



Temporal changes in abundances of large calanoid copepods in the Scotia Sea: comparing the 1930s with contemporary times

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Abstract

To investigate whether impacts of reported climate change in the Antarctic marine environment have affected mesozooplankton populations, we compared the summertime abundances of four species of large calanoid copepods from samples taken during the *Discovery Investigations* (1926–1938) and contemporary times (1996–2013). *Discovery* samples were obtained using an N70V closing net fished vertically through three depth horizons encompassing the top 250 m of the water column, whereas contemporary samples were obtained using a Bongo net fished vertically through 200–0 m. Data from a previous study comparing catch efficiencies of the two nets were used to generate calibration factors which were applied to the N70V abundances. Following further corrections for net depth differences and seasonal biases in sampling frequency, three of the four species, *Calanoides acutus*, *Rhincalanus gigas* and *Calanus simillimus*, were found to be between ~20–55% more abundant in contemporary times than they were 70 years ago. *Calanus propinquus* was marginally more abundant in the *Discovery* era. These results were robust to sensitivity analyses for the net calibration factor, seasonal bias and net depth corrections. Although near-surface ocean temperatures within the Scotia Sea have increased by up to 1.5 °C during the last 70 years, we conclude that the most likely causes of increased copepod abundances are linked to changes in the food-web. In particular, we discuss the reported decrease in krill abundance in the South Atlantic that has potentially increased the amount of food available to copepods while at the same time decreasing predator pressure.

Keywords *Discovery Investigations* · Calanoid copepods · Scotia Sea · Climate change · Trophic cascades

Introduction

The impacts of climate change are being felt worldwide in the marine environment. Species and communities are responding to complex interactions of environmental forcing factors such as increasing temperature, ocean acidification and ocean-atmospheric coupling, which exert their effects over a range of spatial and temporal scales (Richardson 2008; Hátún et al. 2009; Burrows et al. 2011; Richardson et al. 2012; Poloczanska et al. 2013).

In the Southern Ocean, warming has been taking place for at least the last 50–70 years (Gille 2002; Meredith and King 2005; Whitehouse et al. 2008) and has been attributed to near-surface ocean–atmosphere–ice interactions (Turner

et al. 2013). Consequences of warming have included regional changes in sea-ice extent and duration (Stammerjohn et al. 2008) which has subsequently been suggested as a major factor in the recent decline of Antarctic krill and increases in salp abundance (Loeb et al. 1997; Atkinson et al. 2004; Flores et al. 2012).

Impacts of environmental change on other planktonic groups are however less well understood (Constable et al. 2014). Copepoda are the dominant mesozooplankton group in the Southern Ocean but the factors affecting their distribution and abundance have been harder to establish, in part because of a lack of extensive time-series measurements. Changing patterns of atmospheric variability such as the Southern Annular Mode (SAM) which has an important influence on zonal winds (Sen Gupta and McNeil 2012) and the Southern Oscillation Index (SOI) have been linked to changes in plankton abundance. For example, near Elephant Island, Loeb et al. (2009, 2010) found significant correlations between the abundance and concentration of phytoplankton, zooplankton and krill with the SOI which

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exhibited 3–5 year frequencies characteristic of El Niño–Southern Oscillation (ENSO) variability. They found that abundances of *Calanoides acutus*, and *Rhincalanus gigas*, characteristic of the Antarctic Circumpolar Current (ACC), were positively correlated with chlorophyll *a* (Chl *a*) and the SOI. These changes appeared related to the influence of the SOI on water mass movements, with high copepod abundances associated with a southwards movement of ACC waters into the coastal regions off the northern–Antarctic Peninsula. Conversely, during periods when the sign of the SOI was negative, salps tended to become dominant. However, at South Georgia, abundances of krill and copepods were found to be negatively related across a range of scales suggesting direct interactions either as competitor or predator (Atkinson et al. 2001), rather than being solely mediated by ocean–atmosphere coupling. Thus, the balance of zooplankton composition represents a complex of oceanic–atmospheric—sea-ice and competitive interactions which are only just beginning to be teased apart.

Over a longer timescale, Tarling et al. (2018) compared copepod distributions in the Scotia Sea from *Discovery Investigations* (1920s–1930s) and contemporary times (1996–2013) and showed that, over intervening years, populations have essentially remained in the same geographical location despite ocean warming. Had they occupied the same thermal envelope which they inhabited in the 1930s, current distributions would be up to 500 km further south (see also Mackey et al. 2012). Reasons for maintenance of their historical distributions were attributed to food availability and the properties of the underlying water masses where a number of the species over-winter. It was also found that there had been a negligible difference in the rank order of abundance of dominant copepod species sampled over 70 years apart. However, ranked abundance can mask numerical changes, particularly if some species/taxa are extremely abundant and others less so. In this paper, we explore this further and have focussed on the commonly occurring biomass-dominant large calanoid copepods (*C. acutus*, *R. gigas*, *Calanus simillimus* and *Calanus propinquus*). We wished to establish whether abundances were the same between eras and, if not, to seek to understand what factors may lie behind any changes.

Methods

Copepod net sampling and abundance

Net sample stations

We analysed net samples from stations south of the Polar Front in the southwest Atlantic sector of the Southern Ocean, collected as part of the *Discovery Investigations*

(1926–1938) and during contemporary cruises (1996–2013). Our analysis was confined to samples taken in the austral summer months of December–February, between the latitudes of 52–66°S.

The species under consideration have broad and overlapping distributions within the ACC although repeated sampling has shown that *C. simillimus* and *R. gigas* have more northerly distributions compared to *C. acutus* and *C. propinquus* which tend to inhabit colder waters to the south (Atkinson 1998; Schnack-Schiel 2001). The timing of their lifecycles and the presence of populations in near-surface waters vary according to latitudinal progression of the seasons (earlier in the north) with recruitment occurring up to 3 months earlier in some years in the northern parts of the ACC compared to the south (Ward et al. 2006, 2012a). In comparing between the two eras, we have assumed that any changes in the timing of the annual pattern of occurrence of species stages has been captured within the 3 summer months (December, January and February) on which the analysis focussed.

Stations were determined to be south of the Polar Front from the vertical temperature profile recorded at each station (Gordon et al. 1977; Tarling et al. 2018). The *Discovery* sample set accordingly comprised 53 N70V vertical closing net stations supplemented with an additional 10 N70V stations sampled during December 1926 and January 1927, for which catch data were extracted from *Discovery Report 11* (appendix of Hardy and Gunther 1935). The contemporary dataset comprised catches made with a paired Bongo net at 147 stations (Fig. 1).

