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Plasticity in foraging behaviour and diet buffers effects of inter-annual environmental differences on chick growth and survival --Manuscript Draft--

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Abstract:	<p>In marine ecosystems, primary productivity and consequently food availability for higher trophic levels is often strongly affected by the water temperature. Thus, differences in sea surface temperatures (SST) may lead to differences in the diet composition of predators, but this link it is still unknown in many species. By combining GPS tracking and dive analyses on chick-rearing southern rockhopper penguins (<i>Eudyptes chrysocome</i>) with stable isotope analyses and monitoring of chick growth rates and chick survival, we here attempted a comprehensive assessment of the effects of inter-annual environmental variability as indicated by SST and chlorophyll a data.</p> <p>Inter-annual differences in environmental variables around our study colony on New Island, Falkland/Malvinas Islands, contradicted the general expectation, with higher chlorophyll a concentrations coinciding with higher spring SST in 2010/11 compared to 2009/10. Penguins foraged further away from the colony during guard and crèche in 2010/11 compared to 2009/10, while performing deeper dives in 2009/10. Stable isotope mixing models suggested a crustacean-dominated chick diet in 2009/10, compared to a mixture of squid and fish in 2010/11. These differences in foraging behaviour and diet were, however, not reflected in chick growth rates or chick survival, thus had no apparent effect on population trajectories. Consequently, despite significant differences in environmental variables, foraging behaviour and diet, it was not possible to identify a "better" year. Potentially, environmental conditions in both years could still be seen as favourable compared to other years and breeding sites, enabling the parental birds to buffer the environmental differences by plastic foraging behaviour.</p>	
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Plasticity in foraging behaviour and diet buffers effects of inter-annual environmental differences on chick growth and survival

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Abstract

In marine ecosystems, primary productivity and consequently food availability for higher trophic levels is often strongly affected by the water temperature. Thus, differences in sea surface temperatures (SST) may lead to differences in the diet composition of predators, but this link it is still unknown in many species. By combining GPS tracking and dive analyses on chick-rearing southern rockhopper penguins (*Eudyptes chrysocome*) with stable isotope analyses and monitoring of chick growth rates and chick survival, we here attempted a comprehensive assessment of the effects of inter-annual environmental variability as indicated by SST and chlorophyll *a* data.

Inter-annual differences in environmental variables around our study colony on New Island, Falkland/Malvinas Islands, contradicted the general expectation, with higher chlorophyll *a* concentrations coinciding with higher spring SST in 2010/11 compared to 2009/10. Penguins foraged further away from the colony during guard and crèche in 2010/11 compared to 2009/10, while performing deeper dives in 2009/10. Stable isotope mixing models suggested a crustacean-dominated chick diet in 2009/10, compared to a mixture of squid and fish in 2010/11. These differences in foraging behaviour and diet were, however, not reflected in chick growth rates or chick survival, thus had no apparent effect on population trajectories. Consequently, despite significant differences in environmental variables, foraging behaviour and diet, it was not possible to identify a “better” year. Potentially, environmental conditions in both years could still be seen as favourable compared to other years and breeding sites, enabling the parental birds to buffer the environmental differences by plastic foraging behaviour.

Keywords: chlorophyll *a*, *Eudyptes chrysocome*, GPS logger, sea surface temperature, southern rockhopper penguin, stable isotope analysis, stable isotope mixing model

Introduction

In the marine ecosystem, primary productivity and thus – with some time lag – food availability for secondary and higher trophic level consumers such as fish, squid, seabirds and marine mammals, is substantially affected by climate variables like sea surface temperatures (SST) or wind. For example, with increasing SST, the stratification of the surface waters becomes shallower, providing less nutrients for primary productivity compared to a deeper mixed water column (Behrenfeld et al. 2006). On the other hand, very deep mixing of water may also inhibit phytoplankton growth and thus primary productivity (Sverdrup 1953; Smetacek and Passow 1990). A dramatic example of how environmental variability can cause complete breeding failure and even reduce adult survival of seabirds are the regularly re-occurring El Niño Southern Oscillation (ENSO) events in the Pacific Ocean (Schreiber and Schreiber 1984; Anderson 1989; Vargas et al. 2006).

The effects of climate variability on the availability or accessibility of prey for seabirds can best be studied during the breeding season, when seabirds are typical central-place foragers (Ashmole 1971; Orians and Pearson 1979). Due to the needs of their chicks for regular food provisioning, adult birds are then limited in their foraging range, and this is even more so in flightless seabirds like penguins, due to their limitation in traveling speed (Wilson and Wilson 1990; Weimerskirch 2007). Moreover, penguin chicks rely on high quality food and regular provisioning during their nestling period (Heath and Randall 1985) and post-fledging survival in penguins increases with fledging mass (Saraux et al. 2011).

Southern rockhopper penguins (*Eudyptes chrysocome*) are one of the smallest species of penguins (Pütz et al. 2013) and feed on low trophic level prey such as small (partly larval) fish, squid and crustaceans (reviewed in Pütz et al. 2013). Due to their prey spectrum, rockhopper penguins may respond to changes in the food-web caused by changes in primary-productivity more rapidly than larger species that mostly feed on higher trophic prey.

Between-year variability in the timing of and investment into breeding in southern rockhopper penguins was partly explained by the climate indices Southern Annular Mode (SAM) and SST, respectively (Dehnhard et al. 2015). Furthermore, adult survival in this species has been found to be sensitive to SST, with decreased survival under both elevated and very low SST (Dehnhard et al. 2013b), reflecting changes in the underlying food web. This sensitivity of southern rockhopper penguins to SST-related conditions in their foraging habitat might also have contributed to the dramatic population declines observed across their distribution range from the 1930s / 1940s to the early 2000s (Cunningham and Moors 1994; Pütz et al. 2003). Indeed, periods of population declines coincided with elevated ocean temperatures (Morrison et al. 2015), and the recently observed slight population increase on the Falkland Islands (Baylis et al. 2013) as well as at other breeding sites may be due to a current warming hiatus (Morrison et al. 2015).

