

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

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21

22 **Abstract**

23 To investigate whether impacts of reported climate change in the Antarctic marine
24 environment has affected mesozooplankton populations, we compared the summertime
25 abundances of 4 species of large calanoid copepods from samples taken during the *Discovery*
26 *Investigations* (1926-1938) and contemporary times (1996-2013). *Discovery* samples were
27 obtained using an N70V closing net fished vertically through 3 depth horizons encompassing
28 the top 250 m of the water column, whereas contemporary samples were obtained using a
29 Bongo net fished vertically through 200-0 m. Data from a previous study comparing catch
30 efficiencies of the two nets were used to generate calibration factors which were applied to
31 the N70V abundances. Following further corrections for net depth differences and seasonal
32 biases in sampling frequency, three of the four species, *Calanoides acutus*, *Rhincalanus gigas*
33 and *Calanus simillimus*, were found to be between ~20-55% more abundant in contemporary
34 times than they were 70 years ago. *Calanus propinquus* was marginally more abundant in the
35 *Discovery* era. These results were robust to sensitivity analyses for the net calibration factor,
36 seasonal bias and net depth corrections. Although near-surface ocean temperatures within the
37 Scotia Sea have increased by up to 1.5°C during the last 70 years, we conclude that the most
38 likely causes of increased copepod abundances are linked to changes in the food web. In
39 particular, we discuss the reported decrease in krill abundance in the South Atlantic that has
40 potentially increased the amount of food available to copepods while at the same time
41 decreasing predator pressure.

42

43 Key words *Discovery Investigations*, Calanoid copepods, Scotia Sea, Climate change,
44 Trophic cascades

45

46 **Introduction**

47

48 The impacts of climate change are being felt worldwide in the marine environment. Species
49 and communities are responding to complex interactions of environmental forcing factors
50 such as increasing temperature, ocean acidification and ocean-atmospheric coupling, which
51 exert their effects over a range of spatial and temporal scales (Richardson 2008; Hátún et al.
52 2009; Burrows et al. 2011; Richardson et al. 2012; Poloczanska et al. 2013).

53 In the Southern Ocean, warming has been taking place for at least the last 50-70 years (Gille,
54 2002; Meredith and King 2005; Whitehouse et al. 2008) and has been attributed to near
55 surface ocean-atmosphere-ice interactions (Turner et al. 2013). Consequences of warming
56 have included regional changes in sea-ice extent and duration (Stammerjohn et al. 2008)
57 which has subsequently been suggested as a major factor in the recent decline of Antarctic
58 krill and increases in salp abundance (Loeb et al. 1997; Atkinson et al. 2004; Flores et al.
59 2012).

60 Impacts of environmental change on other planktonic groups are however less well
61 understood (Constable et al. 2014). Copepoda are the dominant mesozooplankton group in
62 the Southern Ocean but the factors affecting their distribution and abundance have been
63 harder to establish, in part because of a lack of extensive time-series measurements.

64 Changing patterns of atmospheric variability such as the Southern Annular Mode (SAM)
65 which has an important influence on zonal winds (Sen Gupta et al. 2012) and the Southern
66 Oscillation Index (SOI) have been linked to changes in plankton abundance. For example
67 near Elephant Island, Loeb et al. (2009, 2010) found significant correlations between the
68 abundance and concentration of phytoplankton, zooplankton and krill with the SOI which
69 exhibited 3-5 year frequencies characteristic of El Niño-Southern Oscillation (ENSO)

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

82 Over a longer timescale, Tarling et al. (2018) compared copepod distributions in the Scotia
83 Sea from *Discovery Investigations* (1920s-1930s) and contemporary times (1996-2013) and
84 showed that, over intervening years, populations have essentially remained in the same
85 geographical location despite ocean warming. Had they occupied the same thermal envelope
86 which they inhabited in the 1930s, current distributions would be up to 500 km further south
87 (see also Mackey et al. 2012). Reasons for maintenance of their historical distributions were
88 attributed to food availability and the properties of the underlying water masses where a
89 number of the species over-winter. It was also found that there had been a negligible
90 difference in the rank order of abundance of dominant copepod species sampled over 70
91 years apart. However ranked abundance can mask numerical changes, particularly if some
92 species/taxa are extremely abundant and others less so. In this paper, we explore this further
93 and have focussed on the commonly occurring biomass-dominant large calanoid copepods
94 (*C. acutus*, *R. gigas*, *Calanus simillimus* and *Calanus propinquus*). We wished to establish

95 whether abundances were the same between eras and, if not, to seek to understand what
96 factors may lie behind any changes.

97 **Methods**

98 **Copepod net sampling and abundance**

99 *Net sample stations:* We analysed net samples from stations south of the Polar Front in the
100 southwest Atlantic sector of the Southern Ocean, collected as part of the *Discovery*
101 *Investigations* (1926-1938), and during contemporary cruises (1996-2013). Our analysis was
102 confined to samples taken in the austral summer months of December-February, between the
103 latitudes of 52—66°S.

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

114 Stations were determined to be south of the Polar Front from the vertical temperature profile
115 recorded at each station (Gordon et al. 1977; Tarling et al. 2018). The *Discovery* sample set
116 accordingly comprised 53 N70V vertical closing net stations supplemented with an additional
117 10 N70V stations sampled during December 1926 and January 1927, for which catch data
118 were extracted from *Discovery Report 11* (appendix of Hardy and Gunther 1935). The

119 contemporary dataset comprised catches made with a paired Bongo net at 147 stations (Fig.
120 1).

