



No evidence for a decline in the density of Antarctic krill *Euphausia superba* Dana, 1850, in the Southwest Atlantic sector between 1976 and 2016

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ABSTRACT

The Antarctic marine environment is changing, and changes in the Southwest Atlantic sector have included decreases in sea ice and increases in water temperature. Associated with these changes is a reported 38% and 81% per decade decline in the numerical density (hereafter density) of Antarctic krill *Euphausia superba* Dana, 1850, between 1976 and 2003. Few changes in other components of the ecosystem that could be attributed to such a change, such as a mass decline in krill-dependent predators, have been detected. In an ecosystem so dependent on this keystone species, a massive population decline in krill ought to have had an obvious effect. In the absence of such an effect, it is timely to revisit the issue of the purported decline in krill density. The original analysis that indicated a decline in krill density was based on the 2004 version of KRILLBASE, a database of net samples. We analysed the publicly available and updated version (version 1, accessed 30 November 2017) and our analyses did not suggest a significant decline in krill density. Rather, after accounting for sampling heterogeneity and habitat variables, average krill density appears to have been stable but with considerable inter-annual variability. Since our results were unable to find any evidence for a decline in krill density we recommend a re-appraisal of many of the paradigms that underlie much of the recent thinking about ecosystem change Antarctic waters. Such a revision is necessary to provide a firmer foundation for predictions of the effects of climate change and resource extraction on the Southern Ocean ecosystem.

Key Words: net samples, use of models, populations, Southern Ocean ecosystem

THIRD INTERNATIONAL SYMPOSIUM ON KRILL

INTRODUCTION

Antarctic krill *Euphausia superba* Dana, 1850, hereafter krill, is one of the world's most abundant animals and plays a pivotal role in the Southern Ocean ecosystem as well as supporting the region's largest fishery (Flores *et al.*, 2012; Nicol & Foster, 2016). Large and sustained changes in the krill population would be expected to have important ecological ramifications, and would have consequences for management (Flores *et al.*, 2012).

The Southwest Atlantic sector of the Southern Ocean is believed to be home to 58–71% of the krill population (Atkinson *et al.*, 2004) and is the only region now routinely targeted by the

krill fishery (Nicol & Foster, 2016). The density of krill in the Southwest Atlantic sector was reported to have declined between 38–81% per decade between 1976 and 2003 (Atkinson *et al.*, 2004). Such a massive, long-term decline ought to be reflected in a decline in krill biomass. The relationship between krill biomass and numerical density is not necessarily linear because biomass may be affected by factors such as the size distribution of krill (Atkinson *et al.*, 2009). A biomass decline in line with the reported changes in density would almost certainly have obvious ecological repercussions. These would include declining population trajectories of a wide range of krill-dependent predators or evidence of sustained dietary shifts in specialist krill predators

such as the Antarctic fur seal *Arctocephalus gazelle* (Peters, 1875) and generalist predators such as the Adélie penguin *Pygoscelis adeliae* (Hombron & Jacquinot, 1841). Some studies have indicated changes in some elements of the ecosystem that could be attributed to a scarcity of krill (e.g., Reid & Croxall, 2001, Trivelpiece *et al.*, 2011) but ecosystem-wide changes have so far not been observed (Trathan & Reid, 2009). It is difficult to reconcile an estimated 38–81% decline per decade in krill density with the absence of a subsequent ecological catastrophe.

A long-term sustained decline in krill would also have management consequences. The krill fishery in the Southwest Atlantic sector is managed using a single biomass estimate derived from an acoustic survey conducted in 2000 (Hewitt *et al.*, 2004). If krill has declined at 38% per decade since the 1970s, present-day densities will be 15% of the 1970s density and 48% of its 2000 density. In continuing to use the biomass results from this survey, the implicit assumption is that krill biomass has not changed appreciably since 2000. Determining whether there is any ongoing trend in krill biomass is thus of paramount importance if the fishery is to be managed sustainably.

We investigated variability in krill density over time using the data contained in the database originally used in Atkinson *et al.*, (2004), KRILLBASE, which has been recently updated (Atkinson *et al.*, 2017). Our analyses differed from those in Atkinson *et al.* (2004) by considering variables, such as water temperature as well as the sampling regime, which was unbalanced in both space and time.