While inter-annual and spatial variation in foraging behaviour and chick provisioning rates have been ascribed to differences in ocean productivity (Tremblay and Cherel 2005; Raya Rey et al. 2007), it still remains unclear how environmental variation drives the diet composition in this food-generalist. Hilton et al. (2006) suggested a link between elevated SST and a low trophic level (crustaceans) and thus low quality diet, potentially even driving the population decline. However, this idea was challenged by Morrison et al. (2014) who provided evidence that a more fish-based (higher trophic level diet) may not necessarily result in a better nutritional state of the birds.

By combining GPS tracking and dive analyses of adult birds during the chick-rearing period with dietary (stable isotope) analyses and monitoring of chick growth rates and chick survival, we here attempt a comprehensive assessment of the effects of inter-annual environmental variability on the foraging behaviour, diet and the consequences for the breeding success. By comparing both local SST and spring chlorophyll *a* data as measures of

environmental variability and primary productivity, respectively, between the two study years, we hypothesized that colder conditions would coincide with higher primary productivity and would 1) result in improved foraging conditions for rockhopper penguins, and thus shorter foraging trip distances, which would 2) result in steeper chick growth rates and lower chick mortality. Due to the inconsistency in previous results (Hilton et al. 2006; Morrison et al. 2014), we did not have a clear expectation for the relationship between environmental conditions and dietary composition. We collected tracking data throughout the entire chick-rearing period, and therefore also investigated potential differences in the foraging behaviour between the guard (i.e. early chick-rearing period when males stay with the chicks and only females forage) and crèche stage (both sexes forage, and chicks remain in the colony alone), as well as between sexes. Chicks during crèche have an increased food demand due to their increased size and are fed less frequently but larger meals (Tremblay and Cherel 2003; Raya Rey et al. 2007). Thus, we expected that rockhopper penguins would extend their foraging range from guard to crèche. We furthermore expected – considering the morphological differences between the sexes and dietary differences (Dehnhard et al. 2011; Ludynia et al. 2013) – that the larger males would be able to dive deeper than the females and that sexes would potentially use spatial segregation for intra-specific niche separation.

Notably, our work will not only improve our understanding of how inter-annual environmental variability affects seabirds' foraging and reproductive biology, but also delivers important data about the spatial distribution of foraging rockhopper penguins during chick-rearing. This appears particularly important due to current prospecting for oil and gas in Falkland Island waters and the need for marine spatial planning.

Material and Methods

Sea surface temperatures and chlorophyll a concentration

We downloaded weekly SST data from NOAA (http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.weekly/) for the spatial range of 50.5 to 52.5°S and 60.5 to 63.5°W, i.e. the area utilized by the penguins during the chick-rearing period in both study years (cf. Fig. 1) and the time period from mid-September until mid-February.

Chlorophyll *a* data for the months September to November (austral spring) as well as December to February (austral summer) measured by MODIS-Aqua at a spatial resolution of 4.6 x 4.6 km were downloaded from http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_8day. We calculated the average chlorophyll *a* concentration within the spatial range of 50 to 55°S and 60 to 65°W and furthermore downloaded the plotted data (originating from the same sensor) for the entire region from <http://oceancolor.gsfc.nasa.gov/cms/>.

GPS deployments,

Fieldwork was conducted in the “Settlement Colony” on New Island, in the west of the Falkland Islands/ Islas Malvinas (51°42’S, 61°18’W) as part of an ongoing study on southern rockhopper penguins (e.g. Poisbleau et al. 2008; Dehnhard et al. 2013b). During the breeding seasons 2009/10 and 2010/11, we equipped a total of 23 males (during crèche only) and 40 females (26 and 14 for guard and crèche, respectively) with GPS temperature-depth data loggers (GPS-TD, earth&Ocean technologies, Kiel, Germany), recording the GPS positions, dive depth (using a pressure sensor) and temperature (see Table 1 for exact dates and approximate age of their chicks). Sexes were distinguished according to bill size (males have on average 13% longer and thicker bills than females; Poisbleau et al. 2010).

GPS data loggers were deployed on the birds' lower back using Tesa tape (following Wilson et al. 1997). Devices weighed 75 g, and measured 96x39x26.5 mm, representing 2.9% of the adult body mass, and about 6–10% of the birds' cross-section (Ludynia et al. 2012). Extreme care was taken to minimize stress to the captured adults and to protect chicks from potential predators. Handling time was kept to a minimum, mostly below 15 minutes and always below 20 minutes. The head was covered during handling in order to minimize stress. Birds were released a few metres away from their nests. All birds returned to their nests and attended their chicks shortly after being released.

Data from 54 birds was used in the analyses presented here (see Table 1), as some devices malfunctioned or had to be taken off when males delayed their departure at the beginning of the crèche stage. In general, GPS loggers were recovered after a single foraging trip, but in few cases, birds conducted several (max. 5) foraging trips before devices could be retrieved. Certain trip parameters could not be calculated for all birds if, for example, the battery life ended before the return of the bird.

