratory season, the relative ranks are invariant to temporal shifts in the migratory season. Mothers with calves, and also most large whales without calves, are known to migrate relatively late (Angliss *et al*., 1995; Nerini *et al*., 1984; Rugh, 1990). This paper measures the effects on relative rank of these covariates, both within all captures and within the recaptures.

A mixed effects linear model was used with normally distributed individual effects, and with fixed effects for length, being associated with a calf and for differences in years between recapture and capture. The response variable is the logistic transform of the relative rank (rank divided by number of captures in the survey plus one).

METHODS

The data are summarised in Tables 1 and 2 and Figs 1 and 2. They were obtained through systematic aerial photographic surveys during the spring migration at Barrow, Alaska (Rugh *et al*., 2008). The length measurements were obtained from the photographic images when possible. When duplicate images have been obtained for a whale, the average value of lengths was considered as a length value for this whale. The mean measured length of the 1,782 captures in the subset where length is recorded is 12.03m and among the 40 recaptured individuals where length is recorded is 13.88m.

To investigate possible persistence over the years in relative rank within individuals, the ranks of the 40 individual whales that were photographically captured in more than one year were examined. The matching protocol was stringent to avoid false positive matches (Rugh *et al*., 1998; Schweder *et al*., 2009) and it was assumed that the recorded recaptures were real. There may have been, however, unrecognised recaptures because many bowhead whales were not marked uniquely enough to be consistently recognised in aerial photographs. The relative ranks at capture and recapture are shown in Fig. 2.

Among the 40 whales, 38 were seen in two years, and two whales were seen in three different years, making 42 recognised between-year recaptures. When length was recorded for both capture and recapture its mean was used for both captures. This was done to reduce the effect of measurement errors (9 of 28 whales had a smaller recorded

Table 1

Number of captures, number of whales that were re-captured later (First), number of whales captured for the second time (Second), number of captures where length of the individual is measured (Length) and where a calf is associated (Calf).

Year	Captures	First	Second[1]	Length	Calf
1984	21	1	0	0	0
1985	792	18	0	501	4
1986	552	12	7	236	26
1987	365	4	0	0	0
1989	482	3	11	188	22
1990	463	1	8	224	17
1991	426	2	5	243	16
1992	443	1	10	214	1
1994	250	0	1	176	0
Total	3,794	42	42	1,782	86

[1]Two individuals that were captured in three different years, and give two pairs of recaptures each.

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Table 2

Bowhead whales resighted during the spring migration past Point Barrow, Alaska. Whale numbers are as defined in the database. Date at capture (Sighting 1), date at recapture (Sighting 2), length at capture (Length 1) and length at recapture (Length 2) are given.