Net sample analysis

During sample analysis, the copepodite stages and adults of large calanoid copepod species were either enumerated from complete samples, or the whole sample placed in a Folsom plankton splitter and fractionated into replicate aliquots until countable numbers (~200 individuals) were estimated to be present. Abundances of taxa were standardised to numbers per net sample and the amount of water each net filtered was estimated based on mouth area and distance towed, to derive individual species concentrations (ind. m⁻³). Of the large calanoid species, four were consistently present across the majority of samples and became the focus of subsequent numerical analyses, those species being *R. gigas*, *C. acutus*, *C. simillimus* and *C. propinquus*.

Data preparation

Accounting for different integrated depths

At each *Discovery* station samples were collected from three depth horizons (50–0, 100–50 and 250–100 m) and

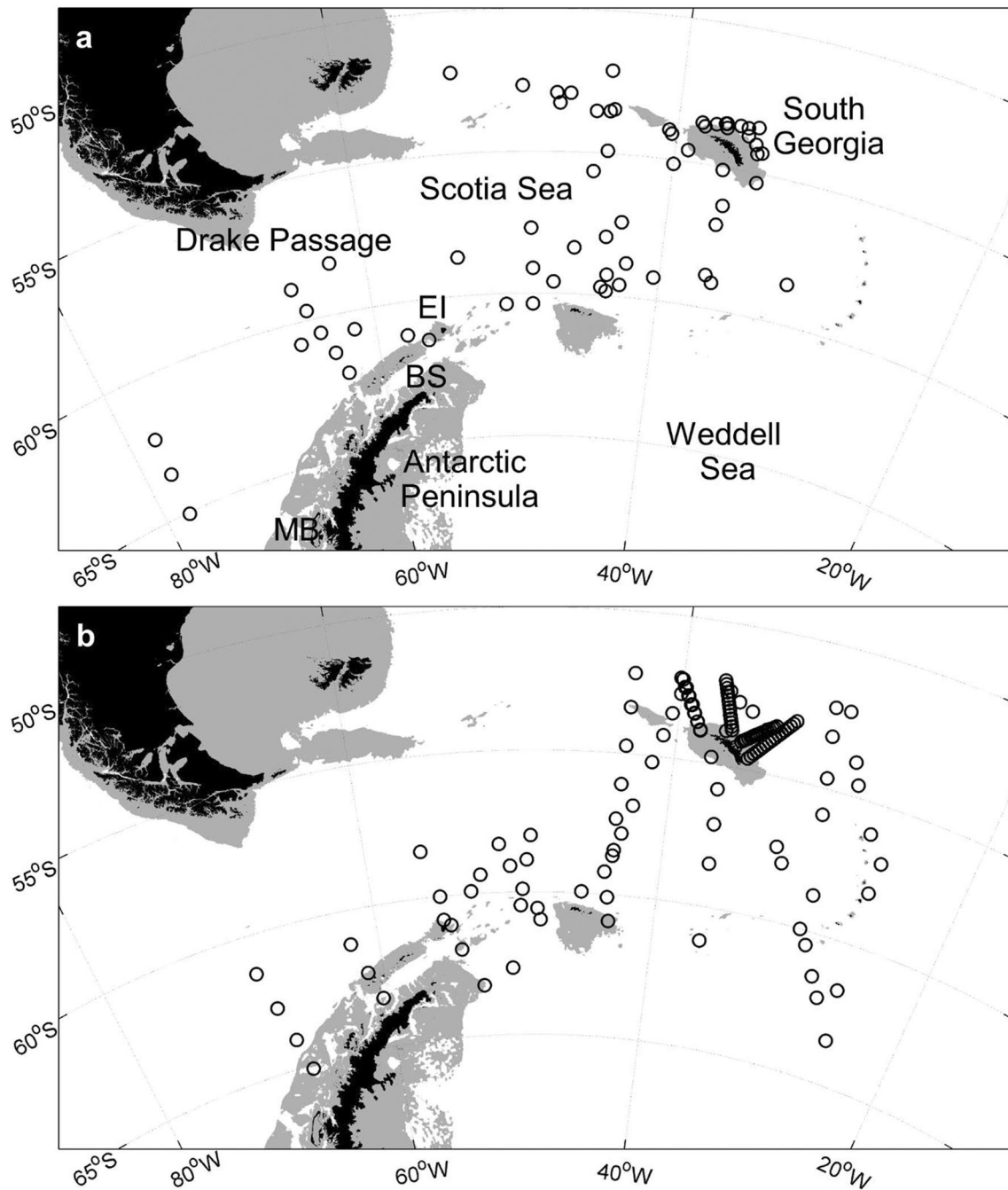


Fig. 1 Zooplankton sample distribution. **a** *Discovery Investigations* (1926–1938). **b** Contemporary era (1996–2013). Bathymetry shallower than 500 m is shaded grey. Place name abbreviations on (a) are Bransfield Strait (BS), Elephant Island (EI), Marguerite Bay (MB)

abundances integrated from 250 to 0 m. Contemporary samples were collected between 200 and 0 m. Copepod abundances were determined in terms of concentrations as individuals per cubic metre (ind m^{-3}) for both sets of samples. However, the majority of copepods reside in the top 200 m at this time of year (Atkinson 1991; Atkinson and Sinclair 2000) which potentially reduces concentrations in

the *Discovery* samples relative to the contemporary samples because of the extra 50 m depth contributing to overall sample volume. Therefore, we multiplied *Discovery* abundances by 1.25 to account for this potential bias. Both sets of samples were subsequently multiplied by 200 m to derive a depth integrated abundance value for the 0–200 m surface layer (ind. m^{-2}).

Accounting for net type bias

Different net types were used in the two eras of sampling. The *Discovery Investigations* collected N70V samples from nets deployed vertically between the 3 horizons (see above) within the surface 250 m (Kemp et al. 1929). Mesh sizes in this net decrease in stages from 5 mm in the upper part, to 440 μm and then 195 μm in the mid and lower parts respectively (measurements are metric equivalents of the original imperial units; see Kemp et al. 1929). In contrast, the contemporary samples were collected from Bongo net deployments (net dia. 0.61 m, 200 μm mesh net) fished vertically from 200 to 0 m.

To enable a comparison between the two net types, an N70V net was reconstructed using nylon mesh of the nearest metric equivalent to the imperial measurements of the bolting silks originally specified in Kemp et al. (1929). The nets were fished alongside each other at a series of stations in Marguerite Bay on the Antarctic Peninsula and across the Scotia Sea to determine a broad spectrum calibration factor (Ward et al. 2012b). For the present study, we re-analysed these data to establish species-specific inter-calibration factors for the four principal calanoid species under consideration.