121

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

131

132 *Data preparation*

133 *Accounting for different integrated depths:* At each *Discovery* station samples were collected
134 from 3 depth horizons (50-0, 100-50 and 250-100 m) and abundances integrated from 250-0
135 m. Contemporary samples were collected between 200-0 m. Copepod abundances were
136 determined in terms of concentrations as individuals per cubic metre (ind m⁻³) for both sets of
137 samples. However, the majority of copepods reside in the top 200 m at this time of year
138 (Atkinson 1991; Atkinson and Sinclair 2000) which potentially reduces concentrations in the
139 *Discovery* samples relative to the contemporary samples because of the extra 50 m depth
140 contributing to overall sample volume. Therefore, we multiplied *Discovery* abundances by
141 1.25 to account for this potential bias. Both sets of samples were subsequently multiplied by
142 200 m to derive a depth integrated abundance value for the 0–200 m surface layer (ind. m⁻²).

143 *Accounting for net type bias:* Different net types were used in the two eras of sampling. The
144 *Discovery Investigations* collected N70V samples from nets deployed vertically between the
145 3 horizons (see above) within the surface 250 m (Kemp et al. 1929). Mesh sizes in this net
146 decrease in stages from 5 mm in the upper part, to 440 μm and then 195 μm in the mid and
147 lower parts respectively (measurements are metric equivalents of the original imperial units;
148 see Kemp et al. 1929). In contrast, the contemporary samples were collected from Bongo net
149 deployments (net dia. 0.61 m, 200 μm mesh net) fished vertically from 200-0 m.
150 To enable a comparison between the two net types, an N70V net was reconstructed using
151 nylon mesh of the nearest metric equivalent to the imperial measurements of the bolting silks
152 originally specified in Kemp et al. (1929). The nets were fished alongside each other at a
153 series of stations in Marguerite Bay on the Antarctic Peninsula and across the Scotia Sea to
154 determine a broad spectrum calibration factor (Ward et al. 2012b). For the present study, we
155 reanalysed these data to establish species-specific inter-calibration factors for the four
156 principal calanoid species under consideration.
157 One particular issue was to take into account the different developmental stages (CI to adult)
158 of the sampled copepods, since the changes of size may alter respective catchabilities and
159 retentions by the two different nets. We therefore compared the abundances of each
160 individual developmental stage of each of the 4 species in every calibration station of Ward et
161 al. (2012b) to determine the average residual difference (*Res*), as follows:

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

165 Eq. 1

166

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

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

178

179

$$180 \quad SRes_{s,d} = Res_{s,d} \times Pr_{s,d}$$

181 Eq. 2

182

183 $SRes_{s,d}$ was divided by the average abundance of the N70V calibration hauls to produce a
184 normalised developmental stage specific calibration factor ($Cal_{s,d}$) which was then summed
185 across all stages to produce a species specific calibration factor (Cal_s):

186

$$187 \quad Cal_{s,d} = \frac{SRes_{s,d}}{(\sum_{station=1}^n N_{N70,s}) / n}$$

188 Eq.3

189

190

191

$$Cal_s = \sum_{d=d_1}^{d=d_t} Cal_{s,d}$$

192 Eq. 4

193 where d_1 is development stage 1 (CI), d_t is final adult stage (male and female).

194 *Discovery* sample abundances ($N_{DI,s}$) were then multiplied by $1+Cal_s$ to determine a

195 calibrated abundance ($N_{Dical,s}$) with which to compare against contemporary abundances

196 ($N_{C,s}$):

197

198

199

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

200 Eq. 5

201

202 *Accounting for seasonal bias:* Further data analyses revealed a seasonal trend in datasets

203 whereby there was a substantial increase in abundances in January compared to December

204 and February in both the *Discovery Investigations* and contemporary sample sets. However,

205 sampling effort varied between the two eras, with there being a proportionally greater

206 sampling effort in January in the contemporary dataset compared to the *Discovery* dataset. To

207 account for this potential bias, we resampled the two datasets so that there was even selection

208 of datapoints across the three months. For both the *Discovery* and contemporary datasets

209 ($N_{Dical,s}$ and $N_{C,s}$), 10 datapoints were selected at random (with replacement) from each of the
210 three months and combined to make a new resampled dataset of 30 datapoints, for which an
211 average was determined. The process was repeated 100 times for each species, to which
212 statistical tests were then applied (see below).

213 *Sensitivity analyses*

214 To determine the sensitivity of the inter-era comparison of species abundance to the various
215 stages in data preparation, a series of sensitivity analyses were run. The two main treatments
216 to the original datasets were the inter-calibration of abundances caught by the two different
217 nets and the resampling to account for seasonal sampling bias, so the objective of the
218 sensitivity analysis was to determine whether species specific abundances remained
219 significantly different between eras when treatments were altered. For the calibration factor
220 sensitivity tests, the factors were increased by 25%, 50% and 100% or removed completely.
221 Multiplying the calibration factor by percentages below 0 was not considered given that this
222 would always act to increase the level of difference between the two eras. For the seasonality
223 sensitivity tests, runs were carried out to determine the effect of removing the resampling
224 process. The 1.25 multiplication factor to the *Discovery* nets was also removed in a further
225 test to determine its implications.

226 *Statistical tests*

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

233 **Results**

234 *Calibration*

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

245 The calibration factor also required the residual difference in species and stage specific
246 abundances to be determined in matched Bongo and N70 hauls. In these hauls, it was found
247 that more individual copepods were captured by Bongo nets than N70V nets, with the
248 majority of residual differences (i.e. Bongo minus N70V, $Res_{s,d}$) being positive (Fig.3). The
249 residual differences were much greater in *C. acutus* and *C. simillimus* than they were in *R.*
250 *gigas* and *C. propinquus*. In *C. acutus*, some of the greatest differences were observed in the
251 early developmental stages, although CIV also exhibited a high value for $Res_{s,d}$. Only CI and
252 CII showed notably high values for $Res_{s,d}$ in *C. simillimus* with a further minor peak in the
253 females. *R. gigas* exhibited a similar peak in $Res_{s,d}$, but there was little pattern in the low
254 values of $Res_{s,d}$ in *C. propinquus*.

