Estimates of population growth rates of humpback whales (*Megaptera novaeangliae*) in the wintering grounds off the coast of Brazil (Breeding Stock A)

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ABSTRACT

Humpback whales wintering off the eastern coast of Brazil were heavily exploited by commercial whaling in the Southern Hemisphere. During recent years, clear signs of recovery have been observed, but few estimates of population growth rate exist. In this study, quantitative estimates of rates of population increase are obtained from sighting per unit of effort data (1995-1998) using generalized linear models and maximum likelihood estimation. The error distributions considered for the models were Poisson and negative binomial. Predictors of the number of sightings included the year, month and 2-week periods during which the sightings were made. Predictors were treated as factors or numeric variables. For the numeric variables, quadratic dependence was also considered for each predictor to allow for possible non-linear relationships. Using AICc as a model selection criterion, the best model included year and month as continuous predictors. The data indicated strong support for the negative binomial over the Poisson models, but did not support models based on a finer temporal scale than month. Assuming year to be a linear predictor, the best estimate of the growth rate for the population wintering off Brazil was 7.4%/year (95% CI = 0.6-14.5%/year) during the period 1995-1998. This estimate provides additional quantitative evidence that this population has been increasing and is consistent with the observed growth rates of other humpback whale stocks.

KEYWORDS: HUMPBACK WHALE, INDEX OF ABUNDANCE, MODELLING, TRENDS, BREEDING GROUNDS, SOUTH ATLANTIC OCEAN

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are present along the eastern coast of Brazil during winter and spring, where breeding and calving takes place (e.g. Martins *et al.*, 2001; Zerbini *et al.*, 2004; Andriolo *et al.* 2006). By late spring, whales migrate through offshore areas to the Scotia Sea in the southern South Atlantic Ocean (Zerbini *et al.*, 2006a and b) and concentrate in feeding grounds near South Georgia and the South Sandwich Archipelago (Stevick *et al.*, 2006; Zerbini *et al.*, 2006, 2008a). This population is referred to as the 'Breeding Stock A' (BSA) by the International Whaling Commission (IWC, 1998, 2005).

Individuals from this population were hunted by coastal and small scale offshore operations in the wintering grounds off the coast of Brazil from at least the 17th century (Ellis, 1969; Lodi, 1994). The introduction of modern whaling techniques in the early 1900s increased catches in the wintering grounds but, most importantly, promoted the expansion of whaling to high density areas in feeding grounds in the Antarctic Ocean (e.g. Tønessen and Johnsen, 1982; Williamson, 1975; Findlay, 2001). The bulk of the feeding ground catches of BSA whales occurred around South Georgia, where approximately 27,000 whales were taken between 1904 and 1920 (Findlay, 2001; Allison, 2006). This substantial catch severely reduced the population to a point where humpbacks became rare in the South Atlantic Ocean. Protection from whaling was imposed by the IWC in the late 1960s, but some whales were taken illegally by the Soviet fleet in both the feeding and the wintering grounds in subsequent years (*e.g.* Yablokov *et al.*, 1998).

Contemporary studies of humpback whales off the coast of Brazil commenced in the late 1980s. Research initially focused on the Abrolhos Bank area (~18°30'S, 38°30'W) (e.g. Siciliano, 1995; 1997; Martins *et al.*, 2001), which is considered the main breeding ground for the species in the western South Atlantic Ocean (Andriolo *et al.*, 2006). However, studies expanded to other areas along the Brazilian coast as the population expanded its distribution to historical wintering habitats (*e.g.* Zerbini *et al.*, 2004; Andriolo *et al.*, 2006).

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During the past 20 years, the population of humpback whales breeding off the coast of Brazil has shown clear signs of recovery. Sightings, strandings and occasions where whales were seen interacting with fisheries have become more common (Siciliano, 1987; Pizzorno *et al.*, 1998; Zerbini and Kotas, 1998) and whales have been observed reoccupying historical areas of distribution (e.g. the northeastern coast of Brazil, Zerbini *et al.*, 2004) after being nearly absent for several decades (Antonelli *et al.*, 1987). Despite that, the rate at which recovery is occurring is poorly known. Freitas *et al.* (2004) estimated that the annual growth rate of this population was 30.6% (95% CI = 2.6-60.0%) from a time series (1996-2000) of mark-recapture abundance estimates. While the precision is low and the point estimate is well above the maximum plausible for humpback whales (10.6%/year, Clapham *et al.,* 2006), this estimate provides additional evidence that the population is increasing.