Temperature and depth sensors were set to 1 s sampling intervals, GPS sampling intervals varied between two minutes in 2009/10 (both sexes) and for females in 2010/11 and five minutes for males in 2010/11, in order to maximize data acquisition. Additionally, while birds were at sea, the GPS units were programmed to attempt to record positions upon each surfacing. Pressure data were recorded with a resolution corresponding to 3.5 cm of depth, while temperature data had a resolution of 0.0058 K. GPS positions, temperature and pressure data were downloaded from the device upon retrieval of the logger.

Chick growth rates and isotope samples

Rockhopper penguins exhibit an extreme egg-size dimorphism paired with a reverse hatching asynchrony, with the smaller and first-laid (A-)eggs hatching on average one day after the

second laid and 28% larger (B-)eggs (Poisbleau et al. 2008; Demongin et al. 2010a). Due to the size-dimorphism between siblings, A-chicks usually die few days after hatching as they cannot compete for food with their larger sibling (Gwynn 1953; Warham 1975; Poisbleau et al. 2008). However, A-eggs may serve as an insurance for the loss of the B-egg or -chick (St. Clair and St. Clair 1996; Poisbleau et al. 2008; Dehnhard et al. 2014), and occasionally parents manage to raise both chicks (Poisbleau et al. 2008). We therefore distinguished between A- and B-eggs and their subsequent survival.

At the beginning of December and before chicks hatched, we marked 30 study nests in the colony, each of which contained two eggs at that stage. We distinguished between A- and B-eggs based on their size-difference, and marked them with non-toxic paint marker. Parental birds of these nests were not deployed with GPS loggers at any time. Nests were checked daily until hatching of both eggs, and chicks were thereafter weighed on average every three days from hatching to fledging. Protocols on weighing and individual marking of chicks followed Poisbleau et al. (2008). Body mass increase in rockhopper penguin chicks is linear in the first 45 to 50 days of age, and may drop after day 55 of age (see Fig. 2; also Poisbleau 2008). We used linear regression models (based on least squares) to determine the slope of mass increase with age (hereafter growth rate) from 0 to 45 days of age individually for each chick that survived until fledging. We furthermore used the last body mass recording of each chick before fledging as a proxy for fledging mass. Overall chick survival was calculated separately for A- and B-chicks as the number of chicks fledged / number of chicks hatched.

When chicks were 18 days old (22 to 31 Dec 2009 and 21 Dec 2010 to 4 Jan 2011, respectively), we collected a blood sample ($< 500 \mu\text{l}$) from the brachial vein (25 gauge needle) for stable isotope analyses (N = 20 analysed samples from 2009/10 and N = 19 samples from 2010/11). Blood sampling had no detectable adverse effects. After

centrifugation and separation, red blood cell samples were frozen (-20°C) and later dried in a drying furnace (60°C).

Prey isotope samples

In marine food webs, the combination of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) stable isotope ratios allow to estimate an animals' trophic position in the food web (Minagawa and Wada 1984; Owens 1987) and to obtain broad-scale spatial information about foraging grounds (reviewed in Rubenstein and Hobson 2004). By incorporating isotope data from both prey and consumers into stable isotope mixing models, one can furthermore reconstruct the proportions of prey types in a consumer's diet (see Boecklen et al. 2011 for a review). We therefore included data on potential prey species, all of which have been documented to be regular food items in southern rockhopper penguins (e.g. Clausen and Pütz 2002; Raya Rey et al. 2007). Isotope data from Argentine shortfin squid *Illex argentinus*, great hooked squid *Moroteuthis ingens* and Patagonian longfin squid *Loligo gahi* that were collected in the summers 2009/10 and 2010/11 around the Falkland Islands were obtained from Quillfeldt et al. (2015). We furthermore included isotope data from Falkland herring *Sprattus fuegensis* and the myctophid *Gymnoscopelus nicholsi* (known to be preyed upon by southern rockhopper penguins; Raya Rey et al. 2007) from Quillfeldt et al. (2015), even though fish-sampling did not entirely match timewise with sampling of rockhopper penguins. In addition, we collected krill samples (*Euphausia lucens* and *E. valentini*.; hereafter referred to as euphausiids) from stomach contents of freshly dead southern rockhopper penguin chicks that died from natural causes (hypothermia, nest abandonment, predation) and were found in the breeding colony.

Stable isotope analysis

224 Due to their small size, we pooled 2–5 euphausiid specimen for each analysed isotope sample
225 (N = 3 in 2009/10 and N = 4 in 2010/11). Euphausiid samples were fat extracted using a
226 Soxhlet apparatus with a methanol:chloroform 2:1 solvent. Subsamples for carbon
227 measurements were additionally acid washed with HCl. Stable carbon and nitrogen isotope
228 analyses of euphausiids from 2009/10 were analysed at the NERC Life Sciences Mass
229 Spectrometry Facility, Glasgow, and from 2010/11 at the IZW Berlin. Stable isotope analysis
230 of penguin blood was carried out at the Leibniz Institute for Zoo and Wildlife Research in
231 Berlin, Germany for the samples from 2009/10 and at the Laboratory of Oceanology,
232 University of Liège, Belgium, for the samples from 2010/11. The use of laboratory standards
233 (see below) assured accurate measurements and facilitated the comparability of results
234 between laboratories. Dried red blood cells were homogenized and ground to a fine powder.
235 In Berlin, stable carbon and nitrogen isotope analyses were carried out on 0.35 mg aliquots,
236 weighed into tin cups. Stable carbon and nitrogen isotope ratios were measured
237 simultaneously by continuous-flow isotope ratio mass spectrometry using a Flash Elemental
238 Analyser (Thermo Finnigan, Bremen, Germany) linked to a Delta V Advantage Isotope Ratio
239 Mass Spectrometer (Thermo Finnigan, Bremen, Germany). Two laboratory standards were
240 analysed for every ten samples, allowing any instrument drift over a typical 14-h run to be
241 corrected. Stable isotope ratios were expressed in δ notation as parts per thousand (‰)
242 deviation from the international standards V-Pee dee belemnite (carbon) and AIR (nitrogen),
243 according to the following equation $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ where X is ^{15}N or ^{13}C
244 and R is the corresponding ratio $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. Based on internal standards (N = 165,
245 tyrosin; Roth, Germany), the analytical precision (± 1 SD) equalled $\pm 0.16\text{‰}$ and $\pm 0.29\text{‰}$
246 for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively. In Liège, stable isotope ratio of carbon and nitrogen were
247 measured on 0.8 mg aliquots, in continuous flow by mass spectrometry (Isoprime 100,
248 Isoprime, UK) coupled to an elemental analyser (Vario Microcube, Elementar, Germany).