One particular issue was to take into account the different developmental stages (CI to adult) of the sampled copepods, since the changes of size may alter respective catchabilities and retentions by the two different nets. We therefore compared the abundances of each individual developmental stage of each of the 4 species in every calibration station of Ward et al. (2012b) to determine the average residual difference (Res), as follows:

$$Res_{s,d} = \frac{\sum_{station=1}^n (N_{B,s,d} - N_{N70,s,d})}{n} \quad (1)$$

where N is abundance (ind. m^{-2}) of either the calibration Bongo net, B , or the calibration N70V net, $N70$, s is species and d is developmental stage from CI to adult (male and female).

It was also necessary to take into account the relative contribution of each of these developmental stages to total species abundance. In certain *Discovery* samples, some individuals had previously been removed and although numbers taken were specified on sample labels, stage distributions were not. Data taken from Hardy and Gunther (1935) were also simply reported as species numbers rather than by stage. Therefore, it was necessary to infer typical proportional stage distributions from the contemporary samples. Hence, $Res_{s,d}$ was multiplied by the relative proportion of stages within species in the contemporary samples ($Pr_{s,d}$), so that a standardised residual difference, $SRes_{s,d}$, could be determined as follows:

$$SRes_{s,d} = Res_{s,d} \times Pr_{s,d} \quad (2)$$

$SRes_{s,d}$ was divided by the average abundance of the N70V calibration hauls to produce a normalised developmental stage specific calibration factor ($Cal_{s,d}$) which was then summed across all stages to produce a species-specific calibration factor (Cal_s):

$$Cal_{s,d} = \frac{SRes_{s,d}}{(\sum_{station=1}^n N_{N70,s})/n} \quad (3)$$

$$Cal_s = \sum_{d=d_1}^{d=d_t} Cal_{s,d} \quad (4)$$

where d_j is development stage 1 (CI), d_t is final adult stage (male and female).

Discovery sample abundances ($N_{DI,s}$) were then multiplied by $1 + Cal_s$ to determine a calibrated abundance ($N_{Dical,s}$) with which to compare against contemporary abundances ($N_{C,s}$):

$$N_{Dical,s} = N_{DI,s} \times (1 + Cal_s). \quad (5)$$

Accounting for seasonal bias

Further data analyses revealed a seasonal trend in datasets whereby there was a substantial increase in abundances in January compared to December and February in both the *Discovery Investigations* and contemporary sample sets. However, sampling effort varied between the two eras, with there being a proportionally greater sampling effort in January in the contemporary dataset compared to the *Discovery* dataset. To account for this potential bias, we resampled the two datasets so that there was even selection of datapoints across the 3 months. For both the *Discovery* and contemporary datasets ($N_{Dical,s}$ and $N_{C,s}$), 10 datapoints were selected at random (with replacement) from each of the 3 months and combined to make a new resampled dataset of 30 datapoints, for which an average was determined. The process was repeated 100 times for each species, to which statistical tests were then applied (see below).

Sensitivity analyses

To determine the sensitivity of the inter-era comparison of species abundance to the various stages in data preparation, a series of sensitivity analyses were run. The two main treatments to the original datasets were the inter-calibration of abundances caught by the two different nets and the resampling to account for seasonal sampling bias, so the objective of the sensitivity analysis was to determine whether species-specific abundances remained significantly different between eras when treatments were altered. For the calibration factor

sensitivity tests, the factors were increased by 25, 50 and 100% or removed completely. Multiplying the calibration factor by percentages below 0 was not considered given that this would always act to increase the level of difference between the two eras. For the seasonality sensitivity tests, runs were carried out to determine the effect of removing the resampling process. The 1.25 multiplication factor to the *Discovery* nets was also removed in a further test to determine its implications.

Statistical tests

Comparisons of abundances between eras were tested either using an unpaired *t* test or a Mann–Whitney Rank Sum test (*U* test), the latter being used in instances where the datasets failed a priori tests for normality (Shapiro–Wilk test) or equal variance. A Kruskal–Wallis 1-way ANOVA on ranks test was applied to differences between months. Tests producing significant differences were further tested using a Dunn’s Method all Pair-wise Multiple Comparison Procedure.

Results

Calibration

To determine the calibration factor, it was necessary to consider the relative proportion of stages within species in the contemporary samples (Fig. 2). Although there was interspecific variation in the relative abundance of developmental stages, the CIII and CIV stages were generally among the most frequent (Fig. 2). For instance, CIII was the most frequent stage in *R. gigas*, with stages CII and CI also being relatively abundant. A similar pattern was apparent in *C. propinquus* although stage CI was comparatively low in abundance while CIV had a similarly high frequency to stage CII. In *C. acutus* and *C. simillimus*, the later developmental stages (CIV and CV) had higher frequencies than the earlier developmental stages. Adult females were more abundant than males in all species, although both were relatively infrequent compared to the earlier developmental stages.

The calibration factor also required the residual difference in species and stage specific abundances to be determined in matched Bongo and N70 hauls. In these hauls, it was found