Whale no.	Sighting 1	Length 1	Sighting 2	Length 2
1058	18/05/1985	13.46	13/05/1986	12.88
1184	07/05/1987	N/A	23/04/1992	15.17
1880	08/05/1991	13.59	13/05/1992	N/A
1890	08/05/1984	N/A	23/04/1992	13.37
1921	02/05/1985	10.15	05/05/1990	10.55
1937	11/05/1985	13.23	27/04/1992	13.36
2024	14/05/1985	10.37	12/05/1986	N/A
2037	17/05/1985	14.97	29/05/1986	15.17
2200	22/05/1985	16.31	26/05/1991	16.16
2217	23/05/1985	14.63	10/05/1991	14.49
2246	26/05/1985	13.39	06/05/1989	14.05
2247	26/05/1985	13.38	17/05/1989	N/A
2291	27/05/1985	13.50	18/05/1989	N/A
2312	29/05/1985	14.59	19/05/1990	13.71
2347	31/05/1985	14.56	11/05/1986	14.67
2371	01/06/1985	15.05	26/05/1992	15.46
2374	01/06/1985	13.88	29/05/1986 [1]	14.29
2384	02/06/1985	12.97	15/05/1989	14.01
2392	02/06/1985	14.45	22/05/1986	13.97
2392	22/05/1986	13.97	18/05/1989 [2]	14.66
2403	02/06/1985	14.34	19/05/1986	13.98
2428	06/06/1985	16.70	27/05/1989	16.01
3963	11/05/1986	9.80	14/05/1992	11.26
4020	11/05/1986	13.33	06/05/1989	13.79
5149	09/05/1992	13.57	25/05/1994	14.45
7946	06/05/1986	12.99	03/05/1989	13.60
8002	11/05/1986	13.44	10/05/1991	14.17
8015	11/05/1986	13.51	02/06/1990 [1]	13.80
8026	11/05/1986	N/A	16/05/1992	13.71
8033	11/05/1986	14.60	19/05/1990	14.72
8090	14/05/1986	N/A	19/04/1989	12.84
8135	22/05/1986	13.65	21/04/1989	13.05
8142	22/05/1986	13.78	19/05/1990	13.34
8250	04/05/1987	N/A	11/05/1990	14.56
8288	08/05/1987	N/A	25/05/1991 [1]	16.03
8312	18/05/1987	N/A	11/05/1990	13.76
8622	19/05/1986	13.55	26/05/1989 [1]	13.94
8744	20/04/1989	12.61	13/05/1992	13.56
8824	25/04/1989	12.75	14/05/1992	14.57
9304	31/05/1989	N/A	29/05/1990	14.18
9304	29/05/1990	N/A	10/05/1991 [1, 2]	14.95
10573	11/05/1991	14.68	26/05/1992	15.26

[1]Accompanied by a calf. [2]Third resighting.

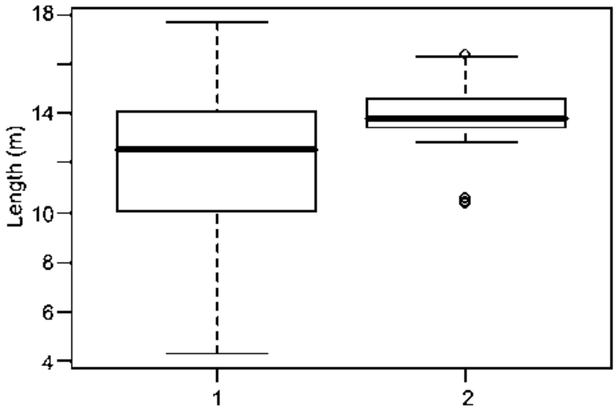

Fig. 1. Boxplot of length data for all captures (1) and for captures with recaptures (2).

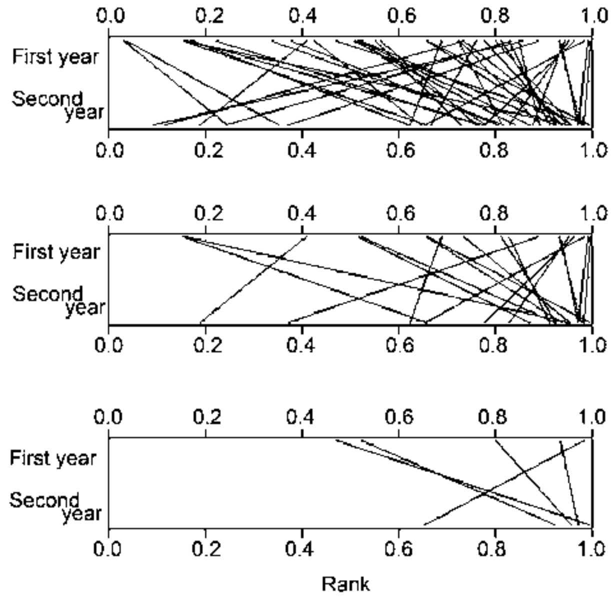

Fig. 2. The relative ranks at capture (first year) and recapture (second year) for all whales (top); for large whales (length more than average 13.88m) (middle); and for whales with calves (the whales were seen with calves only in the second year) (bottom).

length at recapture than at capture). When length for one capture or recapture was not recorded, the recorded capture or recapture length of that individual was imputed. Any bias introduced by this was small since bowhead whales grow slowly (Angliss *et al*., 1995; Koski *et al*., 2006), particularly after sexual maturity.