MATERIALS AND METHODS

Data description

KRILLBASE has been added to substantially since 2004, and now contains many more records than were originally available to Atkinson *et al.*, (2004). We used this updated KRILLBASE database (version 1, accessed 30 November 2017) comprising 14,543 krill density records. (Atkinson *et al.*, 2017). We isolated a subset of 7,670 KRILLBASE records that covered the Southwest Atlantic sector (-70° to -30° and latitude range -69° to -51°), and the ‘modern era’, from 1976 to 2016, in order to be consistent with the data used in Atkinson *et al.* (2004).

KRILLBASE contains data on location (KRILLBASE data fields: LATITUDE, LONGITUDE), density (NUMBER_OF_KRILL_UNDER_1M2) and net-type (NET_TYPE). KRILLBASE records include densities arising from ‘target trawls’, which are non-random net samples collected in response to the presence of acoustically detected krill. Target trawls, identified as those that sampled a near constant depth (range less than 10 m), were excluded from our analyses because of their non-random nature (Atkinson *et al.*, 2017). We excluded 127 records from further analysis because of missing information in some of the data fields.

To avoid double counting of samples, we removed the stratified hauls (multiple records from the same site) but retained the stratified pooled hauls (density estimated from pooled data from multiple net hauls at different depths at the same site) as this data type is similar to the far more common KRILLBASE haul data type. After these exclusions we were left with 7,075 records.

To account for the wide geographic range of the KRILLBASE data, we allocated each haul to the same spatial grid used by Atkinson *et al.* (2004), i.e. grid cells with dimensions 9° of longitude and 3° of latitude (Fig. 1). Following Atkinson *et al.* (2004), we removed cells with fewer than 50 records, cells that contained data from fewer than five years. To ensure that sufficient data were available to account for any net-type sampling variation, we removed net-types that were used fewer than 30 times, leaving 5,962 records for subsequent analysis (Supplementary material Table S1). Although this method differed from the approach in

Atkinson *et al.* (2004), our method enabled the effect of net-type to be considered during modelling. The remaining data comprised entirely of individual hauls from three net-types (NET_TYPE): Isaacs-Kidd, RMT8, and 2 m fixed-frame net. The usage of different nets varied between different time periods (Table 1), which is why it is important that net-type is accounted for in analysing trends.

Statistical modelling

We explored the inter-annual variability in krill density using data from individual records, rather than by cell means, using a two-component statistical hurdle model. We did this for two reasons. Firstly, krill live in swarms and have a highly patchy distribution so systematic surveys often result in large numbers of samples containing no krill. To account for this, we first asked the question ‘are krill present?’ (i.e., the hurdle). Secondly, for records where krill were present, we modelled krill density, ρ , given their presence in a record (denoted as $z = 1$), i.e. conditional density ($\rho | z = 1$). Using a hurdle model avoided the need to add an arbitrary constant to krill densities before \log_{10} transforming highly skewed net density data.

Both modelling stages used mixed effects models that include both fixed and random (population level) effects. Generalised additive mixed models (GAMMs) (Wood, 2006) were used for both the krill presence-absence and the conditional density models. Models were fitted using R (version 3.4.3; R Core Team, 2017) and the *gam4* (version 1.8.23; Wood, 2006) and *lme4* (version 0.2.5; Bates *et al.*, 2015) packages.

Selection of fixed effects structure

Any inter-annual trend in krill density is likely to be driven by a variety of environmental and sampling variables. We investigated the variables within KRILLBASE that helped to describe krill density. We developed eight combinations of explanatory variables for both the krill presence-absence and conditional density model (Supplementary material Tables S2 and S3, respectively), and used the Akaike information criterion (AIC) (Akaike, 1987) to select two models (Burnham & Anderson, 2003), one for describing krill presence-absence, the other for conditional density. Explanatory variables were represented as either single coefficients or smooth functions. Net-type specific inter-annual trends were captured using an interaction term (SEASON: NET_TYPE; e.g. candidate model M8; Supplementary material Table S2). Sampling variability within season was considered using the day of sampling since 1 October variable (DAYS_FROM_1ST_OCT) and diel vertical migration (DAY_NIGHT). Habitat variables of seabed depth (WATER_DEP_MEAN_WITHIN_10KM) and climatological temperature (CLIMATOLOGICAL_TEMPERATURE) were included as fixed effects since temperature is a fundamental driver of krill reproduction (Constable & Kawaguchi, 2017), moult frequency (Kawaguchi *et al.*, 2007), and growth (Wiedenmann *et al.*, 2008).