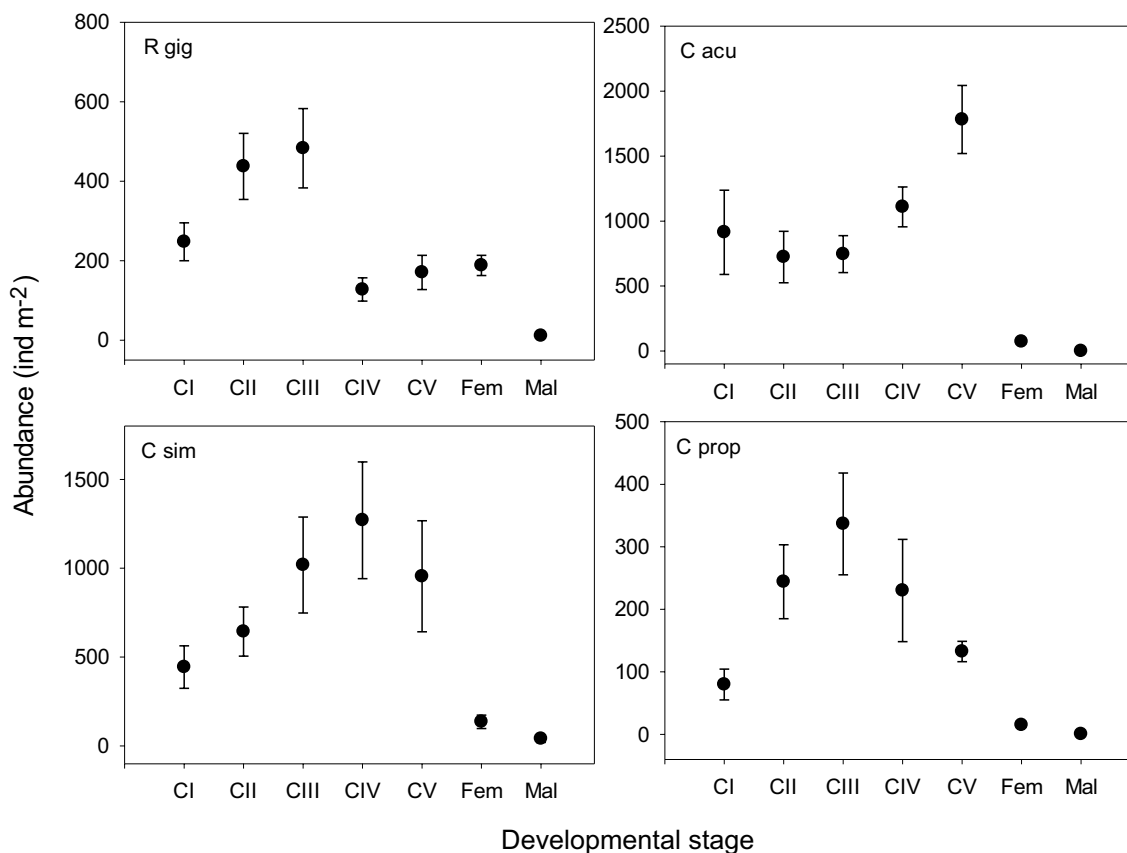


Fig. 2 Development stage abundance (contemporary data only): Average (SE) depth integrated abundance (ind m⁻²) of developmental stages of *Rhincalanus gigas*, *Calanoides acutus*, *Calanoides simillimus* and *Calanoides propinquus* from Bongo net samples in the contemporary era

that more individual copepods were captured by Bongo nets than N70V nets, with the majority of residual differences (i.e. Bongo minus N70V, $Res_{s,d}$) being positive (Fig. 3). The residual differences were much greater in *C. acutus* and *C. simillimus* than they were in *R. gigas* and *C. propinquus*. In *C. acutus*, some of the greatest differences were observed in the early developmental stages, although CIV also exhibited a high value for $Res_{s,d}$. Only CI and CII showed notably high values for $Res_{s,d}$ in *C. simillimus* with a further minor peak in the females. *R. gigas* exhibited a similar peak in $Res_{s,d}$, but there was little pattern in the low values of $Res_{s,d}$ in *C. propinquus*.

The calibration factor ($1 + Cal_s$) is a function of both the residual difference between calibration hauls and relative proportion of stages within species (Table 1). The highest calibration factors were observed in *C. acutus* and *C. simillimus*, for which the highest values for $Res_{s,d}$ were observed. However, the corresponding stage distribution downweighs the calibration factor in *C. acutus* in relation to *C. simillimus*. The calibration factors for *R. gigas* and *C. propinquus* were low since both have comparatively low species abundances and low residual differences.

Comparison of abundances between eras

There were substantial differences in species abundances between the three summer months included in the analysis, with abundance levels in January being almost double those of December and February in both the *Discovery Investigations* and contemporary samples (Fig. 4). The difference between months was significant in both eras (*Discovery Investigations*, Kruskal-Wallis test, $H=7.328$, 2 df, $p=0.026$; Contemporary, $H=7.475$, 2 df, $p=0.024$).

There was a difference in sampling effort between the respective months, with January containing the highest sampling effort in the contemporary dataset and the lowest in the *Discovery Investigations* dataset (Fig. 4). This necessitated data resampling in order to dampen any temporal bias in the comparison of abundances between the two datasets (see "Methods").

The calibrated abundances of *R. gigas*, *C. acutus* and *C. simillimus* in the *Discovery* samples were considerably and significantly lower than those in the contemporary samples (Fig. 5) (*Discovery* vs Contemporary; *R. gigas*: Mann-Whitney *U* Test, $T=6590.000$ $n(\text{small})=100$ $n(\text{big})=100$,