255 The calibration factor ($1+Cal_s$) is a function of both the residual difference between
256 calibration hauls and relative proportion of stages within species (Table 1). The highest

257 calibration factors were observed in *C. acutus* and *C. simillimus*, for which the highest values
258 for $Res_{s,d}$ were observed. However, the corresponding stage distribution downweighs the
259 calibration factor in *C. acutus* in relation to *C. simillimus*. The calibration factors for *R. gigas*
260 and *C. propinquus* were low since both have comparatively low species abundances and low
261 residual differences.

262 *Comparison of abundances between eras*

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

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

274 The calibrated abundances of *R. gigas*, *C. acutus* and *C. simillimus* in the *Discovery* samples
275 were considerably and significantly lower than those in the contemporary samples (Fig.5)
276 (*Discovery* vs Contemporary; *R. gigas*: Mann-Whitney U Test, $T = 6590.000$ $n(\text{small})= 100$
277 $n(\text{big})= 100$, $p<0.001$, *C. acutus*: $T = 7590$, $n(\text{small})= 100$ $n(\text{big})= 100$, $p<0.001$; *C.*
278 *simillimus*: $T = 7053.000$ $n(\text{small})= 100$ $n(\text{big})= 100$, $p<0.001$). In the case of *C. acutus*,
279 calibrated abundances were around 80% of the values observed in contemporary times
280 (means \pm SE of 3553 ± 101 ind m^{-2} and 4374 ± 116 ind m^{-2} respectively) while, in *R. gigas*

281 and *C. simillimus*, *Discovery* samples were between 65% and 70% of contemporary values
282 (respective means \pm SE of 1020 ± 22 ind m^{-2} and 1525 ± 47 ind m^{-2} for *R. gigas* and $2377 \pm$
283 70 ind m^{-2} and 3711 ± 139 ind m^{-2} for *C. simillimus*). However, in *C. propinquus*, the
284 opposite trend was observed, with values being significantly higher in the *Discovery* era
285 (mean \pm SE of 903 ± 21 ind m^{-2} versus 812 ± 41 ind m^{-2} for contemporary era), although the
286 absolute or proportional differences (91 ind m^{-2} and 90% respectively) were not as substantial
287 as for the other species.

288 Levels of significance in these results were relatively insensitive to the calibration factor
289 (Table 2). When removing the calibration factor altogether or increasing its value by 25% or
290 50%, values in contemporary times were still significantly larger in *R. gigas*, *C. acutus* and *C.*
291 *simillimus*. Only when the calibration factor was increased by 100% was there any change to
292 this result, with *C. acutus* no longer significantly more abundant in the contemporary era.
293 Greater sensitivity was exhibited in relation to seasonality in abundance levels, with the
294 removal of the resampling procedure to dampen the effect of different levels of sampling
295 effort between months increasing the level of difference between eras, with even *C.*
296 *propinquus* now exhibiting significantly greater abundances in contemporary times. Removal
297 of the 1.25 multiplication factor to accommodate the different integrated depth intervals
298 between the *Discovery* and contemporary nets had a similar effect, with abundances being
299 significantly greater in contemporary times in all species.

300

301 **Discussion**

302 In this study we have demonstrated that 3 of the 4 species of large calanoids studied have
303 increased in abundance within the Scotia Sea over the past 70 years. Over the same period the
304 Southern Ocean has changed profoundly. There have been significant increases in
305 temperature and, in some regions, reductions in sea-ice, alongside a decline in krill biomass

306 (Atkinson et al. 2004). The commercial extinction of the great whales during the 20th century
307 is also conjectured to have had significant impacts on the functioning of food-webs (Laws
308 1977, 1985; Willis 2007, 2014; Smetacek 2008; Nicol et al. 2010).

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

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

318 *Calibration factor*

319 The survey data from which we generated the calibration factors were originally reported in
320 Ward et al. (2012b). When considered across the entire catch, that study estimated that the
321 Bongo net caught ~3 times as many individuals as the N70 net. This increased to ~4 times
322 greater when limited only to copepod developmental stages or individuals that were <0.5 mm
323 body length. However, between body lengths of 1 and 7 mm, the Bongo net caught between
324 1.5 and 2 times as many individuals as the N70 net. Given the large dependence of
325 Bongo:N70 abundance ratio on body size, we considered it necessary to develop a specific
326 calibration factor for each of our four chosen calanoid copepod species that took
327 developmental stages into account. We could only examine developmental stage composition
328 in the contemporary samples, since specimens had been previously extracted from *Discovery*
329 *Investigation* samples without any record of their respective developmental stages. The

330 contemporary samples showed that mid developmental stages (CII to CIV) dominated the
331 summertime populations of three of the four calanoid species, the exception being *C. acutus*,
332 where the dominant stage was late development stage, CV. *Calanoides acutus* is the only one
333 of the four calanoid species known to enter true diapause for a large part of the year (Drits et
334 al. 1994). Tarling et al. (2004) showed that the population in the Scotia Sea consists of a
335 mixture of 1-year or 2-year life-cycle types, with CV being the dominant overwintering stage.
336 CV therefore dominate the summertime population of *C. acutus* since their abundance
337 comprises both 1 and 2 year old individuals. The other calanoid species appear to have
338 summertime populations that are dominated by newly recruiting individuals from that same
339 season. Although we cannot be certain that summertime populations had the same structure
340 during the *Discovery Investigations* era as during contemporary times, we deliberately
341 designed our analysis to encompass all of the summer months so as to average over any
342 minor variations in life-cycle phenology between the two eras.