Random effects structure

The presence-absence model and conditional density model used a similar random effects structure, both having grid cell as a random effect. In the case of the conditional density model, the grid cell random effect was extended to a ‘slopes and intercepts’ model which allows for year-trend to vary across a population of cells represented by the spatial grid from Atkinson *et al.* (2004).

There is often strong spatial and temporal dependency in net hauls, such that densities in adjacent hauls are correlated and are not independent samples. Assuming independence would be invalid and would result in an overestimation of the amount of information in the dataset, and hence an underestimation of the variance, it would in effect be pseudo-replication (Millar & Anderson, 2004). To overcome this pseudo-replication we used the survey, as denoted using the organisation, year and designation

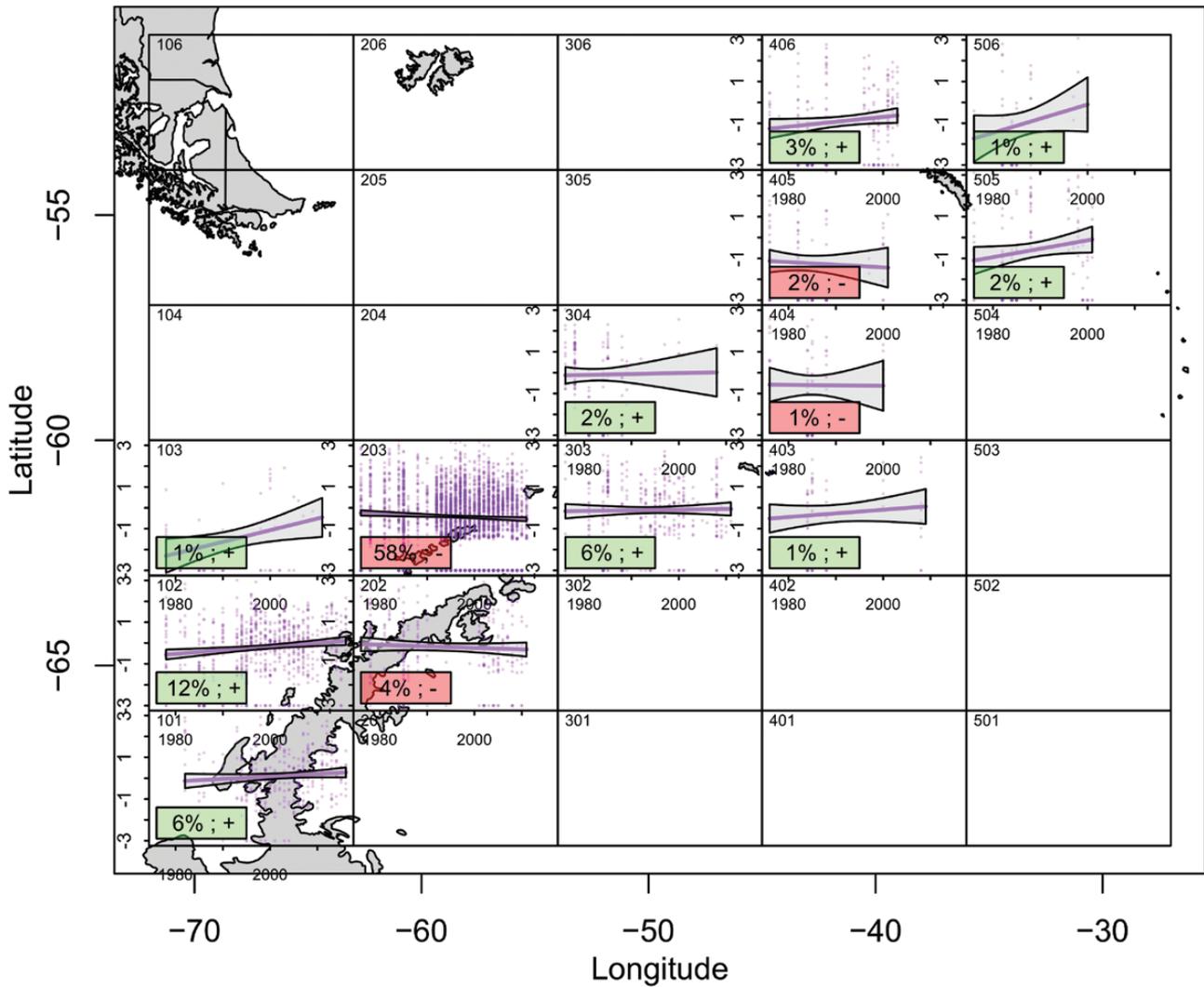


Figure 1. Spatio-temporal variation in density (ρ) of krill (*Euphausia superba*) in the Southwest Atlantic. Each purple dot represents density from haul data ($\log_{10}(\rho+c)$), where $c = \min(\rho)/2$ (Atkinson *et al.*, 2004). A linear regression (purple line) was fitted to the transect means in each of the grid cells to aid clarity. The linear regression (95% confidence intervals) is shown in grey. The percentage of hauls falling in each grid cell is given in the lower left of each grid cell. The krill population trend in each cell is colour coded (+, in green) for increasing krill, (-, in red) for decreasing.

code from the KRILLBASE STATION field, and included survey as an additional random effect (Millar & Anderson, 2004).

Krill presence-absence model

Krill presence-absence was modelled using a generalised additive mixed model (Supplementary material Table S2). Differences in sampling effort were accounted for by using records of the volume of water sieved by a net. The probability of capturing some krill should be greater when larger volumes of water have been

sampled. Lecomte *et al.* (2013) showed by simulation and using bottom trawl data from commercial fishery catches of dover sole *Microstomus pacificus* (Lockington, 1879) and Pacific Ocean perch *Sebastes alutus* (Glibert, 1890) the importance of including the sampled volume of water as a covariate in the presence-absence model component of a hurdle model. We ran our presence-absence models with two datasets: one that contained only data where the volume of water sampled was recorded ($N = 3,874$, years 1992 to 2016), and the other that contained all the data ($N = 5,962$, seasons 1976 to 2016), where volume was not always

