research article

Wintering, rather than breeding, oceanic conditions contribute to declining survival in a long-distance migratory seabird

Running page head: oceanic conditions influence survival

Inês Alexandre Machado dos Santos[1 §], Katherine R. S. Snell[1,2 §]*, Rob SA van Bemmelen[3], Børge Moe[4] & Kasper Thorup[1]

[1] University of Copenhagen, Copenhagen, 2100, Denmark [2] MPI-AB, Radolfzell, 78315, Germany [3] Waardenburg Ecology, Culemborg, 4101 CK, the Netherlands and Wageningen Marine Research, IJmuiden, 1976 CP, the Netherlands [4] NINA, Trondheim, 7485, Norway

[§] contributed equally * corresponding author ksnell@ab.mpg.de

ABSTRACT

Steep declines in Arctic skua populations have been reported during the last half of the 20th century in the southern extent of their breeding range. We used 24 years of available ringing and re-encounter data from the Faroe Islands, North Atlantic, to determine if patterns in survival probabilities can be explained by large scale climatic events. Having first determined the migratory phenology and wintering regions, we tested the North Atlantic Oscillation (NAO) index during breeding and Oceanic Niño

index (ONI) during the non-breeding period within a capture-mark-recapture framework to model direct and time-lagged effects of the environment on annual survival. We found differential effects in the two age-classes examined: young and adults. Overall, three models were equally supported. We found strong support for a substantial decrease in adult annual survival over the study period, from ca. 0.93 probability of survival in 1985 to ca. 0.77 in 2008, and support for a decrease in young survival over the duration of the study period. Furthermore, we found support for increased chick survival following an El Niño winter. We suggest this reflects a potential carry-over effect of El Niño conditions positively impacting the performance of the parents in the subsequent breeding season, leading to improved chick survival prospects. The negative trend of adult survival cannot be attributed to the oceanic climate oscillations tested here; however, this result may account for the substantial population declines observed during the last decades.

Keywords: mortality, carry-over effects, CMR modelling, *Stercorarius parasiticus*

1. INTRODUCTION

Seabirds occupy the upper trophic level and are important in island- and marine ecosystem processes, function and resilience (Paleczny et al., 2015). Their distribution and population dynamics are strongly connected with their feeding ecology and patterns of food availability which are dependent on climatic and oceanographic factors, such as water temperature and currents (Meier et al., 2017). Therefore, changes in any such environmental variables can substantially influence seabird survival and fitness (Champagnon et al., 2018; Irons et al., 2008; Waugh et al., 2015). Steep declines in seabird numbers have been reported during the last half of the 20th century. Palenczny et al. (2015) assessed the population trend of the world's monitored seabirds from a global dataset representing ca. 19% of the global seabird population and found an overall decline of 69.7% in between 1950-2010: a pattern reflected in the population trends of seabirds in the Atlantic Arctic (Irons et al., 2008). Moreover, population declines are more apparent in migratory species (Kubelka et al., 2021).

Given that a broad range of factors that may affect demographic parameters, identifying the factors responsible for population dynamics is often difficult. Unravelling effects of different factors is especially challenging for migratory species, as they depend on multiple, widely separated areas that may contrast in their (rate of change in) conditions. As migratory species spend the majority of their annual cycle on migration or overwintering, the habitat conditions experienced during these periods are likely to influence adult and post-fledging juvenile survival. Likewise, conditions on breeding grounds influence reproductive success, with decreases in productivity in years where conditions are poorer (Fife et al., 2018). In addition to these within-season effects, conditions experienced in one season can affect the condition and performance of

individuals in later seasons (Harrison et al., 2011). The effects of climate on species survival have received increased interest during the last few decades due to accelerated climate change (Ballerini et al., 2015; Jóhannesson et al., 1995; Salas et al., 2017). As shown in several studies, climate indices can influence survival and breeding success of both migrant and non-migrant birds (Boano et al., 2010; England, 2000; Genovart et al., 2013; Irons et al., 2008; Waugh et al., 2015). For example, Blue-footed booby (*Sula nebouxii*) in the Gálapagos suffered increased mortality during an El Niño year, when sea surface temperature was elevated; similarly, chick growth rates of Dark-rumped petrel (*Pterodroma phaeopygia*) were retarded during the 1983 nesting season, one of the strongest El Niño events since records began (England, 2000). The influence of climate indices on seabird survival rates are likely explained by the important impact of stochastic ocean scale environmental processes on ecosystem cascades affecting nutrients, temperature and primary productivity (Polis et al., 1997), which in turn affect food availability for seabirds. Despite anecdotal correlation between climate indices, formally linking survival and reproductive rates to climate indices such as the El Niño Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO) can be a first step towards understanding drivers of population dynamics (Descamps et al., 2010).