In addition to body length, an indicator covariate for being associated with a calf and also the difference in years between recapture and capture were used in a logistic mixed regression of the relative ranks of recaptures which is denoted 'time'. Large whales are known to be late migrants. The covariate time was introduced to see whether migration tends to be later the older the whale is when controlling for length.

Logistic mixed model

Years is denoted by y and recaptured whales by i. A logistic mixed model was considered with three whale-specific covariates denoted as 'calf', 'length' as explained above, and 'time'. The latter is zero at capture and the number of years from capture to recapture. Length was measured in meters, but with mean length for all length-measured individuals subtracted. The response of whale i in year y

$$\text{rank}_{iy} = \frac{r_{iy}}{n_y + 1}$$

where r_{iy} is the sequence number of the capture among the n_y captures that year.

For recaptured individuals the model is:

$$\ln\left(\frac{\text{rank}_{iy}}{1-\text{rank}_{iy}}\right) = \beta_0 + \beta_c \cdot \text{calf}_{iy} + \beta_l \cdot \text{length}_{iy} + \beta_t \cdot \text{time}_{iy} + \xi_i + \varepsilon_{iy}. \quad (1)$$

where β_0, β_c, β_l and β_t are regression coefficients, ξ_i is a whale-specific random variable that represents the degree of consistency with which whale i positions itself in the migration sequence in different years, and ε_{iy} is a residual term. The clusters, i.e. the data referring to individual whales, are assumed independent.

The random individual effects and the residual terms are assumed to be independent and normally distributed with mean zero, and with $\text{Var}(\xi_i) \equiv \sigma^2$ and $\text{Var}(\varepsilon_i) \equiv \theta^2$.

Dependence between any two responses, rank_{iy} and $\text{rank}_{i\hat{y}}$, for the same whale captured in years y and $\hat{y}$ respectively can be expressed by the correlation between the logistic transforms

$$\rho \equiv \mathrm{Cor}(\ln(\frac{\mathrm{rank}_{iy}}{1-\mathrm{rank}_{iy}}), \ln(\frac{\mathrm{rank}_{iy'}}{1-\mathrm{rank}_{iy'}})) = \frac{\sigma^2}{\theta^2+\sigma^2}. \quad (2)$$

Large individuals, and also mothers with calf, are known to be late migrants (Angliss *et al*., 1995; Koski *et al*., 2006; Nerini *et al*., 1984; Rugh, 1990). How much they delay their migration in terms of relative rank was measured by the logistic regression effects of the covariates calf and length on the relative migration rank for all the 1,782 captures for the subset of the data where length is measured. Here the fact that 42 of the captures were known recaptures was discarded, and model (1) was used, but with covariate time and random individual effect ξ_i excluded. The index i now runs over all the captures.

A quadratic version of the model was also fitted to the capture-recapture data,

$$\ln(\frac{\mathrm{rank}_{iy}}{1-\mathrm{rank}_{iy}}) = \beta_0 + \beta_c \cdot \mathrm{calf}_{iy} + \beta_l \cdot \mathrm{length}_{iy} + \beta_t \cdot \mathrm{time}_{iy} + \beta_{ll} \cdot \mathrm{length}^2_{iy} + \beta_{tt} \cdot \mathrm{time}^2_{iy} + \beta_{cl} \cdot \mathrm{calf}_{iy} \cdot \mathrm{length}_{iy} + \beta_{ct} \cdot \mathrm{calf}_{iy} \cdot \mathrm{time}_{iy} + \beta_{lt} \cdot \mathrm{length}_{iy} \cdot \mathrm{time}_{iy} + \xi_i + \varepsilon_{iy}. \quad (3)$$

This model was also used for all the 1,782 captures, but with covariate time (and the linked parameters to that covariate) and random individual effect ξ_i excluded.