Table 1. Nets used in the Southwest Atlantic data set analysed. PA, krill presence-absence data; CD, conditional density (density of krill present in a net; additional net information in Table 3 of Atkinson *et al.* (2017); *number of nets takes into account ‘survey’ record types that have multiple net samples in a single record.

Data type	Net name	Number of records	Number of nets*	Nominal mouth area m ⁻²	Number of years
PA	Isaacs-Kidd	2986	2986	3.08	20 (1992 to 2011)
PA	2 m fixed frame net	888	888	4.00	24 (1993 to 2016)
CD	Isaacs-Kidd	2779	2779	3.08	23 (1984 to 2011)
CD	RMT8	1416	1416	8.00	20 (1976 to 2003)
CD	2 m fixed- frame net	843	843	4	24 (1993 to 2016)

recorded. The full presence-absence model is described by equation S1 (Supplementary material Statistical modelling).

Conditional density

In the second component of our hurdle model we modelled \log_{10} transformed krill density (ρ) conditional on presence ($\log_{10}(\rho | z=1)$) using a GAMM (Supplementary material Table S3). Our models did not assume that krill density could only change at a constant rate over years. In the candidate models (Supplementary material Table S3) krill density year-trend was modelled as a smooth, cubic regression spline, fixed effect (row Mc7; Supplementary material Table S3), and in a separate model (row Mc8; Supplementary material Table S3) as a linear trend. The full model is described by equation S2 (Supplementary material Statistical modelling).

Confidence intervals and prediction

Confidence intervals of krill presence-absence and conditional density were estimated using a parametric bootstrap ($N = 1,000$) of the fitted model parameters. Predictions of krill conditional density trend (equation S3, Supplementary material Statistical modelling) were combined across net-types using a weighted average, with weights being the inverse of the standard error of predictions (equation S4; Supplementary material Statistical modelling). Unconditional krill density predicted using the sum of the \log_{10} predicted probability of presence and \log_{10} conditional krill density (equation S5; Supplementary material Statistical modelling).