Pure gasses of CO₂, NO₂ and SO₂ were used and calibrated against certified reference materials, i.e. sucrose (IAEA-C6; $\delta^{13}\text{C} = -10.8 \pm 0.5\text{‰}$), ammonium sulfate (IAEA-N2; $\delta^{15}\text{N} = +20.3 \pm 0.2\text{‰}$). The analysis' performance was assessed by procedural blanks, replicated samples and in-house standard (i.e. glycine). Analytical precision (\pm S.D.) on replicated samples equaled ± 0.21 and $\pm 0.10\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

Statistics

All statistical analyses were performed in R (version 3.1.0; R Development Core Team 2014). As GPS devices obtained positions in different time intervals, we linear interpolated between recorded positions for standardized kernel analysis using the FillGap software (Jensen Software Systems, Germany). We used the package *adehabitatHR* (Version 0.4.6; Calenge 2006) in the free software R (R Development Core Team 2014) to calculate kernel estimations of the utilization distribution (UD; function *kernelUD*). The 20, 40, 60 and 80% UD kernels are given and we calculated the similarity between the 80% UD kernels using Bhattacharyya's affinity (BA) following Fieberg & Kochanny (2005). BA can range from 0 (no overlap) to 1 (identical UDs). Maximum distance to the colony was calculated for the furthest recorded position from the colony and distance travelled was calculated as the sum of all distances between actual recorded positions. Birds do not necessarily travel in a straight line between two recorded positions, therefore distance travelled can always be considered an underestimation of the actual distance.

Pressure data was analysed using a custom-written Matlab script (see Mattern et al. 2007 for details), defining dives as being of at least three metres depth.

Trip parameters (trip duration, distance travelled and maximum distance) and dive parameters (dive depth and dive duration) were all highly correlated with each other (all Pearson's $R >$

0.80, all $p < 0.001$). We therefore restricted statistical analyses to one trip and one dive parameter, and chose maximum distance to the colony (as this is more accurately measured than distance travelled) and average dive depth (using all dives per individual bird), but – for comparison with other studies – present the metrics for the other dive and trip parameters (Table 1). Running linear mixed effects models in the package *nlme* (Pinheiro et al. 2013), we started with two separate global models that contained maximum distance and dive depth as dependent variables, respectively. Year, breeding stage (guard or crèche) and sex (male or female) were included as fixed factors as well as the two-way interactions year*breeding stage and year*sex. We included bird identity as random factor in the model for maximum distance and trip nested in bird identity as random effect in the model for dive depth. We followed Ratcliffe et al. (2013) and conducted backwards-stepwise model selection, at first identifying the best random-effects model structure by comparing models with and without trip effect (nested in bird identity – only in the model for dive depth) that were fitted with restricted maximum likelihood (REML). We did not test for the performance of a model without bird identity, as removal would have violated the premise of independent data. After validating the best random-effects model structure, we continued with the validation of the fixed effects model structure, starting with the interaction effects and fitting models with maximum likelihood (ML).

To compare chick growth rates and fledgling masses (each as dependent variables in separate models), we used linear models with year as fixed effect. Chick survival between the years was tested separately for A- and B-chicks, using Chi-square tests based on expected and observed values of the numbers of hatchlings and fledglings.

For penguin isotope data, we again conducted a linear model, with year as fixed effect. We furthermore tested for correlations between body mass (at day 18, when blood samples were collected) and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values separately in both years, in order to assess

potential effects of nutritional status on discrimination rates (Lee Cruz et al. 2012), and thus potential implications for the interpretation of our results.

We present likelihood ratio (LR) for linear mixed effect model outputs, and F-values for linear models. df values are presented in subscript. In order to estimate the variance explained by fixed and random effects (for linear mixed effect models), we followed Nakagawa and Schielzeth (2013) and calculated marginal R^2 values (reflecting the variance explained only by fixed effects) and conditional R^2 values (reflecting the variance explained by both fixed and random effects).

Diet composition and isotopic niches

We used the package *SIAR* 4.2.0 (Parnell and Jackson 2013) in R to determine both diet composition and isotopic niche metrics. Diet composition was estimated by applying the SIAR mixing model. We used the same isotopic discrimination rates between diet and blood as previously applied for southern rockhopper penguins (Dehnhard et al. 2011): $\delta^{13}\text{C} = 0.6\text{‰}$, $\delta^{15}\text{N} = 2\text{‰}$. SD was set to 0.5‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, which is at the upper end of the range of values suggested by Caut et al. (2009). We included the prey species as separate sources in the mixing model, and ran SIAR models separately for the two breeding seasons.