In this study, general linear models (GLMs) are applied to sighting data collected in the Abrolhos Bank (Martins *et al.*, 2001) in an attempt to estimate the growth rate of the population between 1995 and 1998. This estimate provides additional quantitative information on the growth rate of this stock to be incorporated in population assessment models (Zerbini *et al.*, 2008b).

METHODS

The Data

Sighting and effort data were gathered to investigate the distribution, seasonality and habitat use of whales in the Abrolhos Bank from June to November over the period from 1992 to 1998. However this information was collected in a systematic and comparable fashion only over the period from 1995 to 1998, as described by Martins *et al.* (2001). Cruises were conducted for four days each week with searches carried out by a team of three observers under relatively good weather and sea conditions (wind speed <20 knots). The ship followed pre-determined transects in the Abrolhos Bank area at an average speed of nine knots. When a group of whales was sighted, the vessel deviated from the trackline to conduct photo-identification and biopsy sampling for as much as 30 minutes, after which it returned to the previous course. On some occasions, when the density of whales in the area was high, the trackline would be abandoned for the day in order to allow photo-identification and biopsy sampling from other whale groups. Martins *et al.* (2001) stratified the data into two-week periods each year, resulting in a total of eight periods per year (Table 1).

Modelling framework and Data Analysis

The sightings-per-unit-of-effort (SPUE) data were analyzed using a GLM framework, which extends the standard linear model by assuming a non-Gaussian error structure, and utilizes a ‘link’ function that transforms non-linear data to fit the assumptions of linear models (McCullagh and Nelder, 1989; Venables and Ripley, 2002). The GLM framework has seen widespread applications in ecology, particularly for problems involving count data (Link and Sauer, 2002). The simplest GLM for count data customarily assumes a Poisson error distribution, and a logarithmic link function. This model has also been termed a log-linear regression model, because the logarithm of the Poisson parameter (*u*) is taken to be a linear function of the parameters and data:

$$\log(u) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + X_3$$

where *u* represents the mean number of humpback sightings, B_0, B_1, B_2 are regression coefficients, X_1 and X_2 are covariates, and X_3 represents an optional offset term (or covariate with a coefficient of 1.0) to account for unequal search effort between sampling occasions (e.g. Coronado and Hilborn, 1998).

One problem with assuming that error is Poisson distributed is that the error variance is constrained to be equal to the mean (*u*). An alternative to the Poisson model is the negative binomial model (Hilborn and Mangel, 1997). The negative binomial distribution is more flexible than the Poisson distribution because it includes an additional overdispersion parameter (θ), which allows the error variance to include a term that is a function of the mean. The negative binomial is often better suited to ecological data, because many such data sets may include correlated observations, an excess of zeros (‘zero-inflated’; Hilborn and Mangel, 1997). The overdispersion parameter of the negative binomial distribution allows for the aggregated distribution of individuals (such as those encountered in the Abrolhos Bank area), whereas the Poisson distribution assumes individuals to be randomly distributed.

In this analysis, both Poisson and negative binomial models were applied to the sighting data from the humpback whale wintering in the Abrolhos Bank (Table 1). Covariates considered as predictor variables of humpback sightings included Year and either Month or Period (the 2-week block during which the sighting was made). Month, Period and Year were considered both as continuous variables and factors (Month = 7-12; Period = 1-10; Year = 1995-1998), but the Month and (two-week) Period were not allowed to act as predictors in the same model to avoid redundancy.. To determine whether there was evidence for a non-linear relationship between sightings and temporal variables, possible quadratic dependence was also explored.

Due to possible correlations in the data, models were fitted to observations from the 1st period only in each month, the 2nd period only in each month, and finally to the entire data set. Because the total number of observations was relatively small (n = 40, 20 records from each period), we used the Akaike Information Criterion corrected for small sample sizes (AICc) as a model selection criterion to indicate the most appropriate model (Burnham and Anderson, 2002). Addressing model selection in a statistical framework allowed evaluation of which hypotheses about predictor variables and error structures are best supported by the data.