Like many populations of vulnerable seabird species in Northwest Europe (Dias et al., 2019), Arctic skua (*Stercorarius parasiticus*) populations are declining rapidly (Perkins et al). The Arctic skua is a migratory seabird with a circumpolar breeding range in high temperate to high Arctic zones. It is long-lived, with immature birds recruiting to the breeding population from an age of 4 years (Furness, 1987; O'Donald, 1983). They exhibit typical kleptoparasitic behaviour, making them highly dependent on other seabirds (Furness 1987), most of which have also experienced sharp population declines

(BirdLife International, 2016). Although the Arctic skua is listed as of 'least concern' globally, with a world population estimated at 4-600 000, it is considered 'endangered' within the European Union (Burfield & van Bommel, 2004). This assessment is mainly based on declines reported from the United Kingdom (Perkins et al., 2018), where the species declined by *ca.* 80% during 1992-2015 and from the Faroe Islands, where the population declined from 1200-1500 pairs in 1981 (Bengtson & Bloch, 2003) to *ca.* 414 pairs in 2017 (Santos, 2018). The proposed drivers of these declines are geographically limited but, in the United Kingdom and Norway, associations were found with predation of young and food shortages (Perkins et al., 2018; van Bemmelen et al., 2021).

The decline of European Arctic skua populations has hitherto been mainly attributed to the effects during the breeding periods on reproduction, and adult survival was considered to be sufficiently high to maintain a stable population. However, a full understanding of the population declines also requires potential effects from the breeding and non-breeding periods, on both adult and immature mortality, to be quantified (Flack et al., 2022). We hypothesise that for long-lived, long-distance migratory seabirds the non-breeding environmental conditions rather than breeding conditions influence population dynamics. Here, we investigated annual survival of adult and immature Arctic skuas breeding in the Faroe Islands. Within a formal capture-mark-recapture framework we explored annual survival, trends in annual survival and the influence of oceanic scale climatic events, precisely the El Niño Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO), using a ringing dataset spanning over two decades. We predict that wintering conditions, the largest component of the annual cycle , will influence annual survival of both young and adults, with El

Niño years having an overall negative effect due to increased water temperatures leading to reduced marine productivity. Furthermore, in long-lived species, we expect adult survival to be largely buffered against environmental variability; as such, mortality will firstly be greater in chicks than adults, and secondly, instead of only affecting survival, poor feeding conditions may be expected to carry over to the breeding performance due to the adults' poorer condition upon arrival and a subsequent increased mortality of offspring.

2. MATERIALS & METHODS

2.1 Study Species and sites

The Faroe Islands (61°53'33" N, 6°58'22" W) are located between the UK and Iceland, in the middle of the North Atlantic current which creates stable temperatures and a maritime climate (Fosaa et al., 2004). The Faroese archipelago consists of 18 islands and is an important breeding site for seabirds (Bakken, 2006). Ringing of Arctic skuas has been conducted since 1924 across the archipelago but was not systematic (Hammer et al., 2014).

As part of a tracking programme covering the Atlantic Arctic Marine areas (AMAs), tracking data was obtained from 20 birds in the Fugloy colony from 2016-7 (Kuletz et al., 2017) (fig. 1). Full details of the analysis and interpretation of light level data are detailed in van Bemmelen et al. (##). The Faroese Arctic skua population winter on the Patagonian Shelf, Discovery Seamounts, coastally from the Iberian plain to Cape Verde Islands, the Gulf of Guinea, and off the Namibian coast and the Cape of Good Hope (Fig. 1). Spatio-temporal data was used to select appropriate environmental indexes. Mean arrival and departure dates were 27 April and 8 August for breeding and 9 September and 21 March for over-wintering sites, respectively.