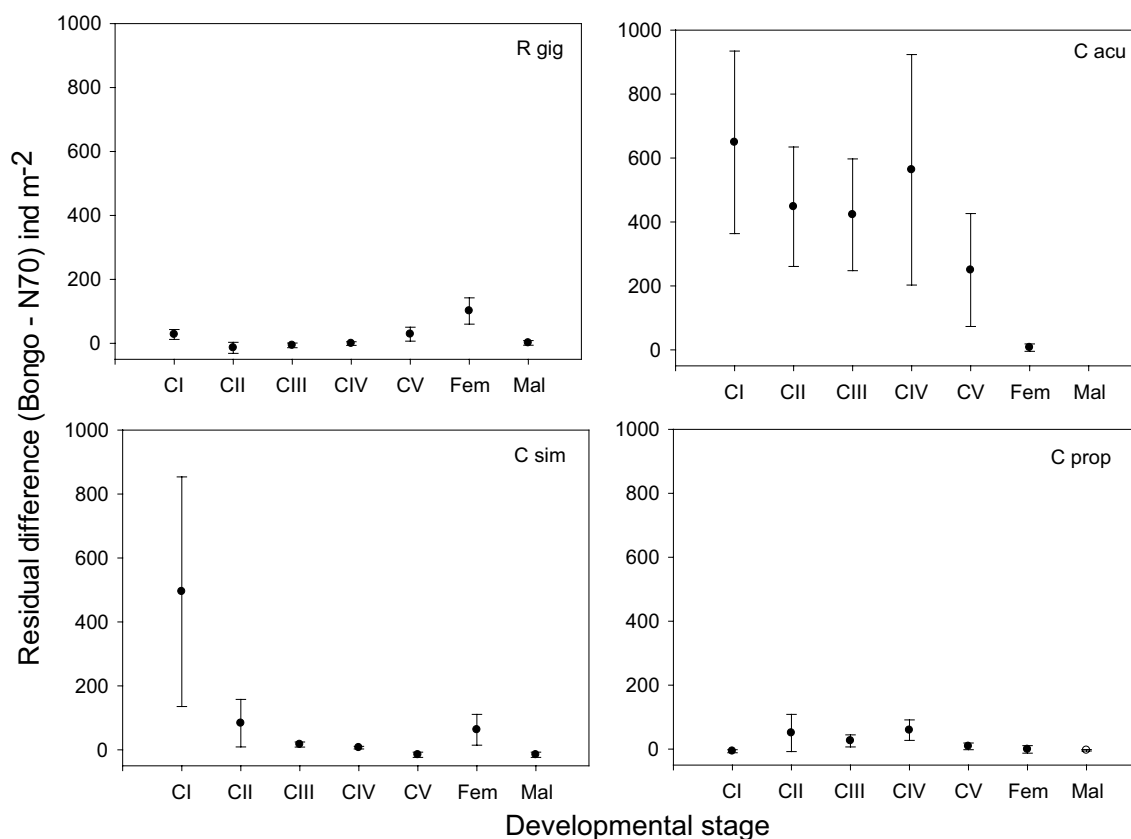


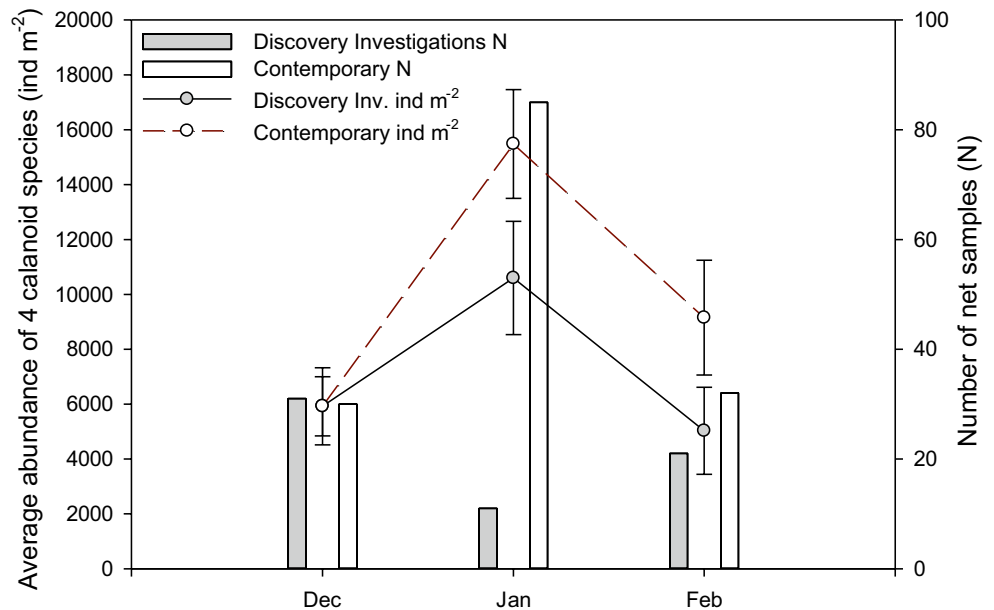
Fig. 3 Residual difference species stage: Residual difference ($Res_{s,d}$ ind m^{-2}) between abundances of *Rhincalanus gigas*, *Calanoides acutus*, *Calanoides simillimus* and *Calanoides propinquus* individual

developmental stages estimated by Bongo nets and N70V nets in simultaneous calibration hauls

Table 1 Calibration factor: Parameters derived in order to determine a Calibration factor (Cal_s) for *Rhincalanus gigas*, *Calanoides acutus*, *Calanoides simillimus* and *Calanoides propinquus* to standardise abundance estimates of N70V catches during the *Discovery Investigations* against contemporary Bongo catches

	Mal	Fem	CV	CIV	CIII	CII	CI	Calibration factor ($1 + Cal_s$)
<i>R. gigas</i>								
Residual difference ($Res_{s,s}$ ind m^{-2})	1.609	101.527	28.931	-0.420	-6.327	-13.995	28.051	
Stage proportions ($Pr_{s,d}$)	0.013	0.211	0.137	0.064	0.213	0.235	0.127	
Normalised proportional difference ($Cal_{s,d}$)	0.000	0.193	0.036	0.000	-0.012	-0.030	0.032	1.219
<i>C. acutus</i>								
Residual difference ($Res_{s,s}$ ind m^{-2})		7.413	249.952	563.340	422.820	447.800	649.381	
Stage proportions ($Pr_{s,d}$)		0.060	0.393	0.255	0.116	0.077	0.100	
Normalised proportional difference ($Cal_{s,d}$)		0.000	0.090	0.132	0.045	0.032	0.060	1.359
<i>C. simillimus</i>								
Residual difference ($Res_{s,s}$ ind m^{-2})	-15.543	62.503	-15.543	6.633	16.450	83.075	494.562	
Stage proportions ($Pr_{s,d}$)	0.016	0.145	0.116	0.184	0.235	0.192	0.112	
Normalised proportional difference ($Cal_{s,d}$)	-0.002	0.062	-0.012	0.008	0.026	0.109	0.379	1.571
<i>C. propinquus</i>								
Residual difference ($Res_{s,s}$ ind m^{-2})	-3.855	-1.188	8.542	59.011	25.490	50.165	-6.674	
Stage proportions ($Pr_{s,d}$)	0.001	0.073	0.227	0.256	0.245	0.149	0.049	
Normalised proportional difference ($Cal_{s,d}$)	0.000	-0.001	0.018	0.144	0.059	0.071	-0.003	1.289

Fig. 4 Seasonality: Average (SE) abundance (ind m^{-2}) and number of net-catches (N) in individual summer months in *Discovery Investigations* and contemporary sample sets