Results

Sea surface temperatures and chlorophyll a concentration

While average local SST were similar in both years (mean SST of $7.57^\circ\text{C} \pm 1.96$ SD in 2009/10 and $7.73^\circ\text{C} \pm 1.51$ SD in 2010/11), conditions differed on a temporal scale. Spring temperatures (September to November) were up to 2°C higher in 2010/11 than in 2009/10, while summer temperatures (December to February) showed the opposite pattern (Fig. 3).

Chlorophyll *a* concentrations, indicating the strength of the phytoplankton bloom, were markedly lower in the austral spring 2009/10 ($1.64 \text{ mg/m}^3 \pm 1.91 \text{ SD}$) than in 2010/11 ($2.82 \text{ mg/m}^3 \pm 2.51 \text{ SD}$; Fig. 4), while this pattern was weaker in summer ($2.01 \text{ mg/m}^3 \pm 1.82 \text{ SD}$ in 2009/10 and $2.19 \text{ mg/m}^3 \pm 1.49 \text{ SD}$ in 2010/11; Fig. 4).

Foraging trip and dive behaviour

Kernel analysis showed that birds of both sexes used larger areas, and foraged much further away from the colony during the breeding season 2010/11 compared to 2009/10 (Fig. 1). Females increased their foraging area from guard to crèche in both years, although the area used during guard in 2010/11 was larger than that used during crèche in 2009/10. Comparing both sexes during the crèche stages showed that females had a much larger range than males, especially in 2010/11. However, similarity calculations of the 80% UD between paired data sets (years and sexes) showed little difference in the degree of similarity in areas used with BA values ranging from 0.505 (least similarity) between females during the guard stage in 2009/10 and 2010/11 to 0.697 (highest similarity) between females during guard and crèche 2009/10 (Fig. 1).

For maximum distance, neither the interaction between year and breeding stage ($\text{LR}_1 = 0.06$, $P = 0.815$), nor the interaction between sex and year ($\text{LR}_1 = 0.81$, $P = 0.369$), breeding stage ($\text{LR}_1 = 1.19$, $P = 0.275$) or sex ($\text{LR}_1 = 1.52$, $P = 0.217$) had a significant effect on maximum distance and were consequently removed from the model. The only variable with a significant effect on maximum distance was year ($\text{LR}_1 = 3.905$, $P = 0.048$), which explained 4.1% of the variance (marginal R^2 -value). Altogether (including the variance explained by bird ID), this final model explained 11.6% of the variance (conditional R^2 value). Thus, birds foraged further away from the colony in 2010/11 compared to 2009/10. The best random effects model structure for dive depth included trip nested within bird ID.

Removal of the nested trip effect led to a significant increase in variance ($LR_1 = 1043.82$, $P < 0.001$, reduction of conditional R^2 by 6.0%). Neither the interaction between year and breeding stage ($LR_1 = 0.06$, $P = 0.814$) nor the interaction between sex and year ($LR_1 = 0.34$, $P = 0.561$) had an effect on dive depth. Dive depth furthermore did not differ significantly between guard and crèche ($LR_1 = 0.04$, $P = 0.843$) or between males and females ($LR_1 = 1.73$, $P = 0.188$). However, birds dived deeper in 2009/10 than in 2010/11 ($LR_1 = 7.76$, $P = 0.005$), and this final model (with year as only fixed effect) explained 24.0% of the total variance (conditional R^2 -value), of which 2.4% were attributed to the year-effect (marginal R^2 -value).

Penguin chick isotopes, diet composition, growth rates and survival

Penguin chicks had significantly lower $\delta^{15}N$ and lower $\delta^{13}C$ values in 2009/10 than in 2010/11 ($F_1 = 313.18$, $P < 0.001$ for $\delta^{15}N$ and $F_1 = 47.36$, $P < 0.001$ for $\delta^{13}C$; Fig. 5). $\delta^{15}N$ and $\delta^{13}C$ values were not correlated with body mass at 18 days (all Pearson's $R < 0.18$, all $p > 0.447$). SIAR mixing models based on penguin and prey isotope values suggested that the chicks' diet during guard 2009/10 was dominated by euphausiids (average 72.0%), followed by *Sprattus fuegensis* (average 11.1%; Fig. 6). The average proportion of *Gymnoscopelus nicholsi* and the three squid species was below 5%. Contrastingly, during guard in 2010/11, euphausiids were estimated to have a subordinate role in chick diet (average 3.6%). Estimated chick diet consisted of a mixture of *Loligo gahi* (average 50.6%), *Illex argentinus* (average 23.7%) and *Sprattus fuegensis* (average 13.1%), with a lower proportion of *Gymnoscopelus nicholsi* and *Moroteuthis ingens* (average 3.7 and 5.3%, respectively; Fig. 6).

Chick growth rates ($51.8 \text{ g} \pm 6.7 \text{ SD}$ per day in 2009/10 and $48.7 \text{ g} \pm 5.7 \text{ SD}$ per day in 2010/11) did not differ between the years ($F_1 = 2.75$, $P = 0.105$), neither did fledgling mass ($2097 \text{ g} \pm 269 \text{ SD}$ in 2009/10 and $2147 \text{ g} \pm 159 \text{ SD}$ in 2010/11 ($F_1 = 0.53$, $P = 0.471$) (Fig 2).

Chick survival did not differ significantly between both years for either A-chicks ($\chi^2_1 = 1.32$, $P = 0.251$) or B-chicks ($\chi^2_1 = 0.11$, $P = 0.743$; Table 2).

Discussion

In summary, our results showed significant year differences in the foraging behaviour and diet of southern rockhopper penguins, which, however, did not affect chick growth rates or chick survival. Foraging behaviour did not differ between sexes during the crèche stage or between the guard and crèche stage for females.