2.2 Environmental Variables

Standardised large-scale oceanic indices were selected appropriate for a spatio-temporal schedule of the long-distance migrant. The Oceanic Niño index (ONI), quantifies the phase and strength of El Niño Southern Oscillation (ENSO) events, where negative

values correspond to La Niña years and positive values to El Niño years (NOAA). The North Atlantic Oscillation index (NAO) is numerically consistent with the phases of the NAO (NOAA). Both ONI and NAO data are presented as aggregated 3-month overlapping temporal periods with values ranging from -1.64 to 2.24 and -1.4 to 1.8, respectively (Fig. 2). Wintering and breeding periods were derived from the GLS data. We calculated mean ONI during the stationary non-breeding season (September to March) and mean NAO during the breeding season (May to July; Fig. 2). Values were used as covariates in the survival model both as a direct effect (same year) and as a time-lagged effect from the previous year.

2.3 Survival Analysis

We used a subset (1985 to 2008) of the ringing and recovery data which had the greatest continuity of data (prior to 1985 gaps of >2 years in ringing effort occurred). Where discrepancies made the record unreliable, we excluded these individuals from our dataset (n=2). The dataset totalled 1060 individuals, of which 530 were ringed as chicks and 530 ringed as adults; 85 individuals were subsequently re-encountered (alive and/or dead) during the 24 years (suppl. mat. Fig. A1). An encounter history was created for each individual in the classic 2 age-class structure: for young (1st year) and for adults and including both live and dead encounters. A year was defined as starting on 1 May and ending on 30 April of the following calendar year, to coincide with the birds' breeding cycle. Annual survival was estimated from a formal capture-mark-recapture framework. The Burnham model for joint live and dead encounters (Burnham, 1993) was used with the Mark software (White & Burnham, 1999). This method calculates parameter estimates of apparent survival (S), live capture probability (p), dead recovery

probability (r) and fidelity (F). We modelled fidelity as constant due to known high philopatry and no reported post-natal dispersal between the Faroe Islands and the nearest colonies in the UK (Hammer et al., 2014). As Arctic skuas generally delay breeding until their 4th year (Furness, 1987; O'Donald, 1983), recovery (p) and reporting probability (r) were modelled as a function of 3 age-classes: young, immature (Imm) and adults. During the immature years, birds are thought to be entirely marine (Furness, 1987) as such p(Young), p(Imm) and r(Imm) were fixed to 0. Survival probability (S) was modelled as a function of 2 age-class (Young and Adults) with the assumption that once birds are full-grown immatures, after 1 year, they will have the same mortality as breeding adults. We derived a global combined model (i.e. a single survival probability over all years) and modelled year-dependant survival for each age-class. We then tested the following *a priori* candidate models: linear temporal trends of survival rates for both age-classes combined and for each age-class independently, and the effects of the two environmental covariates (detailed above) on survival probabilities. Model selection was based on the ranking of Akaike's information criteria corrected for small sample size (AICc) and adjusted for median-ĉ (Akaike, 1973). AIC weights and model likelihood were used for comparing model significance. Survival estimates ± SE are given back transformed from the logit link function Beta estimates. Linear trends are visualised with 95% confidence intervals.

3. RESULTS

The combined model (model 5, Table 1) estimated the overall survival of young as 0.43±0.14 and adults 0.92±0.07. The time dependant model to estimate survival for each year, was largely over-parameterised and returned estimates of 10 of the 24 years for adults, ranging from 0.16±0.15 to 0.87±0.51, and 8 years for young, ranging from 0.13±0.12 to 0.66±0.67 (Fig. 3, not included on Table 1 due to the high number of non-estimable parameters).

There was equal support for three models (Table 1). The highest ranked model (model 1), indicates a negative trend for adult annual survival and the influence of a time-lagged effect of ONI (Oceanic Niño Index) on chick survival (Table 1 & suppl mat Table A1). Evidence for a negative trend in adult annual survival is further supported by model 2 (ca. 4 times better supported than model 5, the combined model (based on AICc weights; Table 1 & suppl mat Table A2)).

We find some support for a decreasing trend for young birds also (model 2 and 3 equally supported) with AIC weights 3 times higher than the combined model (Table 1 & suppl. mat. Table A3). Based on model 3, the adults' survival shows a decline of 16% in 24 years, with 0.93±0.05 probability of survival in 1985 and 0.77±0.09 in 2008, whereas chick survival decreases 34%, from 0.60±0.19 in 1985 to 0.26±0.14 on 2008 (Fig. 3). Adult survival estimates from model 1 and 2 were comparable: within the error range of model 3 estimates.