The ultimate objective of this study was to quantify the annual rate of increase, or year effect of the SPUE data over the period 1995-1998, so that this information might be incorporated into the stock assessment of BSA, assuming that it reflects the growth rate of the whole population wintering off eastern South America. The annual growth rate from one year to the next is defined as:

$$\lambda = \frac{N_{t+1} - N_t}{N_t}$$

with the instantaneous rate of change (r) as estimated by the GLM transformed into an annual rate by the relationship: $\lambda = \exp(r) - 1$. Additional objectives were to address: (1) whether there is evidence for over-dispersion in the Abrolhos Bank humpback whale data (whether the negative binomial is favoured over the Poisson distribution), (2) whether there is evidence for quadratic dependence on the Year variable rather than linear dependence, (3) whether Period or Month is a better predictor of the number of sightings, and (4) whether there is evidence for quadratic dependence on either the Period or the Month variable.

RESULTS

A large number of GLMs were evaluated for the full data set (the best fitting model and several related models appear in Table 1). The model of humpback whale sightings with the lowest AICc score was one that assumed a negative binomial error distribution, treated the Year variable as a linear predictor, and assumed quadratic dependence on the Month variable (Fig. 1). This model suggested that the humpback whale population wintering off Brazil increased 7.4%/year (95% CI = 0.6-14.5%/year) from 1995 to 1998. The results for other models (Table 2) are presented in terms of the AICc values relative to the lowest score (this difference being denoted by ΔAICc). As a general rule of thumb, models with ΔAICc values that are less than 2 should be given consideration in addition to the selected model, while models with ΔAICc values that are more than 10 should receive little consideration (Burnham and Anderson 2002).

The first question addressed by the analysis was whether there was more support for the negative binomial error distribution or the Poisson error distribution. For all models considered, the negative binomial model consistently performed better, resulting in lower AICc scores when compared to the corresponding Poisson GLM. The negative binomial models had AICc scores that were at least 30 units better than their Poisson counterparts, indicating that they were strongly preferred by the data. Across models that treated Year as a linear predictor, accepting the negative binomial model resulted in maximum likelihood estimates of the annual growth rate parameter (Year effect) that were 30-50% larger than their Poisson counterparts (Table 2). A second important result was that the standard errors of the Year effect were nearly twice as high for negative binomial models compared to Poisson models, reflecting that the latter's ignoring of correlations between sightings leads to overestimation of precision. Although the autocorrelation between standardized residuals was small for both models, another difference between the negative binomial and Poisson models was that the Poisson models had slightly higher autocorrelation (-0.15 compared to 0.015 for the negative binomial; Fig. 2).

The second issue investigated was whether there was greater support for a model that treated the Year dependence as quadratic. For a negative binomial GLM with quadratic dependence on Month, adding a quadratic term for Year resulted in a ΔAICc value of 0.51, relative to the model that assumed the Year effect was linear, so that the latter was preferred.

As the SPUE data have been broken down into 2-week blocks as well as by month, it was also important to investigate whether either of these predictor variables should be treated as a factor or as a continuous variable.

When Month was used alongside Year as a predictor variable, a GLM that considered quadratic dependence on Month performed better than a GLM that considered Month as a factor (Table 2, ΔAICc = 3.3). Regardless of whether Month was treated as a factor or continuous variable, the overall trend was similar (Fig. 3). The same result was found for the 2-week Period variable – assuming a quadratic dependence on Period resulted in better performance than treating Period as a factor (Table 2, ΔAICc = 12.2). Although the factor model was not favoured over quadratic dependence in either case, it did perform better than models that assumed linear dependence on Month or Period. Unlike the comparison between the Poisson and negative binomial distributions, the choice of predictor variables appeared to have little influence on the Year effect, with all annual growth rate estimates being ~ 7.4% (Table 2).

DISCUSSION

This analysis explored alternative GLM models of humpback whale sighting data, with the aim of finding a model that was best supported by the data. The model that received the most support was a negative binomial GLM that assumed linear dependence on Year and quadratic dependence on Month (Model 1, Table 2). The estimated Year coefficient was 0.071 (SE = 0.033), suggesting that over the period 1995-1998, humpback whale sightings off of Abrolhos Bank increased at 7.4% annually. This estimated annual trend for the corresponding Poisson GLM with a linear Year effect (Model 7, Table 2) was lower (~5%/year), however the data did not support the Poisson model assumption.