To investigate the power of testing for positive correlation, a small simulation study has been carried out. Ranks for all the capture-recaptures were simulated using the logistic mixed model (1), with covariates as observed and with regression coefficients, random individual effects variance and residual variance as estimated. The model was fitted to the simulated ranks and observed data exactly as it was fitted to the observed data. A one-sided likelihood ratio test was performed to calculate p-values for each of 1,000 replicates. Finally, a generalised linear model (GLM) on the logistic scale was applied to obtain a power curve for testing the null hypothesis of $\rho = 0$. Additional repeated simulations were carried out for $\sigma = 1.69$ ($\rho = 0.5$) and $\sigma = 5.1$ ($\rho = 0.9$) to get maximum likelihood estimates for the logistic mixed model with simulated ranks. In addition, simulated results were used to estimate a confidence curve and obtain a confidence interval for ρ as in Schweder *et al*. (2009).

Table 3

Maximum likelihood estimates and standard errors (in parenthesis) for all captures where length of the individual is measured and for captures with recaptures.

	All captures n=1,782	Captures with recaptures n=42[1]
β_0	0.17 (0.04)	1.01 (0.24)
β_c	2.16 (0.19)	1.55 (0.79)
β_l	0.26 (0.02)	0.53 (0.15)
β_t		0.04 (0.08)
σ		2.3e-06 (0.01)
θ	1.65 (0.03)	1.69 (0.13)
- log likelihood	1,784.94	86.10

[1]The 2 whales captured in 3 different years were regarded as 4 cases of recaptures.

RESULTS

The model was fitted by way of the computer package *AD Model Builder* (Otter Research, 2004). Maximum likelihood estimates and standard errors based on the Hessian of the log likelihood are given in Table 3 for the simple logistic regression and the mixed model (1).

The correlation coefficient between ranks (2) is estimated to be 1.9e-12, and is not significantly different from zero (p-value 0.78). Simulation results estimated ρ to be 0.00 with 95% confidence interval (0.00, 0.35). The confidence curve is given in Fig. 3 (right).

The estimated intercept is higher when only captures with recaptures are considered (Table 3). This reflects that well marked whales tend to be long and thus late migrants. Association with a calf and being of a long length have both a significant effect of delaying the migration relative to the other migrants (p-value 0.00, all captures), while the time has no significant effect on the migration rank (Table 3).

Adding quadratic terms, as in (3), did not improve the fit appreciably for the capture-recapture data. The improvement in log likelihood was only 2.11 units on 5 degrees of freedom. There is thus no evidence for interaction or quadratic effects of covariates. For the capture data of size 1,782 the likelihood was improved significantly (22.67 units), but only the quadratic length term β_{ll} is significant.

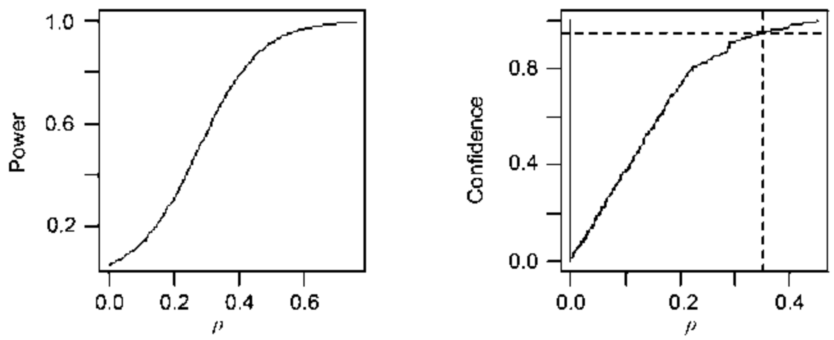

Fig. 3. Power curve of testing for positive temporal correlation in relative ranks within individuals at significance level 0.05 (left) and confidence curve for ρ (right). The horizontal line represents confidence 0.95. The vertical lines indicate 95% confidence interval.