Young survival was influenced in part by ONI from the preceding year. El Niño events were related to an increase in apparent survival while La Niña events a reduction (Fig. 3 & Table 1). When testing for the effect of time-lagged ONI on chicks in isolation (model 4) the model is only weakly supported, suggesting a coupled interaction with a

temporal trend. Model 8, which included temporal trends for both age-classes and ONI carry-over effect on chicks included several non-estimable parameters (Table 1).

No models including the NAO (North Atlantic Oscillation) during breeding season as a covariate were supported.

4. DISCUSSION

Survival rates and productivity are important parameters in population dynamics and in long-lived species, survival probability is the greatest contributing factor. However, the numerous ecological factors that are acting upon survival rates complicate determining the driving factors. Survival rates of seabirds are known to be affected by climatic events. In our study of Arctic skuas breeding on the Faroe Islands, a declining trend in survival of both age-classes and a carry-over effect of ENSO on survival of young birds (1st year) were found. These findings may in part explain the notable decline of the Arctic skua population in the Faroe Islands in recent time, and could be considered influential for other comparable species experiencing similar declines.

As K-selected species, many seabirds share the life history trait of high annual survival rates for adults (Szostek & Becker, 2015). Overall high survival probabilities of this age-class are commensurate with reported values and are expected for Arctic skuas and their sister species (Julien et al., 2013; O'Donald, 1983; Phillips, 2001; van Bemmelen et al., 2021). We found strong support for a negative trend over the 24 year study period. Because annual survival of adults is important for maintaining a stable

population, a decrease of 16% in survival rate in this timeframe is likely to be biologically significant. The number of Arctic skuas breeding in the Faroe Islands has decreased substantially during our study period (Santos, 2018) and the negative trend in adult survival observed on our study might explain this decline. In adults, we found no support for the influence of large-scale oceanic indices, either during the breeding season or non-breeding period, on their survival. This may be due to masking of any effect by the strong downward trend or be due to an environmental variable trending over time (such as air/sea temperature) which were not tested here as it would be difficult to resolve drivers of the decline over correlation. As such, exploration of this pattern demands further investigation, aided in part by our improved understanding of the spatial ecology of this population and species. The closest neighbouring population, in the UK, is also suffering heavy population declines (Jones et al., 2008; Perkins et al., 2018). Here, studies aimed at explaining these population declines have focussed mainly on explaining population dynamics by variation in reproductive success (Perkins et al., 2018), but have left open the possibility that population declines were (also) driven by reduced survival rates due to factors outside the breeding period. Furthermore, Perkins et al. (2018) demonstrated that low breeding success affects the stability of the population. The breeding success of Arctic skuas in the Faroe Islands has received no formal analysis to date, but sharp declines of the population are expected if productivity declined also here, together with the decreases in adult survival observed in our study.

ENSO has been linked with survival in various seabird species (Boersma, 1998; Champagnon et al., 2018; England, 2000). The closest examples, however, only assessed chick survival from birth to fledging. In Kiritimi Island Black noddy (*Anous minutos*) populations, no nestlings survived during an El Niño year, when heavy rains

flooded the nests, and in the Galapagos archipelago reduced chick size and survival was reported in three species during an El Niño year (Jaksic & Fariña, 2010). While we found no direct effect of ENSO on adult survival, we did find some support for an influence of ENSO conditions from the previous year on first year survival. This suggests a carry-over effectfrom the quality of their parents' non-breeding environment to the survival of immatures after fledging. Similarly, Szostek and Becker (2015) found a correlation between primary productivity during winter with recruitment in the following breeding season in common terns *Sterna hirundo*. Primary productivity can be used as proxy for food availability and this suggests that food availability during winter is limiting survival and recruitment success in common terns. As ENSO has effects on primary productivity, ENSO would be expected to correlate with species vital rates, as we found in our study. Potentially, in Arctic skuas, in similarity with common terns, the quality of the environment during winter for adult birds, expressed by food availability, will be reflected on the quality of their chicks and their ability to complete their first year. There is likely to be a disparity between the impact of south Atlantic conditions on locally breeding populations and migratory birds from thousands of kilometres away. While we found some support for a downward trend in survival probability in young, the model including constant probability was equally supported. The coupled interaction with the stochastic ENSO events masking the trend over time may explain this, or simply that this is not as strong a gradient as, for example, in adults.