343 Through combining developmental stage composition with the residual differences in
344 abundance between Bongo and N70 samples for each developmental stage, we derived
345 calibration factors between 1.2 and 1.7. This reflects the fact that even though relatively large
346 residual differences were observed in the early developmental stages, these stages were not
347 that common in the population during the summer. These calibration factors are somewhat
348 lower than those originally proposed by Ward et al. (2012b). That study considered the entire
349 copepod community, which was numerically dominated by smaller species such as *Oithona*
350 *similis* and *Ctenocalanus citer*. The calanoid species we analyse here are comparatively
351 larger in body size even during the earlier developmental stages and the residual differences
352 between the Bongo and N70 nets were correspondingly smaller. Nevertheless, the sensitivity
353 analyses showed that even increasing the value of the calibration factors by 50%, which

354 would act to inflate abundances during the *Discovery* era, did not change the overall pattern
355 of significantly greater abundances in the contemporary era in 3 out of the 4 calanoid species.

356

357 *Climate variability*

358 Recent investigations carried out around the western Antarctic Peninsula and Elephant Island
359 are unanimous in finding links between decadal changes in abundance of plankton and the
360 dominant modes of climate variability such as SAM and ENSO, which importantly influence
361 sea-ice extent (Stammerjohn et al. 2008). It has been suggested that sea ice extent in the first
362 part of the 20th century may have been greater than in recent times (de la Mare 1997; Cotté
363 and Guinet 2007). However data derived from satellite measurements from 1979 – 2006
364 show a positive trend of around 1% per decade reaching a new record maximum for the
365 satellite era in 2012 (Turner et al. 2009, 2014). If ice extent was greater over the Scotia Sea in
366 the early part of the last century we might have expected changes in cycles of productivity
367 and hence in the timing of appearance in surface waters of some species, particularly large
368 calanoids that overwinter at depth and appear in the surface waters in spring. Such a
369 phenological change is not borne out by the data (Fig. 4) which shows similar trends in
370 relative abundance by month.

371 Movements of frontal zones have also been recorded in response to atmospheric forcing.

372 During El Niño events, northwest winds in the vicinity of Drake Passage decrease, allowing
373 colder water from the Weddell Sea to flow north and penetrate into the Bransfield Strait.

374 Increased winds and a southwards movement of the SACCF allows warmer water to mix with
375 cold coastal waters during the La Niña phase (Loeb et al. 2009, 2010). This increased oceanic
376 influence results in more Chl *a*, more copepods and better krill recruitment in the coastal area
377 whereas, under the El Niño regime, salps dominate, Chl *a* is low and krill recruitment is poor.

378 Aside from sea-ice reduction, climate variability also induces physical changes in the marine
379 environment such as water column stability which influences primary productivity and links
380 to species abundance in space and time (Saba et al. 2014; Steinberg et al. 2015). We have
381 only incomplete data on prevailing atmospheric conditions and their impacts during the time
382 of the *Discovery Investigations*. Our data are also insufficient to allow us to test for changes
383 in regional abundance of species across the Scotia Sea which we acknowledge may be a
384 possibility. However, averaged over the entire region, and across two decadal periods,
385 differences in abundances are proportionately large and strongly suggest wider changes
386 within the ecosystem, rather than local displacements of water masses and changes in nutrient
387 supply.

388 *Temperature and food availability*

389 It is hard to see how the observed increases in temperature between eras would impact on
390 population demography and account for the differences observed. The increases of $\sim 1.5^{\circ}\text{C}$
391 are apparent only within the near-surface ocean, although lesser warming has been observed
392 at depth (Gille 2002). We might in any case have expected species to respond differently to
393 changing temperature since we considered species with both warm (*R. gigas* and *C.*
394 *simillimus*) and cold (*C. acutus* and *C. propinquus*) water preferences and yet, with the
395 exception of *C. propinquus*, which showed a marginal decrease in contemporary times, all
396 have increased in overall abundance. In terms of food availability, there have been a number
397 of studies suggesting both recent decreases and increases in primary production in the
398 Southern Ocean during the satellite era. Gregg et al. (2003) found a 10% decline in
399 productivity when comparing satellite mounted Coastal Zone Color Scanner (CZCS) data for
400 the period 1979-1986 compared to more recent SeaWiFS (Sea-viewing Wide Field-of-view
401 Sensor) measurements (1997-2002). In contrast, Smith and Comiso (2008) found that
402 productivity in the entire Southern Ocean showed a substantial and significant increase

403 during their 9-year observation period (1997-2006), with much of this increase due to
404 changes during the austral summer months. However, we have no direct way of knowing how
405 present levels of phytoplankton compare to those found 70 years ago during the *Discovery*
406 *Investigations*.

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

425 The degree of competition for food resources is likely to be highly variable in space and time
426 reflecting plankton densities and distributions as well as conditions conducive to primary
427 production. However, food limitation is commonly observed in the world ocean, particularly

428 among large copepods (Saiz and Calbet 2011). In the Southern Ocean, egg production rates
429 of *C. acutus* and *R. gigas* reach an asymptote at around 3 mg m⁻³ Chl *a* (Shreeve et al. 2002)
430 which is a relatively high concentration for much of the predominantly high nutrient low
431 chlorophyll Southern Ocean. Longhurst (1998) notes that, within the southern part of the
432 ACC, only 5% of underway-sampled chl-*a* concentration data exceeds 1 mg m⁻³ and most are
433 a quarter of this (Treguer and Jacques 1992). Not only copepod abundance but carbon mass
434 and condition have also been found to be related closely to proxies of past production levels
435 such as silicate levels and nutrient deficits (Shreeve et al. 2002; Ward et al. 2007), showing
436 that bottom up control is important. Microphytoplankton (>20 µm) has also been found to
437 account for a large part of the variance in copepod abundance and carbon mass around South
438 Georgia and elsewhere (Berggreen et al. 1988; Paffenhöfer 1988; Shreeve et al. 2002). Krill
439 grazing may selectively remove microphytoplankton, thus disadvantaging large calanoid
440 copepods which require blooms of large diatoms to optimise recruitment (Ward et al. 2005).
441 However, of the 4 species, only *C. propinquus* showed a marginal but significant decrease in
442 contemporary abundance, suggesting other factors may be paramount in this case. All species
443 have broad and overlapping distributions within the ACC but life history traits are variable.
444 For example, *C. acutus* is the most herbivorous and has a clear period of diapause in winter
445 (Atkinson 1998), whereas *C. propinquus* has a closer association with ice-covered waters to
446 the south of the Scotia Sea and, along with the northerly distributed *C. simillimus*, has
447 extended periods of reproduction, with at least part of each population remaining active
448 during winter (Bathmann et al. 1993; Atkinson 1998; Pasternak and Schnack-Schiel 2001). In
449 contrast to *C. acutus* and *R. gigas*, in which wax esters are the main storage lipid,
450 triacylglycerides dominate in both species of *Calanus*, suggesting more or less continuous
451 feeding throughout the year (Hagen et al. 1993; Ward et al. 1996) and it has been found that
452 microzooplankton can form a considerable part of the diet of both *Calanus* species (Hopkins