Year differences in foraging behaviour

Rockhopper penguins foraged further away from the colony in 2010/11 and made shallower dives in that same breeding season, indicating significant year-differences in the foraging behaviour. Alongside, stable isotope mixing models suggested marked differences in the composition of penguin chick diet, with euphausiids dominating the diet in 2009/10, but being nearly absent in 2010/11 when especially squid contributing relatively more to the diet (see detailed discussion about the diet below). We assume that changes in the availability and/or distribution of prey species between the two years, most likely caused by differences in oceanographic conditions, caused these behavioural and dietary changes. Albeit similar on average across the entire breeding season as well as the preceding winter months, we indeed observed distinct differences in local spring SST between the two years. On a larger spatial scale, SST appeared to be generally lower not only in spring but also in summer (contrasting the local pattern) in the breeding season 2009/11 compared to 2010/11 (see Fig. 5 in Quillfeldt et al. 2015). We expected that lower spring SST would improve conditions for phytoplankton growth and thus primary productivity. However, the opposite pattern was

visible, with higher chlorophyll *a* concentrations suggesting a stronger phytoplankton bloom in 2010/11 than in 2009/10. Potentially, the colder spring temperatures in 2009/10 slowed down phytoplankton growth and thus productivity. Based on chlorophyll *a* values, we would therefore have expected better foraging conditions and specifically shorter trip distances in 2010/11 than in 2009/10. However, the opposite was the case, with foraging trips being significantly longer in distance in 2010/11, as birds used pelagic foraging sites that were located further away than the coastal foraging areas used in 2009/10. On the other hand, chick growth rates and survival did not differ between the years, and it is therefore – despite the clear differences in annual primary productivity – difficult to identify which one (if any) of the two study years was “better” for the penguins. In line with this, dive depths showed an opposite pattern compared to foraging range, with penguins diving deeper in 2009/10, when birds foraged in coastal areas, and shallower dives in pelagic areas in 2010/11. Southern rockhopper penguins can reach maximum dive depths of more than 100 m (Schiavini and Raya Rey 2004; Raya Rey et al. 2009) and were thus potentially able to reach prey close to the seafloor in 2009/10. Nevertheless, planktonic euphausiids dominated the prey in 2009/10. Birds in 2009/10 mostly foraged in water depths of 30 – 100 m compared to water depths of >100 m in 2010/11 (see Fig. 1) when squid contributed relatively more to the diet.

Potentially, SST and chlorophyll *a* only affect the abundance of actual prey species with a longer time lag. This could explain the seemingly contradicting patterns between SST, chlorophyll *a* and the penguins’ foraging distance from the colony. However, SST during the winters before both breeding seasons did not differ markedly (see Electronic Supplementary Material). Alternatively, the differential oceanographic conditions may have led to a differential distribution of prey species in both years, with the penguins’ foraging behaviour being determined by prey distribution / availability rather than productivity. This could also explain the significant differences in estimated prey proportions (see below).

The spatial foraging behaviour of rockhopper penguins during the chick-rearing period has so far only been described very briefly, mainly in the context of inter-specific segregation (Boersma et al. 2002; Masello et al. 2010). Maximum distance from colony as described in Masello et al. (2010) for the guard stage (during the breeding season 2008/09, also on New Island), was intermediate compared to our data from 2009/10 and 2010/11. Similarly, maximum distance in our study was broadly in the range of values presented by Boersma et al. (2002) for short trips of less than three days (assuming this was during guard and crèche as the authors did not distinguish between incubation and chick-rearing). Our data on trip durations were similar to those presented by Pütz et al. (2006) for the chick-rearing period, reflecting rather short foraging trips and a low percentage of overnight trips (especially in 2009/10). In contrast, Tremblay & Cherel (2003; 2005) reported that 10–15% of foraging trips were overnight trips, partly spanning several nights, in chick-rearing eastern rockhopper penguins (*Eudyptes chrysocome filholi*) on Kerguelen and Crozet Islands. For Staten Island and Noir Island, Argentina, the percentage of overnight trips in chick-rearing southern rockhopper penguins was even higher (53 and 60%, respectively; Schiavini and Raya Rey 2004; Raya Rey et al. 2009). Although we did not analyse trip duration, we can thus – based on the positive correlation between trip duration and maximum foraging distance – assume that rockhopper penguins outside the Falkland Islands forage further away from colonies than we observed at our study site.

Dives in both study years were deeper and longer compared to those during the guard stage at other sites in the Falkland Islands (Pütz et al. 2006), but in the same range or shallower/shorter compared to dive data recorded for birds from Noir and Staten Islands (Schiavini and Raya Rey 2004; Raya Rey et al. 2009) as well as Kerguelen and Crozet Islands (Tremblay and Cherel 2003), reflecting the overall flexible diving behaviour in this species.

Year differences in chick diet, growth rates and survival

Due to the partly very similar isotope values of prey species, a mismatch in sampling time between some of the fish samples and the penguins, and considering that we may have missed to include isotope data from some important prey species, we here prefer to refer to the prey types (i.e. fish, squid and crustaceans) rather than relying on the SIAR results as exact proportions of specific prey species in the diet. Indicated by the significant changes in penguin isotope values, and subsequent changes in the estimated diet proportions by SIAR models, the diet of rockhopper penguin chicks differed markedly between the two breeding seasons. These year differences and the much lower proportion of euphausiids in 2010/11 in the chick diet was also apparent from visual inspection of chick stomachs (died from natural causes and mainly collected to obtain isotope samples of prey specimen as detailed in the Methods). As chick ages and sizes differed because they were collected throughout the entire breeding season, and stomach contents were often partly digested, we did not conduct standardized stomach content analyses. Nevertheless, stomachs visually contained a higher proportion of fresh squid as well as squid beaks in 2010/11 compared to 2009/10, including the species *Loligo gahi*, *Illex argentinus* and *Gonatus antarcticus* (Dehnhard et al. unpublished data). Furthermore, we identified few specimen of *Sprattus fuegensis* in stomach samples from 2010/11, suggesting that penguins foraged on pelagic prey. Such year differences in diet are in line with previous studies that emphasized the plasticity of rockhopper penguins' diet, with varying amounts of fish, euphausiids and squid species among years (Clausen and Pütz 2002; Raya Rey and Schiavini 2005) and breeding sites (Tremblay and Cherel 2003; see review in Pütz et al. 2013).