The negative binomial model with the lowest AICc score treated Month dependence as quadratic, rather than as a factor variable. The trend in the estimated Month effect is similar, regardless of the model chosen: sightings increase from July to September, and then proceed to decrease from summer to late fall. This is consistent with the seasonal variation in abundance observed for this population off Brazil (Siciliano, 1997). A further question concerning intra-annual trends addressed in this study was whether use of a finer temporal scale (the two-week Period) admitted a better explanation of the variation in the data compared to a coarser scale (Month). The analysis suggested the latter was to be preferred, probably because the observation error associated with the count data may be too high to detect a fine scale temporal trend (e.g. the number of whales in Abrolhos Bank over the course of a particular month).

Ideally, the output from the analysis presented here will be incorporated into the current assessment of this humpback whale stock (Zerbini *et al.*, 2008b). Although sighting data from Abrolhos Bank are not absolute indices of abundance, it is possible to include the annual growth rate (related to the Year effect in these GLMs) into the likelihood as the observed growth rate over the period 1995-1998. It should be noted that there are important tradeoffs in assuming a negative binomial error structure over a Poisson error structure on the estimate of the Year effect. The Year coefficient in the negative binomial model is approximately 45% larger (7.4% compared to 5%) than that for the Poisson model, but the associated standard error for the Poisson model is approximately half that for the negative binomial model.

The year effect estimated by the selected model is taken to correspond to the rate of increase of humpback whales wintering off the coast of Brazil between 1995 and 1998. This estimate (7.4%/year, 95% CI = 0.6-14.5%/year) presents additional quantitative evidence that humpback whale populations are increasing in the western South Atlantic Ocean. In addition, it provides a point estimate for annual growth rate that is realistic from a biological standpoint, when compared to the previous estimate reported by Freitas *et al.* (2004): 30.6% (95% CI = 2.6-60.0%). While the two confidence intervals overlap, the latter has much poorer precision and the point estimate is well above what is considered plausible for humpback whale populations (e.g. Clapham *et al.*, 2006).

Sighting surveys conducted by Martins *et al.* (2001) covered the central portion of the Abrolhos Bank. This region includes most of the population of humpback whales wintering off the coast of Brazil and is considered the optimal habitat for the species on its breeding grounds. Because whales on their wintering grounds would concentrate first on finding optimal habitat, the estimate of growth rate presented here could be biased downwards. Once this area becomes full (saturated), the rate of growth would decrease, and further whales would move to other, non-surveyed, and previously uninhabited regions, which would show a greater rate of growth. The actual population rate of increase would be a combination of the growth in the optimal habitat and the rate of expansion to more peripheral areas.

Rates of increase presented here are consistent with those observed for other humpback whale populations. In the North Atlantic, North Pacific and elsewhere in the Southern Hemisphere, growth rate estimates for humpback whale stock varied between 3% and 15%/year (e.g. Best, 1993; Bannister, 1994; Sigurjónsson and Gunnlaugsson 1990; Stevick *et al.*, 2003; Clapham *et al.*, 2003; Mizroch *et al.*, 2004).

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Table 1 – Sighting and search effort data collected on the Abrolhos Bank, which is a wintering ground for humpback whales from breeding stock A (BSA), from 1995-1998 (after Martins *et al.*, 2001).

Table 2 – Poisson and negative binomial models of humpback whale sightings, using Year, Month, and (two-week) Period as predictor variables. Month and Period may be factors (F), or continuous variables (N) upon which the count depends quadratically. For each model, the estimated Year effect expressed as an annual increase rate and the associated 95% confidence interval (CI) are included. The best model according to the AICc criterion is highlighted in bold.

Fig. 1. Plot showing the observed data (Table 1) and the fit from the model with the lowest AICc (Model 1, Table 2). In addition to the year effect, this model assumes count to be a quadratic function of month. For simplicity, the dashed line has been drawn to show the mean model-predicted number of sightings for each month.