453 et al. 1993; Atkinson 1995, 1996). The extent to which the diet of *C. propinquus* includes sea
454 ice algae is currently debateable. It has generally been found to be more abundant in open
455 water than in the ice and marginal ice zones and was shown to have a higher proportion of
456 empty guts when found under sea ice (Burghart et al. 1999). However, recent data from the
457 Scotia Sea show areas of recruitment for *C. propinquus* and, to an extent, *C. acutus*, which
458 match surface concentrations of an isoprenoid ice-algae biomarker in the wake of the
459 retreating ice edge (Schmidt et al. 2018). It is possible that a reduction in sea ice means that
460 under-ice productivity available to *C. propinquus* has declined or that any historical increase
461 in chlorophyll available to copepods did not occur in the more southern parts of the Scotia
462 Sea.

463 Krill may also directly prey on copepods (Atkinson and Snyder 1997; Atkinson et al. 1999;
464 Cripps et al. 1999; Hernandez Leon et al. 2001), particularly at times of low phytoplankton
465 production and biomass. Through either preying directly upon or outcompeting copepods for
466 food, krill may therefore, to a greater or lesser extent, control copepod population numbers.
467 An overall increase in the number of large calanoids therefore suggests that control on this
468 group has relaxed since the time of the *Discovery Investigations*. The reported decline of krill
469 in the Atlantic sector of the Southern Ocean since the 1970s (Atkinson et al. 2004) could
470 therefore be a mechanism by which competition and or predation has reduced, allowing
471 copepod numbers to increase.

472 *Ecosystem impacts*

473 There is little doubt that a decreased abundance of krill will have had a significant impact on
474 the amount of carbon passing through direct diatom- krill -higher predator food-chains.
475 Copepod and krill food-webs have different characteristics in terms of carbon demand and
476 fate depending on which is the dominant organism. Krill grazing can decrease phytoplankton

477 standing stocks, particularly when swarms are present, although copepods rarely do, unless
478 standing stocks are low (Atkinson 1996; Dubischar and Bathmann, 1997). Within the Scotia
479 Sea, krill and copepods are the dominant crustaceans, with krill tending to be more abundant
480 in the southern part and copepods towards the north (Ward et al. 2012a). In a modelling
481 study, Priddle et al. (2003) found that the biogeochemical consequences of grazing by krill
482 and copepods were also different in terms of nutrient regeneration and resupply to primary
483 producers. In a low krill-high copepod scenario, higher phytoplankton biomass and
484 production, lower mixed layer ammonium, nitrate and silicate concentrations, and higher
485 detrital carbon were predicted than for a high krill low copepod scenario. Phytoplankton
486 chlorophyll biomass was negatively related to krill biomass, and mixed layer nutrients were
487 positively correlated with krill biomass in these data. Both observations and model results
488 suggest that variation in biogeochemical carbon and nitrogen cycles in the South Georgia
489 pelagic ecosystem is determined largely by changes in zooplankton community composition
490 and its impact on phytoplankton dynamics. Contemporary estimates of krill and copepod
491 biomass suggest that copepod standing stocks are at least equal to those of krill or indeed
492 exceed them (Voronina 1998). Estimates of copepod vs krill production around South
493 Georgia (where the biomass of both groups is generally high) suggest that the copepod
494 community as a whole may be 4 times as productive as krill (Shreeve et al. 2005). Over the
495 wider scale, Voronina (1998) estimates that 92% of annual zooplankton production in the
496 Southern Ocean can be attributed to copepods whereas Conover and Huntley (1991) estimate
497 productivity to be 3 times higher than krill-based estimates of ingestion and assimilation.
498 Given that the biomass of baleen whales was so much higher in the past, it is axiomatic that
499 krill biomass must also have been higher than contemporary estimates to support this biomass
500 (Willis 2007, 2014; Smetacek 2008). The balance of production would also have changed

501 but, even with large calanoids being less abundant in the past, as shown by our study,
502 copepods would still have contributed significantly to secondary production.

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

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763 Figure and Table legends

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

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

772

773 Fig. 3 Residual difference species stage: Residual difference ($Res_{s,d}$ ind m⁻²) between
774 abundances of *Rhincalanus gigas*, *Calanoides acutus*, *Calanoides simillimus* and *Calanoides*
775 *propinquus* individual developmental stages estimated by Bongo nets and N70V nets in
776 simultaneous calibration hauls.

777

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

780

781 Fig. 5 *Discovery Investigations* vs Contemporary abundance: Box plot of estimated
782 abundance (ind m⁻²) of *Rhincalanus gigas*, *Calanoides acutus*, *Calanoides simillimus* and
783 *Calanoides propinquus* during the *Discovery Investigations* and contemporary times.
784 Horizontal line represents the median, limits of boxes, 25th and 75th percentiles, limits of
785 whiskers, 10th and 90th percentiles, dots, 5th and 95th percentiles. \wedge indicates abundances
786 during contemporary era were significantly larger than those during the *Discovery*
787 *Investigation* era, \vee , that *Discovery Investigation* era abundances were significantly larger
788 than those in the contemporary era ($p < 0.001$).