Oceanographic conditions are known to affect the spawning migrations and reproductive success of squid species around the Falkland Islands (e.g. Waluda et al. 2001;

Arkhipkin et al. 2004) and similarly the population sizes of euphausiids (Siegel 2000). Subantarctic euphausiids can occur both offshore and in coastal waters (Gibbons et al. 1991), sometimes forming large swarms with high densities (Nicol et al. 1987). The higher proportion of euphausiids in 2009/10 may therefore reflect a high distribution of euphausiid swarms close to the coast in 2009/10, enabling birds to feed close to the colony, while squid was more abundant or easier to catch in 2010/11.

Notably, the higher proportion of euphausiids in the chick diet occurred in the year with colder spring temperatures. These results coincide with data from Morrison et al. (2014), who found a higher percentage of zooplankton prey in eastern rockhopper penguin chick diet in the year with lower SST when parental birds foraged closer to the colony. Together with our results that chick body mass was not linked to stable isotope values, our data may thus add to the growing evidence that higher trophic level prey (i.e. prey with higher $\delta^{15}\text{N}$ values) does not necessarily present higher quality prey for rockhopper penguins (Morrison et al. 2014).

Notably, we applied isotope discrimination factors that were previously used for adult penguins, and this may have biased SIAR estimates, as isotopic differences between adults and chicks can be caused by age- and body-condition related metabolic differences. In blue-footed booby chicks (*Sula nebouxii*), body condition and both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were negatively correlated, suggesting that the individual's nutritional status affects discrimination factors (Lee Cruz et al. 2012). Our results did not confirm such a relationship in southern rockhopper penguin chicks. Moreover, rapid growth in seabird chicks has been shown to lead to a depletion of ^{15}N in red blood cells by 0.37 to 0.55 ‰, while no effect of growth on $\delta^{13}\text{C}$ was found (Sears et al. 2009). A depletion of ^{15}N in this magnitude could have affected the overall SIAR-estimates for prey species estimates to some extent, meaning the proportion of fish and squid species in general might have been underestimated, and the proportion of euphausiids

overestimated. However, as chick mass at the date of blood sampling and growth curves did not differ between the years, a potential physiological effect should have been similar in both years. If at all present, we would thus assume a similar error for SIAR-estimates in both years, which would thus not debilitate the overall and very marked year-differences in diet that we found.

Despite these year differences in foraging behaviour and diet, and thus contrasting our expectations, we did not observe a significant effect on chick growth rates and chick survival. This agrees with Dehnhard et al. (2013a) who found no year-differences in average daily body mass gain of adults during the chick rearing season in both focal years. Chick growth rates in both 2009/10 and 2010/11 were steeper compared to those presented by Tremblay and Cherel (2003) for both Kerguelen and Crozet Islands for the eastern subspecies (*Eudyptes chrysocome filholi*). These differences may thus either reflect differences in productivity between breeding sites and/or be related to the (albeit slight) morphological differences between both subspecies.

In comparison with Demongin et al. (2010b), we found a broadly similar survival rate of chicks from hatching to fledging. As we marked study nests only shortly before the hatching period, we unfortunately cannot directly compare our results with the few other studies that present breeding success (based on the number of chicks fledged per breeding pair; e.g. Poisbleau et al. 2008; Baylis et al. 2013).

Effects of sex and breeding stage

Based on the (albeit small) morphological differences between males and females, we expected that males would be able to dive deeper than females and thus exploit deeper prey sources as seen in other size-dimorphic penguins and seabirds (Kato et al. 2000; Quintana et

al. 2011). Further, sexually different foraging behaviour could help to avoid intra-specific competition for resources during the crèche period, when males join the females to provision chicks with prey. However, we detected no significant differences in the maximum distance or dive depth between sexes and/or breeding stages in either breeding season. While results in 2009/10 may have been affected by the lower sample size for males during crèche compared to females, sample sizes were balanced in 2010/11, and yielded the same (non-significant) results. While confirming results from eastern rockhopper penguins (Hull 2000), our results are in contrast to a study by Raya Rey et al. (2007) who found significant differences in foraging duration between sexes during crèche. While generally weak, sexual differences were also present in the closely related macaroni penguin (*Eudyptes chrysolophus*) (Barlow and Croxall 2002) during crèche.

As the food demand of chicks should increase, while chicks could also tolerate to be fed less frequently, we expected that rockhopper penguins would extend their foraging range from guard to crèche. Thus, we expected to find an increase of maximum foraging distance from guard to crèche. However, this was not the case, as neither maximum distance to the colony nor dive behaviour differed significantly between guard and crèche. This agrees with results from eastern rockhopper penguins from Kerguelen and Crozet (Tremblay and Cherel 2003) but contrasts previous results from southern and northern rockhopper penguins (*Eudyptes moseleyi*) which showed an increase in foraging duration from guard to crèche (Tremblay and Cherel 2003; Raya Rey et al. 2007).