We found no evidence of the effects of NAO on survival of either adults or chicks. This indicates that any environmental influence on survival of both chicks and adults does not occur during the breeding season. One explanation is that all skuas, regardless of age, spend the majority of their annual cycle on the wintering grounds rather than the

breeding region in the north Atlantic (Hurrell et al., 2001; Stenseth et al., 2003). Possibly, the environmental conditions during the breeding season (and the influence of NAO) have greater effects on breeding success than on survival.

While we made attempts to use the best available dataset to cover the range of stochastic environmental events in particular intense El Niño and La Niña events, the structure of the data precluded estimates for all years. While this modelling approach takes into account lack of data in the estimates, a fully time-dependant model was not estimable for all years. This may have a two-fold influence on how the data is interpreted: firstly, we can be relatively confident that winter conditions have little influence on first-year skuas as we did not find a direct effect of ONI on young survival; secondly that the only weak contribution of a carry-over effect may be attributed to the limited range of covariate data. Furthermore, as such, the power to detect an effects of the environment on adult survival may be low. Unfortunately, we could not estimate survival rates for either young or adults following the biggest El Niño year (1997/98) of the 20th century.

Not all variation in survival could be explained by the variables tested in this study. Furthermore, population changes can be investigated with an approach from breeding ecology, which is outwith the scope of this survival study. Future studies should include establish the contribution of other parameters, such as recruitment as a function of climate variables, to also help understand how climate influences survival from birth until the chicks fledge.

5. CONCLUSIONS

From a conservation perspective, studying population dynamics and understanding the underlying process is important for targeting effective conservation measures. Our study contributed to this understanding for the Faroese Arctic Skua population by showing that – in addition to local effects on the breeding grounds on reproduction – the adult survival rate has declined to levels below what is required to sustain a stable population. Additionally, the carry-over effect of ENSO on survival of young birds can inform predictions of population trends, especially those due to climate change effects and the prediction of an increase of ENSO events. We highlight the importance of continuing ringing efforts and longitudinal monitoring programmes, particularly in light of acute conservation threats such as hunting (BirdLife International, 2017) and highly pathogenic strains of avian influenza (Banyard et al., 2022).

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343

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FIGURES

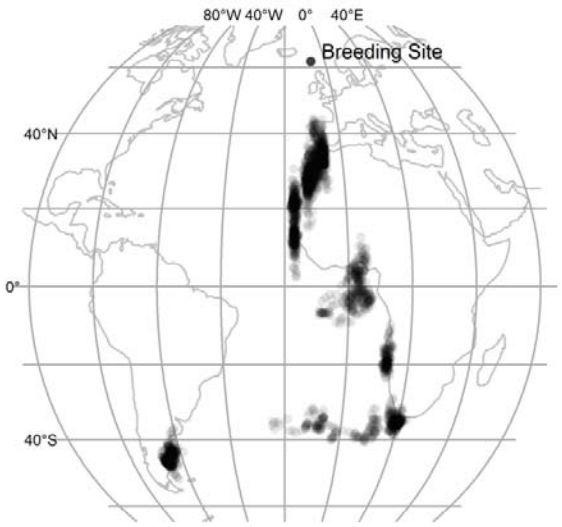

Fig. 1. Non-breeding areas of Arctic skuas breeding in Fugloy, Faroe Islands, based on positional data from 20 GLS tracked birds 2016-7 (van Bemmelen et al. ##). Bird largely over-winter on the Patagonian Shelf, Discovery Seamounts, coastally from Iberian peninsula to the Cape Verde Islands, the Gulf of Guinea, the Angola Current and from the Benguela Current westwards to Tristan da Cunha.