The change in krill density from 1976 to 2016 was examined by calculating the ratio ($R\rho$) of the unconditional density prediction for 2016 to that of 1976, with a ratio below 1 indicating a decline, for each of the bootstrap simulations ($N = 1,000$).

RESULTS

Krill density varied spatially and temporally, and the trend in krill density also varied spatially. Each spatial cell exhibited different slopes and intercepts over time, with nine cells showing an increasing trend and four a decreasing trend (Fig. 1). These differences justify our use of a random effect for slope and intercept. Eight of the 13 spatial cells showed evidence of a non-linear trend (Fig. 1).

The spatial distribution of data within KRILLBASE was also considerably unbalanced, with 58% of the records falling in a single grid cell (number 203; Fig. 1).

Krill presence-absence modelling

Using AIC-based model selection, krill presence-absence was explained using a model comprised of fixed effects with smoothed cubic splines for year, the variable days since 1 October, water temperature, a linear term of seabed depth, and categorical variables of net-type and day or night sampling (Supplementary material Table S4).

Krill presence in net samples showed a statistically significant year-trend smooth ($s(S)$; $P = 0.03$), indicating that krill presence in nets increased with time. Krill were also less likely to be present in deeper waters throughout all years ($\beta_s = -0.21$; $P < 0.001$).

The effect of the net-type differed between the krill presence model that accounted for sampling volume (fitted using a reduced dataset of records, $N = 3,874$) and the model that did not account for sampling volume (fitted to all records, $N = 5,962$). In the model that accounted for sampling volume, net-type was not statistically significant ($P = 0.46$), whereas in the model that did not account for sampling volume, net-type was highly significant ($P < 0.025$). The probability of krill presence was high ($Pr(z=1) > 0.82$; Fig. 2). Average krill presence showed a long-term increase for both the models, although not significantly, with the confidence intervals at the beginning and end of both series overlapping.

Conditional density models

There was no evidence for an inter-annual trend in conditional krill density (Supplementary material Fig. S6). A log-linear interaction between year and net-type (Supplementary material Table S5) showed that different nets result in different estimates of trends in krill density. Inter-annual variation was explained in the selected model using a log-linear season net-type interaction. AIC-based model selection (Supplementary material Table S5) was unequivocal with a $dAIC = 4.1$ between the first model, with a log-linear net-type interaction, and the second ranked model with varying smooth functions of season by net-type. The highest-ranked model (model 1, first row in Supplementary