Fig. 2. Standardized residuals for two selected models in Table 2. The open circles and solid line correspond to the model with negative binomial error structure (Model 1, Table 2), whereas the dashed line and closed circles represent the corresponding model with a Poisson error structure (Model 7, Table 2). In addition to the year effect, these models assume abundance to be a quadratic function of month. The residual with the largest magnitude occurred in the latter half of 1998 surveys.

Fig. 3. Estimated Month effects for a model that treats the Month variable as a factor (solid circles; Model 2, Table 2), and a model that assumes quadratic dependence on Month (open circles; Model 1, Table 2).

Table 1

Period	1995		1996		1997		1998	
	N^o. of sightings	Effort (h)	N^o. of sightings	Effort (h)	N^o. of sightings	Effort (h)	N^o. of sightings	Effort (h)
1-15 July	31	15.4	35	21.3	83	56.6	72	50
16-31 July	78	38.9	44	37	74	38.9	91	42.4
1-15 Aug	44	37.8	106	41.5	118	66	127	68.6
16-31 Aug	142	69.75	153	55.6	177	63	211	106.3
1-15 Sep	60	26	71	26.1	89	29.3	62	26.6
16-30 Sep	108	66.3	121	42.75	127	46.7	54	23.25
1-15 Oct	36	29.5	43	22.1	89	68	121	56.1
16-31 Oct	59	51.3	72	42.1	36	25.25	24	8.16
1-15 Nov	30	36.1	34	36.1	25	29.1	25	22.5
16-31 Nov	4	7.75	22	30.1	53	41.5	12	9.9
Total	592	378.8	701	354.65	871	464.35	799	413.81

Table 2

Model	Error	Number of Parameters	Year Effect	95% CI	Month	Period	ΔAICc
1	**Negative Binomial**	**5**	**7.4%**	**0.6 - 14.5%**	**N**	**-**	**0**
2	Negative Binomial	7	7.4%	0.8 - 14.3%	F	-	3.29
3	Negative Binomial	5	7.4%	0.4 - 14.8%	-	N	3.79
4	Negative Binomial	12	7.4%	1.4 - 13.6%	-	F	16
5	Poisson	11	5.7%	2.2 - 9.2%	-	F	47.03
6	Poisson	6	5.5%	2.1 - 9.1%	F	-	50.97
7	Poisson	4	5.0%	1.6 - 8.6%	N	-	55.73
8	Poisson	4	4.7%	1.3 - 8.2%	-	N	57.24

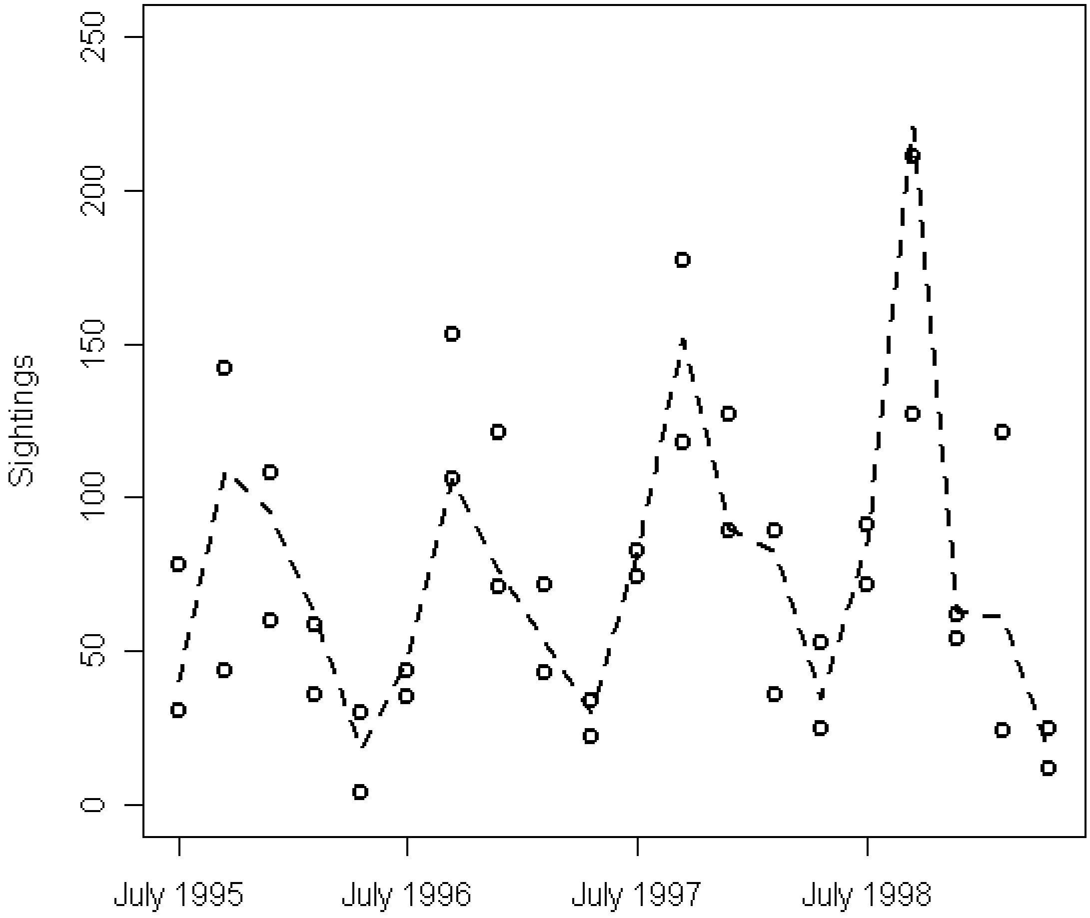
Sightings
0
50
100
150
200
250
July 1995
July 1996
July 1997
July 1998