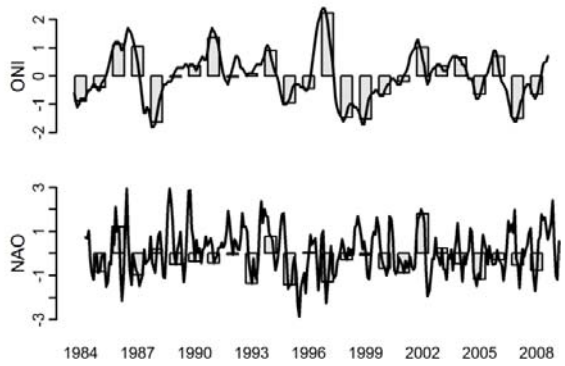

Fig. 2 a. The Oceanic Niño index (ONI) and b. North Atlantic Oscillation index (NAO). Lines represents 3-month rolling aggregate per calendar month. Bars shows the mean aggregate for period of interest: a. non-breeding period (September to March) and b. breeding period (May to July), of which values were used as covariants in the survival models.

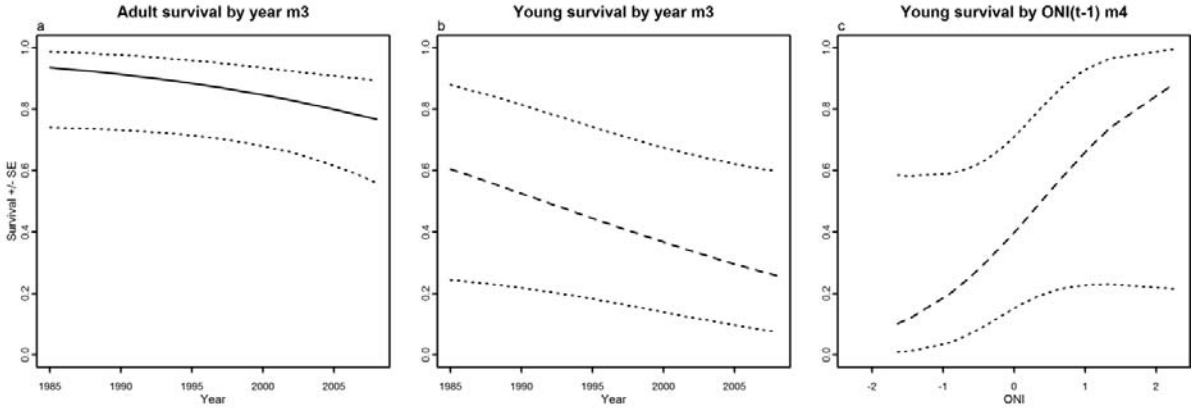

Fig. 3. Best supported models describing variation in survival probabilities for (a) adult and (b-c) young. The derived linear trend with (a-b) year and (c) the time-lagged oceanic Niño index, ONI(t-1), are shown with 95% confidence intervals. Solid lines

indicate strongly supported models, dashed lines are weakly supported (i.e. there is equal support for no trend: model 2).

Table 1. Annual survival model results for Arctic Skuas, temporal trends and environmental parameterization variables, Akaike's information criterion values adjusted for median-$\hat{c}$; (AICc), differences in AICc, weights, model likelihood, number of estimable parameters and deviance. Age represents 2 age-classes. ONI(t-1) is the time lagged (-1 year) Oceanic Niño index. Live capture probability (p), dead recovery probability (r) and fidelity (F) remain constant across models: p(3AGE[Young=Imm=0]),r(3AGE[Imm=0]),F(.). † combined model *Non-estimable

	Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Par	Deviance
1	{S(2AGE+TREND[Adult]+ONI(t-1)[Young])}	2383.7	0.00	0.245	1.00	8	1772.72
2	{S(2AGE+TREND[Adult])}	2384.4	0.70	0.173	0.71	7	1775.45
3	{S(2AGE+TREND[2AGE])}	2385.1	1.38	0.123	0.50	7	1776.13
4	{S(2AGE+ONI(t-1)[Young])}	2385.9	2.19	0.082	0.33	7	1776.94
5	{S(2AGE)}†	2387.2	3.56	0.041	0.17	6	1780.34
6	{S(2AGE+ONI(t-1)[Adult])}	2388.5	4.84	0.022	0.09	7	1779.59
7	{S(2AGE+TREND[Young])}	2389.0	5.32	0.017	0.07	7	1780.07
8	{S(2AGE+TREND[2AGE]+ONI(t-1)[Young])}	2389.5	5.86	0.013	0.05	6	1782.63