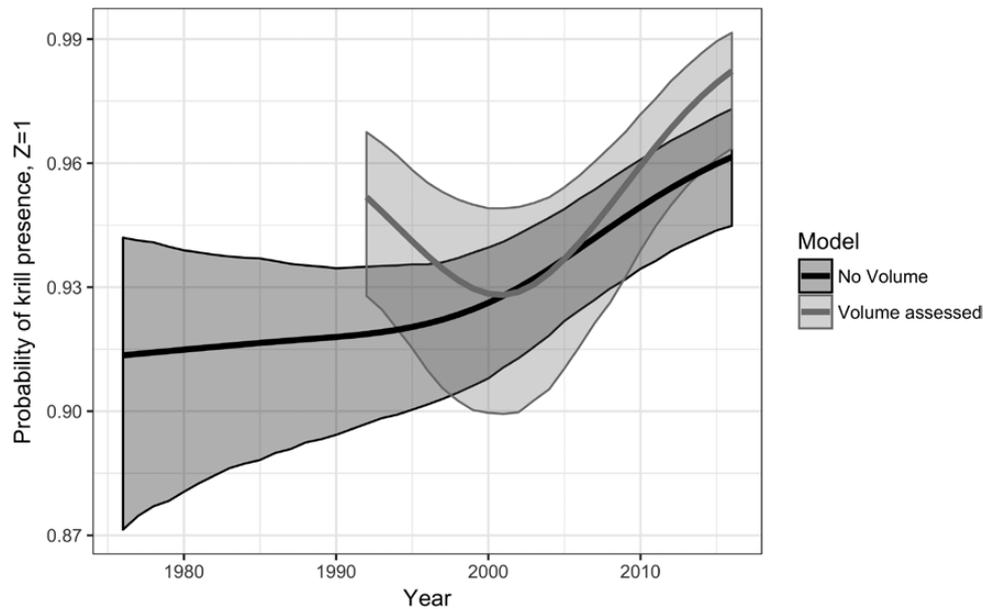


Figure 2. The trend in the probability of the presence of krill (*Euphausia superba*) using two models. Average probability trend is a broad line and the confidence intervals are shaded. The first model (No volume) ignores the volume of water sampled by a net. The second model (Volume assessed) accounts for volume of water sampled where such data is available and so spans a shorter time period.

material Table S5) also included fixed effect smooth terms for water temperature and days since 1 October. Model selection provided strong evidence that inter-annual trend alone is insufficient to model krill density as this model ranked lowest (model 8, last row in Supplementary material Table S5): this means that spatial variability and water temperature need also to be taken into account.

Unconditional density

Average unconditional krill density showed a nonlinear inter-annual trend (Fig. 3). The results suggest no detectable trend in krill density throughout the five decades analysed, although the large confidence intervals may mask shorter-term density fluctuations (Fig. 3). The practical difference between the models for unconditional density, either considering sampling volume or not, is limited, as shown by overlapping confidence intervals (Fig. 3).

The ratio of unconditional krill density predictions for the 2016 season to that of the 1976 season, R_p , was 0.431, the proportion of simulations where R_p was greater than 1, which indicates an increase in krill density.

DISCUSSION

Our analyses, which considered sampling variables (location, net-type, within-season time of sampling, and habitat variables such as seabed depth and temperature), were unable to find evidence for a large-scale and significant negative trend in krill density in the Southwest Atlantic sector during the period 1976–2016 (Fig. 3). The wide confidence bounds (shaded areas Fig. 3) mean that any inter-annual trend in krill density is difficult to detect.

Our models predict that for surveys re-run theoretically 1,000 times through the 1976 to 2016 period, 43% of these theoretical surveys would result in time series that suggested increasing krill density. We argue that this result is inconsistent with having a massive decline in krill density during this period.

Our results did reveal a significant trend for an increased occurrence of krill in shallower water, and for krill to be more likely present in nets towards the end of the time series. It is unclear whether these are real trends or a result of more recent surveys concentrating in areas where krill are more abundant within grid

cells. Our results also demonstrated the effect that the use of different sampling nets has on the estimation of density, highlighting the need to standardise nets used in krill studies.

Several interpretations of ecological changes in the Southwest Atlantic sector have been predicated on a large decrease in the krill population in the 1970s and 1980s driving change in populations of krill predators (Trivelpiece *et al.*, 2011). In the light of our findings, alternative mechanisms to explain observed ecosystem changes will need to be explored. Similarly, much criticism of the krill fishery and its management has been based on the concept of a long-term decline of the krill population that has not been taken account of in the management system (Jacquet *et al.*, 2010; Nicol & Foster 2016). Our results, and those analysing time series of acoustic surveys (Brierley *et al.*, 1999; Reiss *et al.*, 2008; Fielding *et al.*, 2014), suggest a krill population that is stable in the longer term but which exhibits considerable inter-annual fluctuations. These features of the krill population need to be taken into account in the future management of the fishery.

A long-term massive decline in the Southwest Atlantic krill population should elicit a detectable response in the populations of krill predators; an 81% decline per decade since the 1970s would result in a present-day krill density of less than 1% of its 1970s value. A permanent drop in krill density to such levels would be expected to have had a long-lasting deleterious effect on the populations of all predators in the Southwest Atlantic. The observed ecological signal in krill predators is equivocal. Some species of penguins in a number of colonies in the Southwest Atlantic have undoubtedly declined in abundance (Trivelpiece *et al.*, 2011; Lynch *et al.*, 2012), some very large colonies have remained stable (Lynch *et al.*, 2016), whilst other major consumers of krill such as Antarctic fur seals (Trathan & Reid, 2009) have increased in numbers considerably as they recover from historical over-harvesting.