Fig. 1

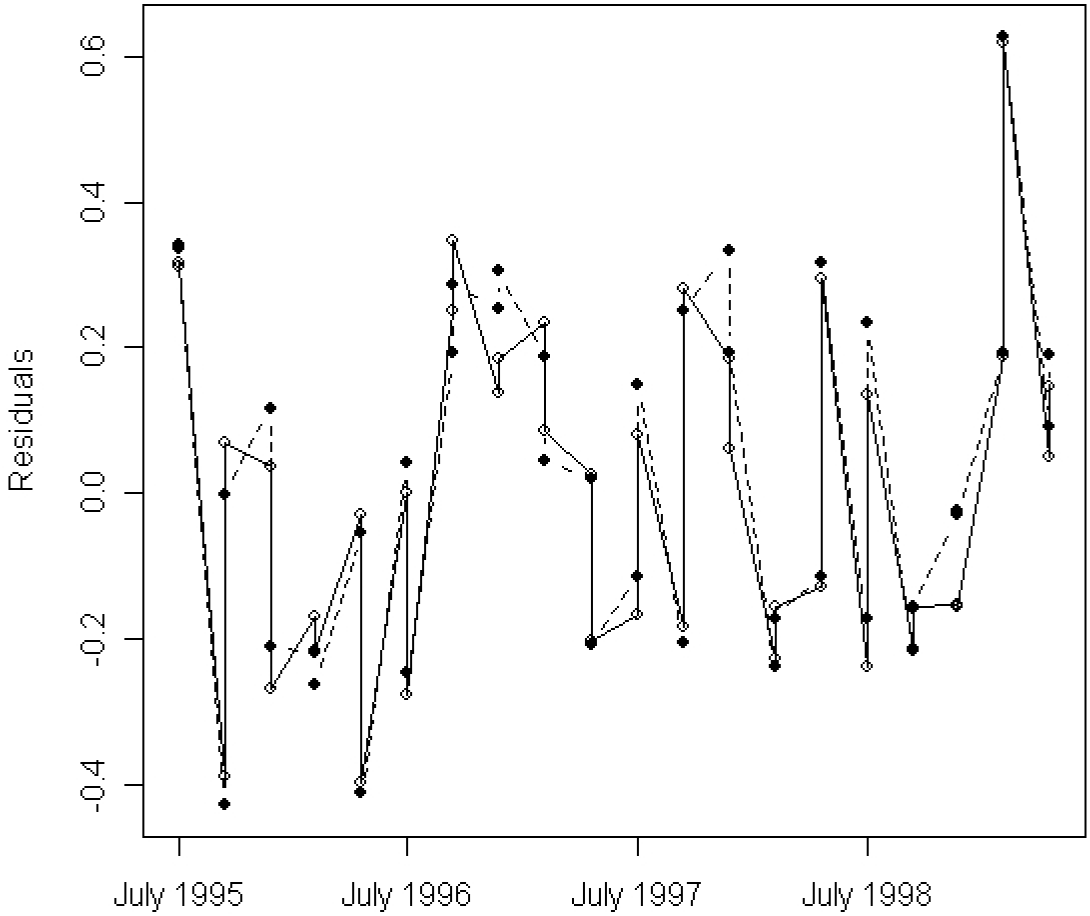
Residuals
0.6
0.4
0.2
0.0
-0.2
-0.4
July 1995
July 1996
July 1997
July 1998