DISCUSSION

To illustrate the regression results, the effect of having a calf associated was explored. Based on all captures, the intercept was estimated to be 0.17, and the effect of having a calf was estimated to be 2.16. An individual of average length without a calf thus has a predicted relative rank of exp(0.17) / (1 + exp(0.17)) = 0.54, while the predicted relative migration rank would be exp(2.16 + 0.17) / (1 + exp(2.16 + 0.17)) = 0.91 if it was associated with a calf. Recall that average length (12.03m) was subtracted from the observed length. The effects on calf and length on relative migration rank are highly statistically significant in the total capture data and in the capture-recapture data the effect of length is strongly significant. The effect of being associated with a calf is only of borderline significance here, but note that there were only five cases of capture-recaptures in which a calf was associated (Fig. 2).

It is important to note that these results are valid when surveys are assumed to cover the migration periods in a consistent pattern. However, if the first few surveys were performed early in the migration and the last few surveys were only able to cover the latter part of the migration, the relative ranks would be measured differently. In this case, an artefact would be observed that indicates a tendency of the recaptures to appear later in the migration than the captures, even when there is no such pattern in the true ranks. Fortunately, except for 1984, 1986, 1987 and 1994, the surveys covered the migration periods consistently (Koski *et al*., 2006). Since only captures for which length of the individual was measured were considered, the surveys in 1984 and 1987 were excluded automatically. Elimination of 1986 and 1994 produced nearly the same results (β_c, β_l and θ were estimated as 2.18, 0.28 and 1.68 respectively). Elimination of these four years, when only captures with recaptures were considered, produced similar results for the parameters β_l, β_t, θ and σ (0.96, 0.07, 1.61 and 1.4e-06 respectively), while the estimate for β_c was different (-1.34). This result is not surprising since four records with calves were removed from the five-records database.

Although the capture-recapture sample size was small, the power of detecting migratory patterns was still reasonable. The power of testing $H_0 : \rho = 0$ at level 0.05 was about 50% when $\rho = 0.23$. Figs 3 and 4 illustrate the power of testing for positive correlation. Fig. 2 and the confidence curve shown on Fig. 3 (right) give additional support to the finding of a low intra-whale correlation in relative rank.

To assess the quality of the linear model, it was used as a predictive tool. First the model was applied only to 1985 and the maximum likelihood estimates obtained from this fit were applied to the year 1986 to obtain predicted ranks and residuals. The model was then fitted to both years 1985 and 1986 to yield predicted ranks for 1989 (years are not consecutive, Table 1), etc. Finally, the model was fitted to all the years 1985-1992 to obtain predicted ranks for 1994. The maximum likelihood estimates based on the sequentially cumulated data used to find predicted ranks, are found in Table 4. It is reassuring that these estimates vary little and hardly show any trends. Predicted ranks, residuals and normal-probability plot of the sequential residuals are found in Fig. 5.

Table 4

Maximum likelihood estimates based on increasing subsets of the data.

Subset	85	85-86	85-89	85-90	85-91	85-92
β_0	0.18	0.12	0.15	0.13	0.11	0.16
β_c	3.31	2.05	2.19	2.38	2.19	2.16
β_l	0.2	0.22	0.25	0.26	0.26	0.27
n	501	737	925	1,149	1,392	1,606

Except for the well-known systematic effect of large whales, and also the late migration of cows with calves, age is not found to significantly affect the migration rank. The main result is however that individual whales appear not to have any persistency from year to year in their relative rank when passing Barrow in the spring migration. In the limited capture-recapture data the estimated intra-whale correlation in relative rank, when controlling for covariates, is indeed small and not statistically significant. The power of testing for positive correlation at a significance level 5% is about 50% when $\rho = 2.8$.