Breeding failures in foragers returning to the same location between foraging trips, i.e. central-placed foragers, occur at South Georgia when acoustically-derived krill density drops below 20–30% of the long-term average (Brierley *et al.*, 1999), but breeding failures do not occur persistently, suggesting that an even greater and continuing decline in krill density is unlikely to have taken place.

During the period of the decline suggested by Atkinson *et al.* (2004), the krill fishery was also operating in the Southwest Atlantic

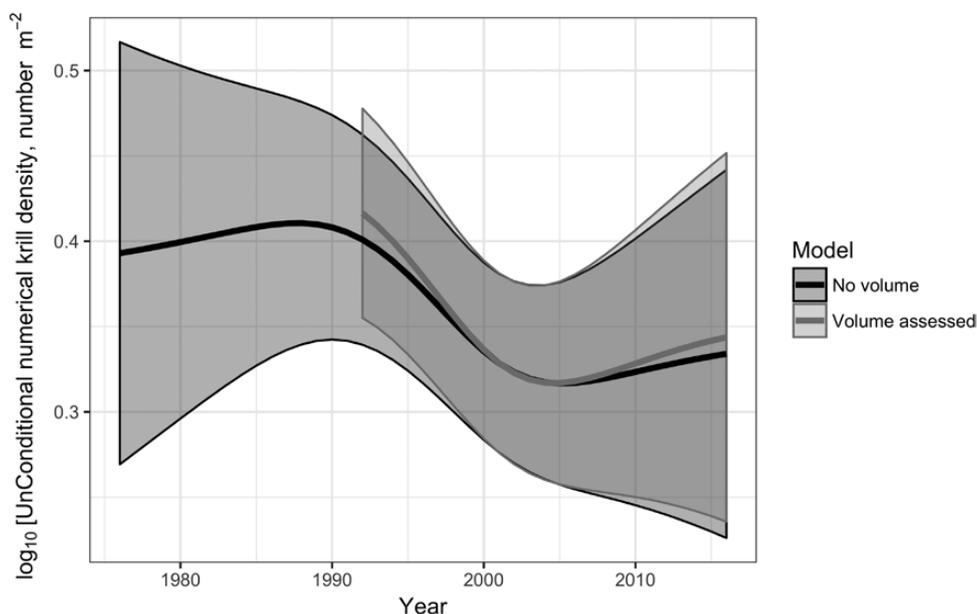


Figure 3. Densities of krill (*Euphausia superba*) considering the krill-presence models: volume not considered (No volume) and volume sampled modelled (volume assessed) and conditional density. Mean unconditional density is shown as solid lines and confidence intervals as shaded areas.

sector. Indices from the fishery show no dramatic change during the 1980s and 1990s that would be consistent with such a major decline in the targeted population (Kawaguchi *et al.*, 2005). Although the annual krill catch declined from a historical high of over 500,000 tonnes during the early 1980s to around 120,000 tonnes in the early 2000s, such decline was a result of economic and political factors, rather than a scarcity of krill (Nicol & Foster 2016).

Given the results of our analysis, and the nature of the data from predator monitoring, acoustic surveys, and fisheries, we suggest that there has been no long-term decline in krill density, or indeed biomass in the Southwest Atlantic sector. Instead, we conclude that the long-term decline in the krill population presented in Atkinson *et al.* (2004) is a consequence of their not considering interactions between krill density and unbalanced sampling in time and space in the data, and not accounting for the different net-types used. Future studies that are designed to investigate trends in krill abundance, distribution, and density will need to be designed using a range of standard techniques (e.g. agreed scientific nets and acoustics) and a rigorous sampling strategy. We suggest that paradigms that underlie much of the recent thinking about climate-driven change in krill populations, and in the Antarctic marine ecosystem more generally, need to be revisited in the light of these findings.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

Statistical modelling.

S1 Table. KRILLBASE data.

S2 Table. Model formulation for krill presence-absence.

S3 Table. Model formulation for krill conditional density.

S4 Table. Model selection results for krill presence-absence.

S5 Table. Model selection results for krill conditional density.

S6 Figure. Krill conditional density predictions.

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