789

790 Table 1. Calibration factor: Parameters derived in order to determine a Calibration factor
791 (Cal_s) for *Rhincalanus gigas*, *Calanoides acutus*, *Calanoides simillimus* and *Calanoides*

792 *propinquus* to standardise abundance estimates of N70Vcatches during the *Discovery*
793 *Investigations* against contemporary Bongo catches.

794

795 Table 2. Sensitivity: Analyses to determine the sensitivity of *Discovery Investigations* and
796 contemporary estimates of species specific abundance to the parameters used in the inter-
797 calibration of the respective nets and the standardisation of differences in sampling effort and
798 sampling protocol. Bold indicates where contemporary abundance is significantly greater
799 than that of the *Discovery Investigations*, italics indicates where *Discovery Investigations*
800 abundance is significantly greater than contemporary era abundance, standard text indicates
801 that no significant differences in abundance exist.

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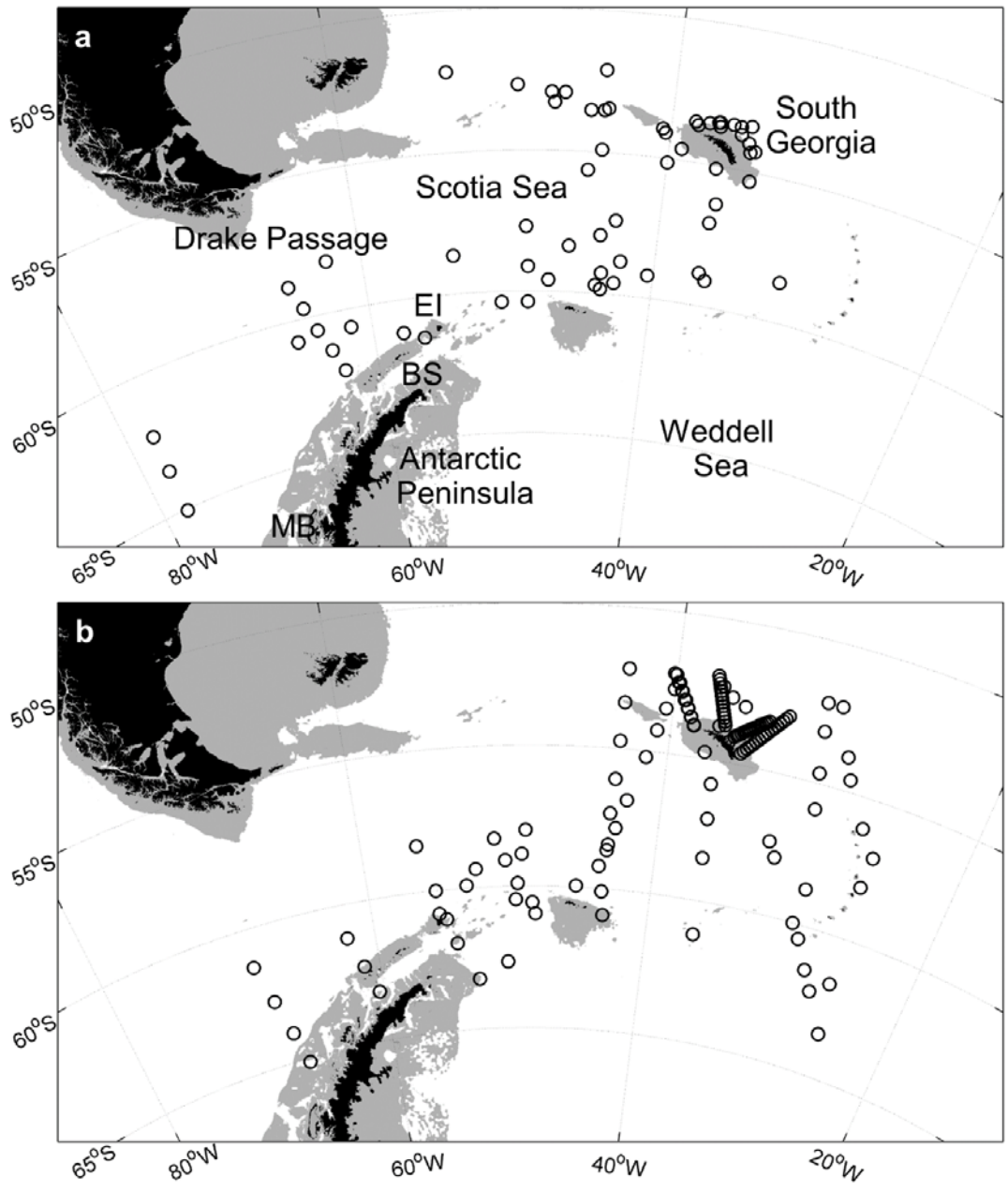