Fig. 2

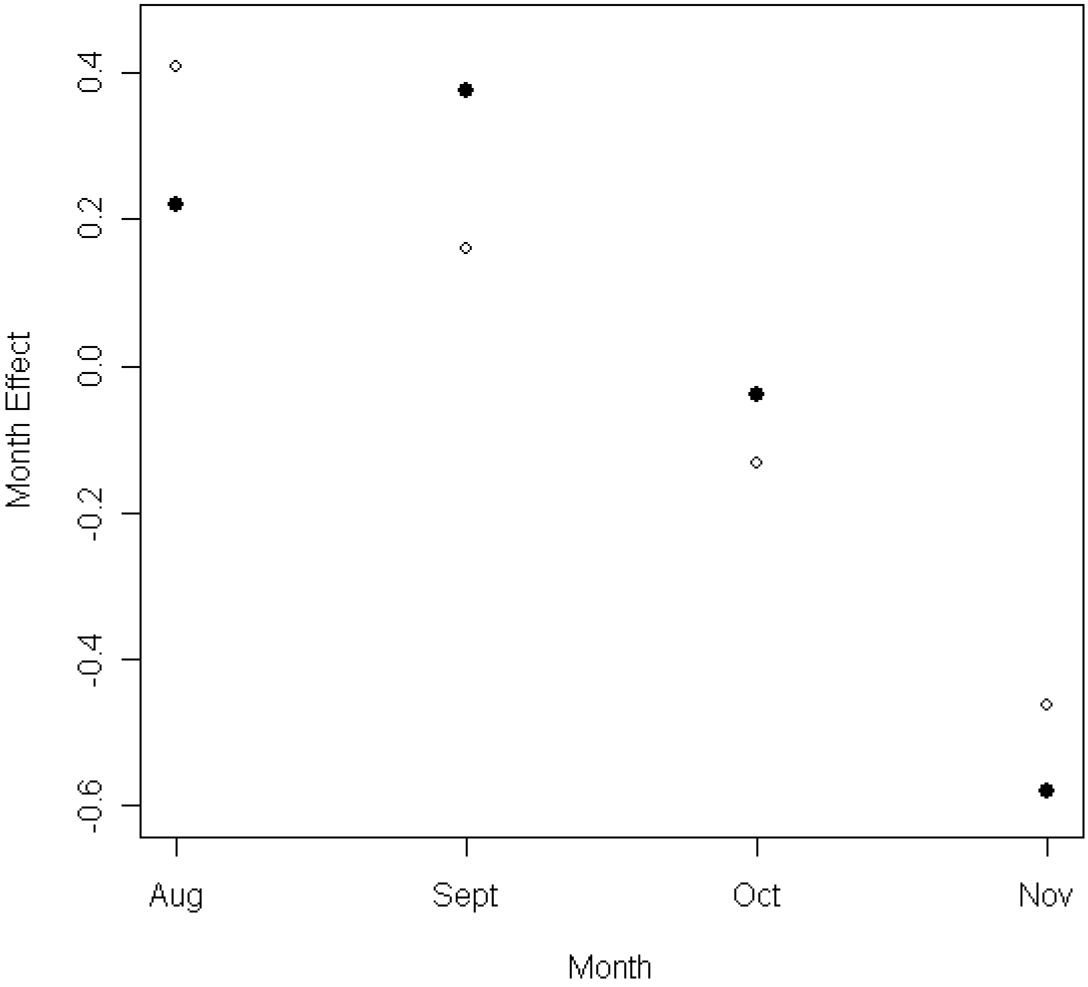

Fig 3