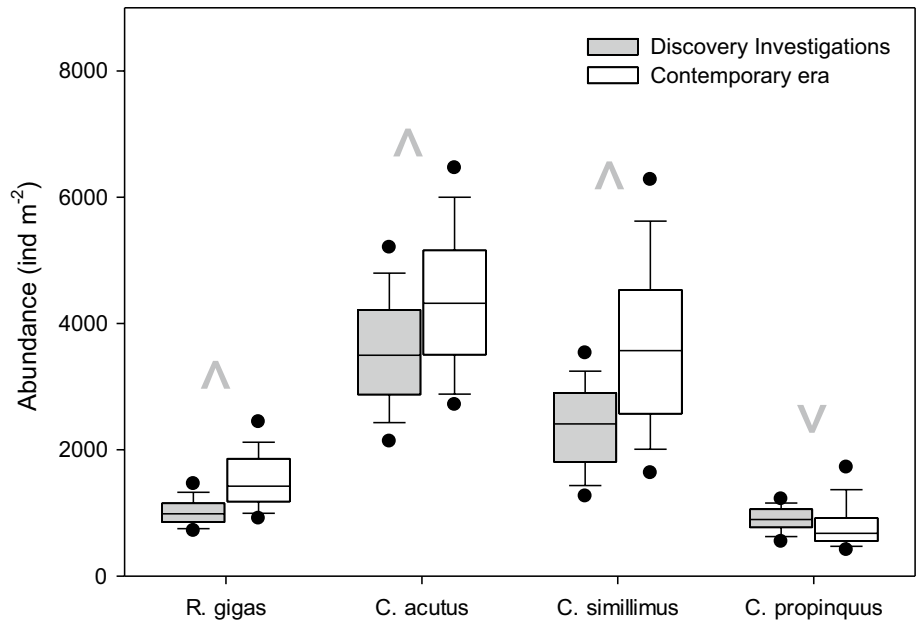


$p < 0.001$, *C. acutus*: $T = 7590$, $n(\text{small}) = 100$ $n(\text{big}) = 100$, $p < 0.001$; *C. simillimus*: $T = 7053.000$ $n(\text{small}) = 100$ $n(\text{big}) = 100$, $p < 0.001$). In the case of *C. acutus*, calibrated abundances were around 80% of the values observed in contemporary times (mean \pm SE of 3553 ± 101 and 4374 ± 116 ind m^{-2} respectively) while, in *R. gigas* and *C. simillimus*, *Discovery* samples were between 65 and 70% of contemporary values (respective mean \pm SE of 1020 ± 22 and 1525 ± 47 ind m^{-2} for *R. gigas* and 2377 ± 70 and 3711 ± 139

ind m^{-2} for *C. simillimus*). However, in *C. propinquus*, the opposite trend was observed, with values being significantly higher in the *Discovery* era (mean \pm SE of 903 ± 21 ind m^{-2} vs 812 ± 41 ind m^{-2} for contemporary era), although the absolute or proportional differences (91 ind m^{-2} and 90% respectively) were not as substantial as for the other species.

Levels of significance in these results were relatively insensitive to the calibration factor (Table 2). When removing the calibration factor altogether or increasing its value

Fig. 5 *Discovery Investigations* versus Contemporary abundance Box plot of estimated abundance (ind m⁻²) of *Rhincalanus gigas*, *Calanoides acutus*, *Calanoides simillimus* and *Calanoides propinquus* during the *Discovery Investigations* and contemporary times. Horizontal line represents the median, limits of boxes, 25th and 75th percentiles, limits of whiskers, 10th and 90th percentiles, dots, 5th and 95th percentiles. ^ indicates abundances during contemporary era were significantly larger than those during the *Discovery Investigation* era, v, that *Discovery Investigation* era abundances were significantly larger than those in the contemporary era (*p* < 0.001)



by 25 or 50%, values in contemporary times were still significantly larger in *R. gigas*, *C. acutus* and *C. simillimus*. Only when the calibration factor was increased by 100% was there any change to this result, with *C. acutus* no longer

significantly more abundant in the contemporary era. Greater sensitivity was exhibited in relation to seasonality in abundance levels, with the removal of the resampling procedure to dampen the effect of different levels of sampling effort

Table 2 Sensitivity: Analyses to determine the sensitivity of *Discovery Investigations* and contemporary estimates of species-specific abundance to the parameters used in the inter-calibration of the respective nets and the standardisation of differences in sampling effort and sampling protocol

	<i>R. gigas</i>		<i>C. acutus</i>		<i>C. simillimus</i>		<i>C. propinquus</i>	
	Disc	Cont	Disc	Cont	Disc	Cont	Disc	Cont
Best run								
Av	1019.84	1525.19	3552.79	4374.24	2376.70	3710.72	902.70	811.96
SE	22.08	47.36	101.39	115.99	70.20	138.52	20.89	41.33
No calibration factor								
Av	733.27	1561.93	2337.57	4191.51	1393.69	3718.40	684.22	774.30
SE	17.99	44.55	61.06	115.45	44.49	160.35	16.64	40.09
Increase of calibration factor by 25%								
Av	934.01	1561.93	3386.55	4191.51	2388.43	3718.40	931.39	774.30
SE	22.92	44.55	88.46	115.45	76.24	160.35	22.64	40.09
Increase of calibration factor by 50%								
Av	974.15	1561.93	3596.35	4191.51	2587.38	3718.40	980.82	774.30
SE	23.90	44.55	93.94	115.45	82.59	160.35	23.85	40.09
Increase of calibration factor by 100%								
Av	1054.45	1561.93	4015.94	4191.51	2985.28	3718.40	1079.69	774.30
SE	25.87	44.55	104.90	115.45	95.29	160.35	26.25	40.09
No normalisation to accommodate seasonal bias in sampling effort								
Av	906.89	1703.46	3597.19	5505.49	1875.33	3610.87	717.53	1029.01
SE	20.41	48.70	107.11	172.16	75.17	150.64	24.11	51.32
Remove 1.25 multiplication factor to <i>Discovery Investigation</i> samples								
Av	653.46	1541.88	2542.84	4084.85	1088.00	3264.01	491.34	728.53
SE	28.29	72.58	148.09	248.98	117.63	219.71	35.96	67.58

Bold indicates where contemporary abundance is significantly greater than that of the *Discovery Investigations*, italics indicates where *Discovery Investigations* abundance is significantly greater than contemporary era abundance, standard text indicates that no significant differences in abundance exist

between months increasing the level of difference between eras, with even *C. propinquus* now exhibiting significantly greater abundances in contemporary times. Removal of the 1.25 multiplication factor to accommodate the different integrated depth intervals between the *Discovery* and contemporary nets had a similar effect, with abundances being significantly greater in contemporary times in all species.

Discussion

In this study we have demonstrated that three of the four species of large calanoids studied have increased in abundance within the Scotia Sea over the past 70 years. Over the same period the Southern Ocean has changed profoundly. There have been significant increases in temperature and, in some regions, reductions in sea-ice, alongside a decline in krill biomass (Atkinson et al. 2004). The commercial extinction of the great whales during the 20th century is also conjectured to have had significant impacts on the functioning of food-webs (Laws 1977, 1985; Willis 2007, 2014; Smetacek 2008; Nicol et al. 2010).

We can rule out methodological differences as the cause of the changes in abundance even though estimates of abundance from the different periods were derived from different nets. Our inter-net calibration determined size-related differences in catch efficiency and appropriate correction factors were applied to N70V catches.

A study carried out in the Weddell Sea comparing historical *Discovery* N70V (1929–1939) and contemporary WP-2 (1989–1993) net samples concluded that there had been marginally significant long-term changes among large calanoids but overall, no consistent trend was apparent (Vuorinen et al. 1997). However, and importantly, no inter-calibration of net performance was carried out.