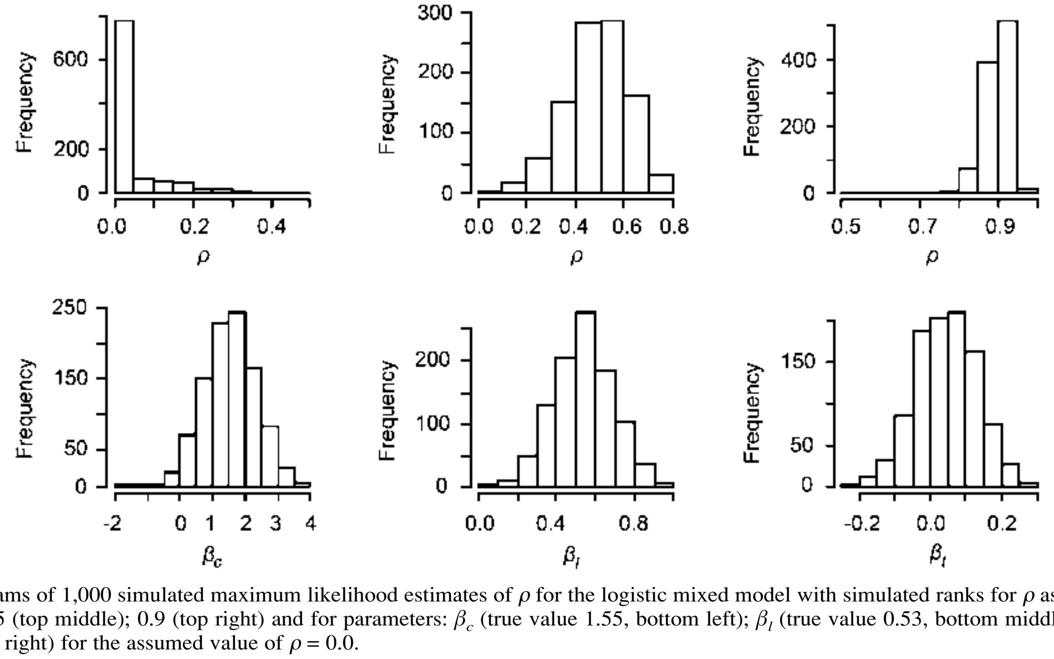

Fig. 4. Histograms of 1,000 simulated maximum likelihood estimates of ρ for the logistic mixed model with simulated ranks for ρ assumed to be: 0.0 (top left); 0.5 (top middle); 0.9 (top right) and for parameters: β_c (true value 1.55, bottom left); β_l (true value 0.53, bottom middle); β_t (true value 0.04, bottom right) for the assumed value of $\rho = 0.0$.

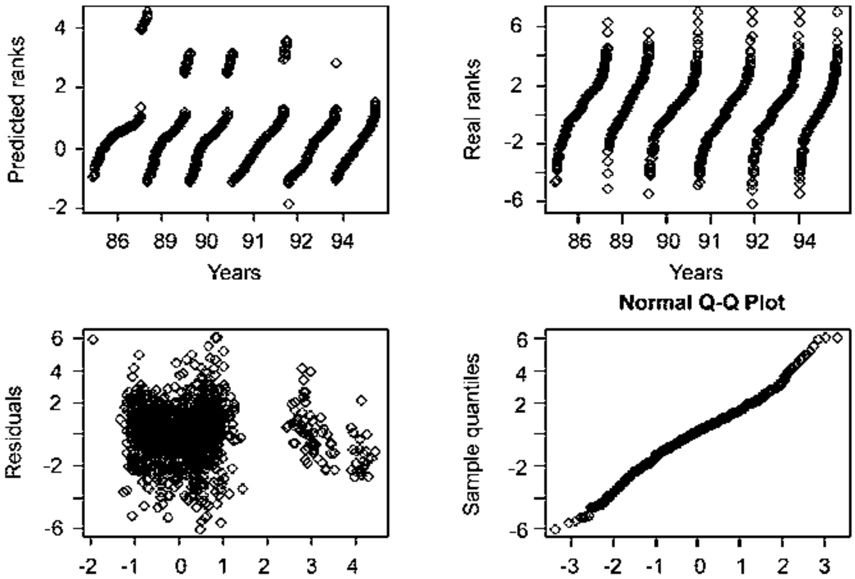

Fig. 5. Predicted ranks (sorted) versus years (top left); real ranks (sorted) versus years (top right); predicted ranks versus residuals for all years (bottom left); normal-probability plot of residuals for all years (bottom right).

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