Fig. 1

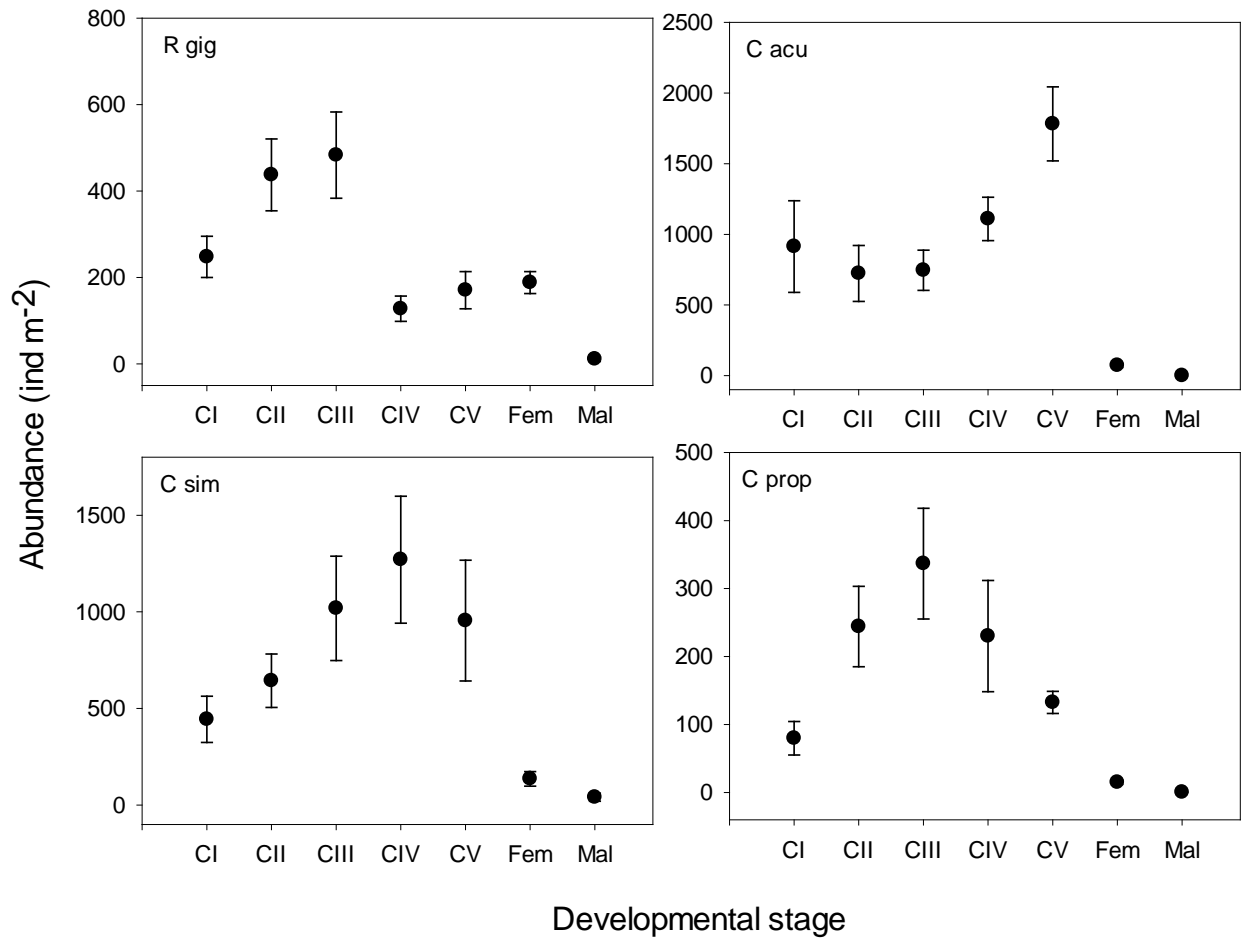


Fig. 2

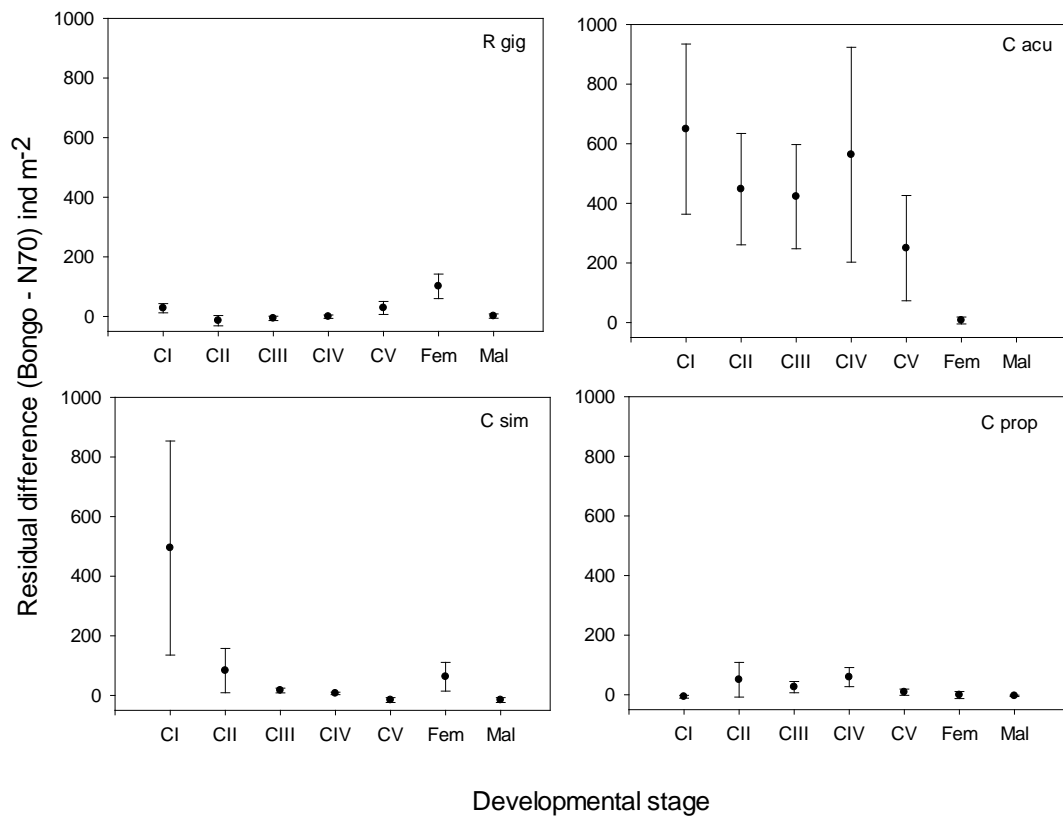


Fig. 3

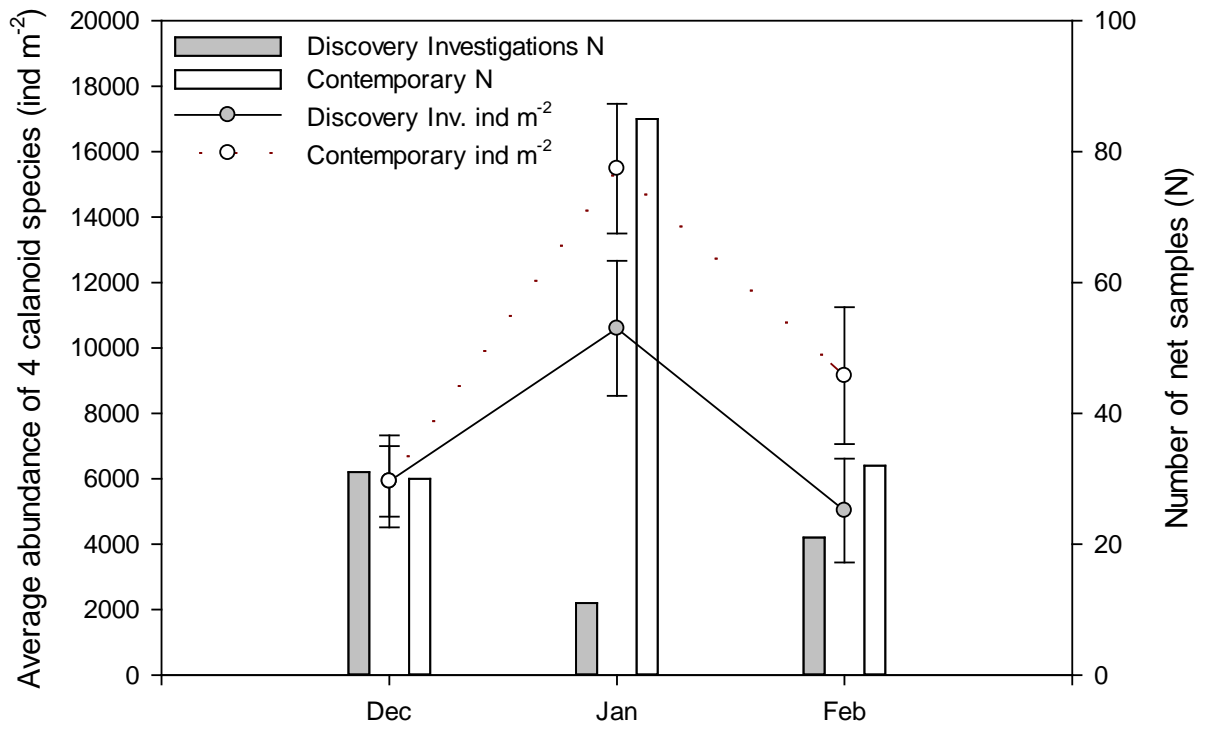


Fig. 4

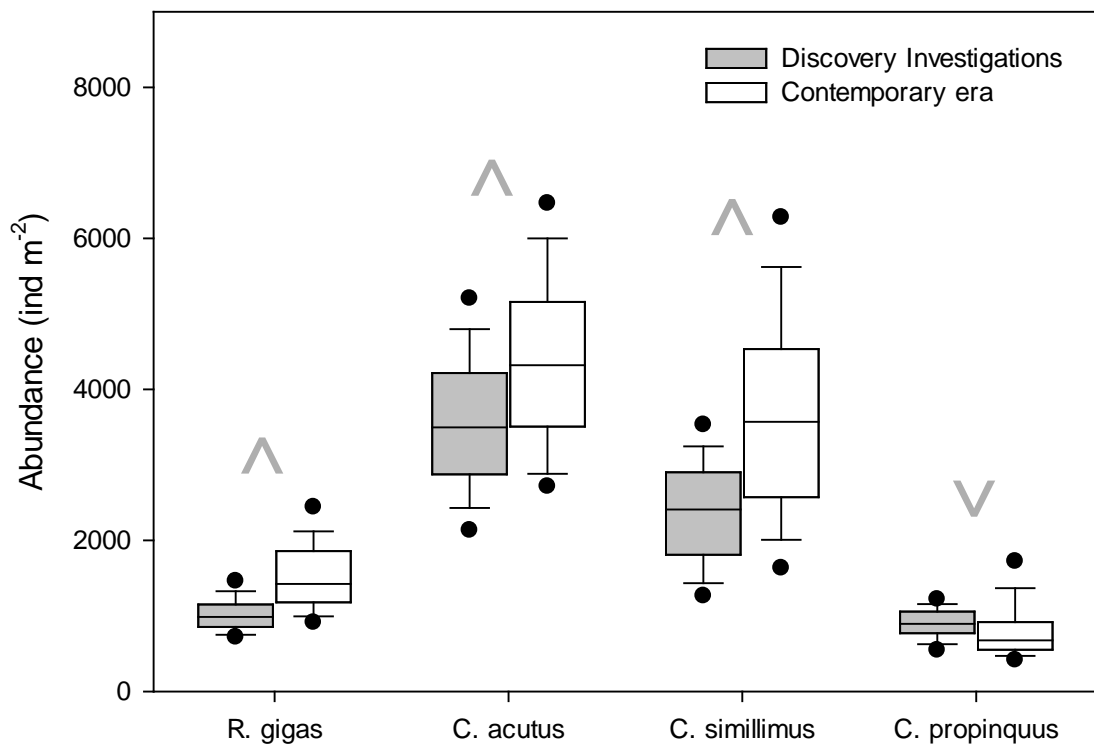


Fig. 5

	Mal	Fem	CV	CIV	CIII	CII	CI	Calibration factor (1+ Cal_s)
<i>R. gigas</i>								
residual difference (Res_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 , 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 , 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 , 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

Table 1

Table 2

	<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 Discovery Investigation 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