Calibration factor

The survey data from which we generated the calibration factors were originally reported in Ward et al. (2012b). When considered across the entire catch, that study estimated that the Bongo net caught ~3 times as many individuals as the N70 net. This increased to ~4 times greater when limited only to copepod developmental stages or individuals that were <0.5 mm body length. However, between body lengths of 1 and 7 mm, the Bongo net caught between 1.5 and 2 times as many individuals as the N70 net. Given the large dependence of Bongo:N70 abundance ratio on body size, we considered it necessary to develop a specific calibration factor for each of our four chosen calanoid copepod species that took developmental stages into account. We could only examine developmental stage composition in the

contemporary samples, since specimens had been previously extracted from *Discovery Investigation* samples without any record of their respective developmental stages. The contemporary samples showed that mid developmental stages (CII–CIV) dominated the summertime populations of three of the four calanoid species, the exception being *C. acutus*, where the dominant stage was late development stage, CV. *Calanoides acutus* is the only one of the four calanoid species known to enter true diapause for a large part of the year (Drits et al. 1994). Tarling et al. (2004) showed that the population in the Scotia Sea consists of a mixture of 1- or 2-year life-cycle types, with CV being the dominant over-wintering stage. CV therefore dominate the summertime population of *C. acutus* since their abundance comprises both 1 and 2 year old individuals. The other calanoid species appear to have summertime populations that are dominated by newly recruiting individuals from that same season. Although we cannot be certain that summertime populations had the same structure during the *Discovery Investigations* era as during contemporary times, we deliberately designed our analysis to encompass all of the summer months so as to average over any minor variations in life-cycle phenology between the two eras.

Through combining developmental stage composition with the residual differences in abundance between Bongo and N70 samples for each developmental stage, we derived calibration factors between 1.2 and 1.7. This reflects the fact that even though relatively large residual differences were observed in the early developmental stages, these stages were not that common in the population during the summer. These calibration factors are somewhat lower than those originally proposed by Ward et al. (2012b). That study considered the entire copepod community, which was numerically dominated by smaller species such as *Oithona similis* and *Ctenocalanus citer*. The calanoid species we analyse here are comparatively larger in body size even during the earlier developmental stages and the residual differences between the Bongo and N70 nets were correspondingly smaller. Nevertheless, the sensitivity analyses showed that even increasing the value of the calibration factors by 50%, which would act to inflate abundances during the *Discovery* era, did not change the overall pattern of significantly greater abundances in the contemporary era in three out of the four calanoid species.

Climate variability

Recent investigations carried out around the western Antarctic Peninsula and Elephant Island are unanimous in finding links between decadal changes in abundance of plankton and the dominant modes of climate variability such as SAM and ENSO, which importantly influence sea-ice extent (Stammerjohn et al. 2008). It has been suggested that sea-ice

extent in the first part of the 20th century may have been greater than in recent times (de la Mare 1997; Cotté and Guinet 2007). However data derived from satellite measurements from 1979 to 2006 show a positive trend of around 1% per decade reaching a new record maximum for the satellite era in 2012 (Turner et al. 2009, 2014). If ice extent was greater over the Scotia Sea in the early part of the last century we might have expected changes in cycles of productivity and hence in the timing of appearance in surface waters of some species, particularly large calanoids that overwinter at depth and appear in the surface waters in spring. Such a phenological change is not borne out by the data (Fig. 4) which show similar trends in relative abundance by month.

Movements of frontal zones have also been recorded in response to atmospheric forcing. During El Niño events, north-west winds in the vicinity of Drake Passage decrease, allowing colder water from the Weddell Sea to flow north and penetrate into the Bransfield Strait. Increased winds and a southwards movement of the SACCF allows warmer water to mix with cold coastal waters during the La Niña phase (Loeb et al. 2009, 2010). This increased oceanic influence results in more Chl *a*, more copepods and better krill recruitment in the coastal area whereas, under the El Niño regime, salps dominate, Chl *a* is low and krill recruitment is poor. Aside from sea-ice reduction, climate variability also induces physical changes in the marine environment such as water column stability which influences primary productivity and links to species abundance in space and time (Saba et al. 2014; Steinberg et al. 2015). We have only incomplete data on prevailing atmospheric conditions and their impacts during the time of the *Discovery Investigations*. Our data are also insufficient to allow us to test for changes in regional abundance of species across the Scotia Sea which we acknowledge may be a possibility. However, averaged over the entire region, and across two decadal periods, differences in abundances are proportionately large and strongly suggest wider changes within the ecosystem, rather than local displacements of water masses and changes in nutrient supply.

Temperature and food availability

It is hard to see how the observed increases in temperature between eras would impact on population demography and account for the differences observed. The increases of ~1.5 °C are apparent only within the near-surface ocean, although lesser warming has been observed at depth (Gille 2002). We might in any case have expected species to respond differently to changing temperature since we considered species with both warm (*R. gigas* and *C. similimus*) and cold (*C. acutus* and *C. propinquus*) water preferences and yet, with the exception of *C. propinquus*, which showed a marginal decrease in contemporary times, all have

increased in overall abundance. In terms of food availability, there have been a number of studies suggesting both recent decreases and increases in primary production in the Southern Ocean during the satellite era. Gregg et al. (2003) found a 10% decline in productivity when comparing satellite mounted Coastal Zone Colour Scanner (CZCS) data for the period 1979–1986 compared to more recent SeaWiFS (Sea-viewing Wide Field-of-view Sensor) measurements (1997–2002). In contrast, Smith and Comiso (2008) found that productivity in the entire Southern Ocean showed a substantial and significant increase during their 9-year observation period (1997–2006), with much of this increase due to changes during the austral summer months. However, we have no direct way of knowing how present levels of phytoplankton compare to those found 70 years ago during the *Discovery Investigations*.

It is also important to consider how changes elsewhere in the ecosystem may have brought about increased abundances by virtue of trophic cascade effects. An increase in abundance could have arisen due to an increase in available food, a relaxation of predation pressure, or both. Antarctic krill (*Euphausia superba*) might provide a key to understanding some of the ecosystem interactions as it has been argued that krill occupy a position in the Southern Ocean food-web whereby they influence trophic levels above and below themselves, in a so called ‘wasp-waist’ ecosystem (Flores et al. 2012; Atkinson et al. 2014). For example, it has been demonstrated that intense krill grazing can alter phytoplankton species composition by preferentially grazing diatoms leading to a dominance of flagellates < 20 µm (Jacques and Panouse 1991; Kopczynska 1992; Granéli et al. 1993). Equally, through fluctuations in biomass, their availability to higher predators varies and can impact breeding success and population size (Trathan et al. 2007). It has been suggested that, historically, both whales and krill were able to act as ‘ecosystem engineers’ in the sense that by virtue of their great abundance they were, and are, important recyclers of nutrients essential for phytoplankton growth (Tovar-Sanchez et al. 2007; Willis 2007, 2014; Smetacek 2008; Nicol et al. 2010; Schmidt et al. 2011). In this way, increased phytoplankton production would have supported a greater krill population ultimately benefiting whales and perhaps placing greater pressure on copepods, both as competitors and as potential prey.

The degree of competition for food resources is likely to be highly variable in space and time reflecting plankton densities and distributions as well as conditions conducive to primary production. However, food limitation is commonly observed in the world ocean, particularly among large copepods (Saiz and Calbet 2011). In the Southern Ocean, egg production rates of *C. acutus* and *R. gigas* reach an asymptote at around 3 mg m⁻³ Chl *a* (Shreeve et al. 2002) which is a relatively high concentration for much of

the predominantly high nutrient low chlorophyll Southern Ocean. Longhurst (1998) notes that, within the southern part of the ACC, only 5% of underway-sampled chl-*a* concentration data exceeds 1 mg m^{-3} and most are a quarter of this (Tréguer and Jacques 1992). Not only copepod abundance but carbon mass and condition have also been found to be related closely to proxies of past production levels such as silicate levels and nutrient deficits (Shreeve et al. 2002; Ward et al. 2007), showing that bottom up control is important. Microphytoplankton ($> 20 \mu\text{m}$) has also been found to account for a large part of the variance in copepod abundance and carbon mass around South Georgia and elsewhere (Berggreen et al. 1988; Paffenhöfer 1988; Shreeve et al. 2002). Krill grazing may selectively remove microphytoplankton, thus disadvantaging large calanoid copepods which require blooms of large diatoms to optimise recruitment (Ward et al. 2005). However, of the 4 species, only *C. propinquus* showed a marginal but significant decrease in contemporary abundance, suggesting other factors may be paramount in this case. All species have broad and overlapping distributions within the ACC but life history traits are variable. For example, *C. acutus* is the most herbivorous and has a clear period of diapause in winter (Atkinson 1998), whereas *C. propinquus* has a closer association with ice-covered waters to the south of the Scotia Sea and, along with the northerly distributed *C. simillimus*, has extended periods of reproduction, with at least part of each population remaining active during winter (Bathmann et al. 1993; Atkinson 1998; Pasternak and Schnack-Schiel 2001). In contrast to *C. acutus* and *R. gigas*, in which wax esters are the main storage lipid, triacylglycerides dominate in both species of *Calanus*, suggesting more or less continuous feeding throughout the year (Hagen et al. 1993; Ward et al. 1996) and it has been found that microzooplankton can form a considerable part of the diet of both *Calanus* species (Hopkins et al. 1993; Atkinson 1995, 1996). The extent to which the diet of *C. propinquus* includes sea-ice algae is currently debateable. It has generally been found to be more abundant in open water than in the ice and marginal ice zones and was shown to have a higher proportion of empty guts when found under sea-ice (Burghart et al. 1999). However, recent data from the Scotia Sea show areas of recruitment for *C. propinquus* and, to an extent, *C. acutus*, which match surface concentrations of an isoprenoid ice-algae biomarker in the wake of the retreating ice edge (Schmidt et al. 2018). It is possible that a reduction in sea-ice means that under-ice productivity available to *C. propinquus* has declined or that any historical increase in chlorophyll available to copepods did not occur in the more southern parts of the Scotia Sea.

Krill may also directly prey on copepods (Atkinson and Snýder 1997; Atkinson et al. 1999; Cripps et al. 1999; Hernández-León et al. 2001), particularly at times of low phytoplankton production and biomass. Through either

preying directly upon or outcompeting copepods for food, krill may therefore, to a greater or lesser extent, control copepod population numbers. An overall increase in the number of large calanoids therefore suggests that control on this group has relaxed since the time of the *Discovery Investigations*. The reported decline of krill in the Atlantic sector of the Southern Ocean since the 1970s (Atkinson et al. 2004) could therefore be a mechanism by which competition and or predation has reduced, allowing copepod numbers to increase.

Ecosystem impacts

There is little doubt that a decreased abundance of krill will have had a significant impact on the amount of carbon passing through direct diatom-krill-higher predator food-chains. Copepod and krill food-webs have different characteristics in terms of carbon demand and fate depending on which is the dominant organism. Krill grazing can decrease phytoplankton standing stocks, particularly when swarms are present, although copepods rarely do, unless standing stocks are low (Atkinson 1996; Dubischar and Bathmann 1997). Within the Scotia Sea, krill and copepods are the dominant crustaceans, with krill tending to be more abundant in the southern part and copepods towards the north (Ward et al. 2012a). In a modelling study, Priddle et al. (2003) found that the biogeochemical consequences of grazing by krill and copepods were also different in terms of nutrient regeneration and resupply to primary producers. In a low krill-high copepod scenario, higher phytoplankton biomass and production, lower mixed layer ammonium, nitrate and silicate concentrations and higher detrital carbon were predicted than for a high krill low copepod scenario. Phytoplankton chlorophyll biomass was negatively related to krill biomass, and mixed layer nutrients were positively correlated with krill biomass in these data. Both observations and model results suggest that variation in biogeochemical carbon and nitrogen cycles in the South Georgia pelagic ecosystem is determined largely by changes in zooplankton community composition and its impact on phytoplankton dynamics. Contemporary estimates of krill and copepod biomass suggest that copepod standing stocks are at least equal to those of krill or indeed exceed them (Voronina 1998). Estimates of copepod vs krill production around South Georgia (where the biomass of both groups is generally high) suggest that the copepod community as a whole may be four times as productive as krill (Shreeve et al. 2005). Over the wider scale, Voronina (1998) estimates that 92% of annual zooplankton production in the Southern Ocean can be attributed to copepods whereas Conover and Huntley (1991) estimate productivity to be three times higher than krill-based estimates of ingestion and assimilation. Given that the biomass of baleen whales was so much higher in the past, it is axiomatic that krill biomass

must also have been higher than contemporary estimates to support this biomass (Willis 2007, 2014; Smetacek 2008). The balance of production would also have changed but, even with large calanoids being less abundant in the past, as shown by our study, copepods would still have contributed significantly to secondary production.

Our previous analysis has shown that over the last 70 years, despite warming, the geographical distribution of the plankton community of the Scotia Sea has not changed (Tarling et al. 2018). This study has shown that, despite the rank order of species abundance staying broadly the same, there have been changes in absolute abundance of biomass-dominant copepod species. The factors we consider responsible are linked through to changes occurring within the food chain brought about by decreasing krill abundance both as a result of warming induced habitat loss and also the commercial exploitation of whales.

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Compliance with ethical standards

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