Conclusions

Our results underline the high plasticity of rockhopper penguins in their foraging behaviour and diet. Seen in a larger context and in comparison with other studies, it appears that – despite the obvious differences in foraging behaviour and diet between both years –

conditions during our two-year study period were still favourable. This may be highlighted by the fact that chick growth rates and survival did not differ between both years. Parents were therefore seemingly able to buffer the effects of longer foraging distances, so that there were no apparent effects on population trajectories.

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Table 1. Trip and dive parameters (mean \pm SE) of female and male southern rockhopper penguins during guard and crèche 2009/10 and 2010/11.

	2009/10			2010/11		
	Fem. Guard	Fem. crèche	Males crèche	Fem. Guard	Fem. crèche	Males crèche
Sample size*	8(10)	8(10)	3(3)	14(16)	9(14)	9(22)
Timing of GPS-deployments	10–20 Dec	6–26 Jan	14–26 Jan	17–29 Dec	8–25 Jan	4–19 Jan
Approximate chick age [days]**	4–14	31–51	39–51	8–20	31–48	26–41
Trip duration [h]	10.94 \pm 0.76	13.22 \pm 0.78	10.93 \pm 2.52	16.88 \pm 1.86	23.58 \pm 8.98	10.86 \pm 1.89
Distance travelled [km]	29.88 \pm 2.00	43.31 \pm 4.66	37.42 \pm 11.39	59.60 \pm 7.65	81.73 \pm 31.75	39.88 \pm 8.31
Maximum distance [km]	10.17 \pm 0.73	17.22 \pm 2.19	16.39 \pm 5.23	22.90 \pm 3.06	27.52 \pm 8.65	17.02 \pm 3.79
Total number of dives	3169	3354	775	5246	5973	6233
Number of dives per trip	316.90 \pm 17.60	335.40 \pm 22.72	258.33 \pm 82.73	419.68 \pm 43.04	426.64 \pm 100.23	283.32 \pm 54.99
Dive depth [m]	25.68 \pm 0.27	25.50 \pm 0.32	26.28 \pm 0.67	22.42 \pm 0.17	20.95 \pm 0.17	19.42 \pm 0.17
Dive duration [s]	74.14 \pm 0.38	70.91 \pm 0.45	70.22 \pm 1.10	63.84 \pm 0.36	74.52 \pm 0.41	66.73 \pm 0.34

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* number of birds and number of trips in parenthesis

** based on average age of study nest chicks during the deployment period

Fem.: females

Table 2. Southern rockhopper penguin chick survival from hatching to fledging in the two breeding seasons 2009/10 and 2010/11. Data are presented separately for A- and B-chicks

	Number of chicks hatching	Number of chicks fledging	chick survival
2009/10			
A-chicks	7	4	0.57
B-chicks	21	18	0.86
Total	28	22	0.79
2010/11			
A-chicks	18	4	0.22
B-chicks	23	17	0.74
Total	41	21	0.51

Fig. 1. Utilization distribution (UD) kernels of female rockhopper penguins during guard (top row), crèche (middle row) and male rockhopper penguins during crèche (bottom row) in 2009/10 (left column) and 2010/11 (right column). Note that the geographic range differs between years, with a smaller area shown for 2009/10 than 2010/11, reflected by the red frame shown in the top right plot. Given are the 20, 40, 60 and 80% UD kernels (black to light grey). Blue arrows and boxes refer to the similarity between groups for the 80% UD using Bhattacharyya's affinity. The white circle marks the position of the study colony on New Island.

Fig. 2. Body mass increase (mean \pm SD) of southern rockhopper penguin chicks with age. Only chicks that survived until fledging were included (N = 22 in each year). The timing of blood sampling for isotope analyses (on day 18) is indicated with an arrow.

Fig. 3. Weekly mean sea surface temperatures (SST) \pm SD in the foraging area of southern rockhopper penguins (50.5 to 52.5°S and 60.5 to 63.5°W) during the breeding seasons 2009/10 and 2010/11. Arrows indicate the timing of GPS-deployments, chick blood sampling in relation to arrival dates, chick hatching and chick fledging dates.

Fig. 4. Chlorophyll *a* concentration as an indicator of primary productivity in austral spring and summer 2009/10 (left) and 2010/11 (right) in the study area. Plotted data were obtained from remote sensing by NASA (MODIS-Aqua). The black ring marks the position of New Island.

Fig. 5. Stable isotope values (‰) of southern rockhopper penguin chicks (scatter plots) and prey species (means \pm SD) of potential prey species in 2009/10 (top) and 2010/11 (bottom). Prey values were corrected using the discrimination factors given in the Methods. SPR = *Sprattus fuegensis* Falkland herring, GYN = *Gymnoscopelus nicholsi* Lanternfish, ILL = *Illex argentinus* Argentine shortfin squid, ING = *Moroteuthis ingens* Greater hooked squid, LOL = *Loligo gahi* Patagonian squid, EUP = euphausiids (*Euphausia lucens* and *E. valentini*)

Fig. 6. Proportion of estimated prey species in the diet of southern rockhopper penguin chicks during the breeding seasons 2009/10 (top) and 2010/11 (bottom) Estimates are from SIAR mixing models and box plots present the 95, 75 and 25% credibility intervals in different shades of grey. SPR = *Sprattus fuegensis* Falkland herring, GYN = *Gymnoscopelus nicholsi* Lanternfish, ILL = *Illex argentinus* Argentine shortfin squid, ING = *Moroteuthis ingens* Greater hooked squid, LOL = *Loligo gahi* Patagonian squid, EUP = euphausiids (*Euphausia spp.* & *Thysanosessa macrura*).

Figure 1
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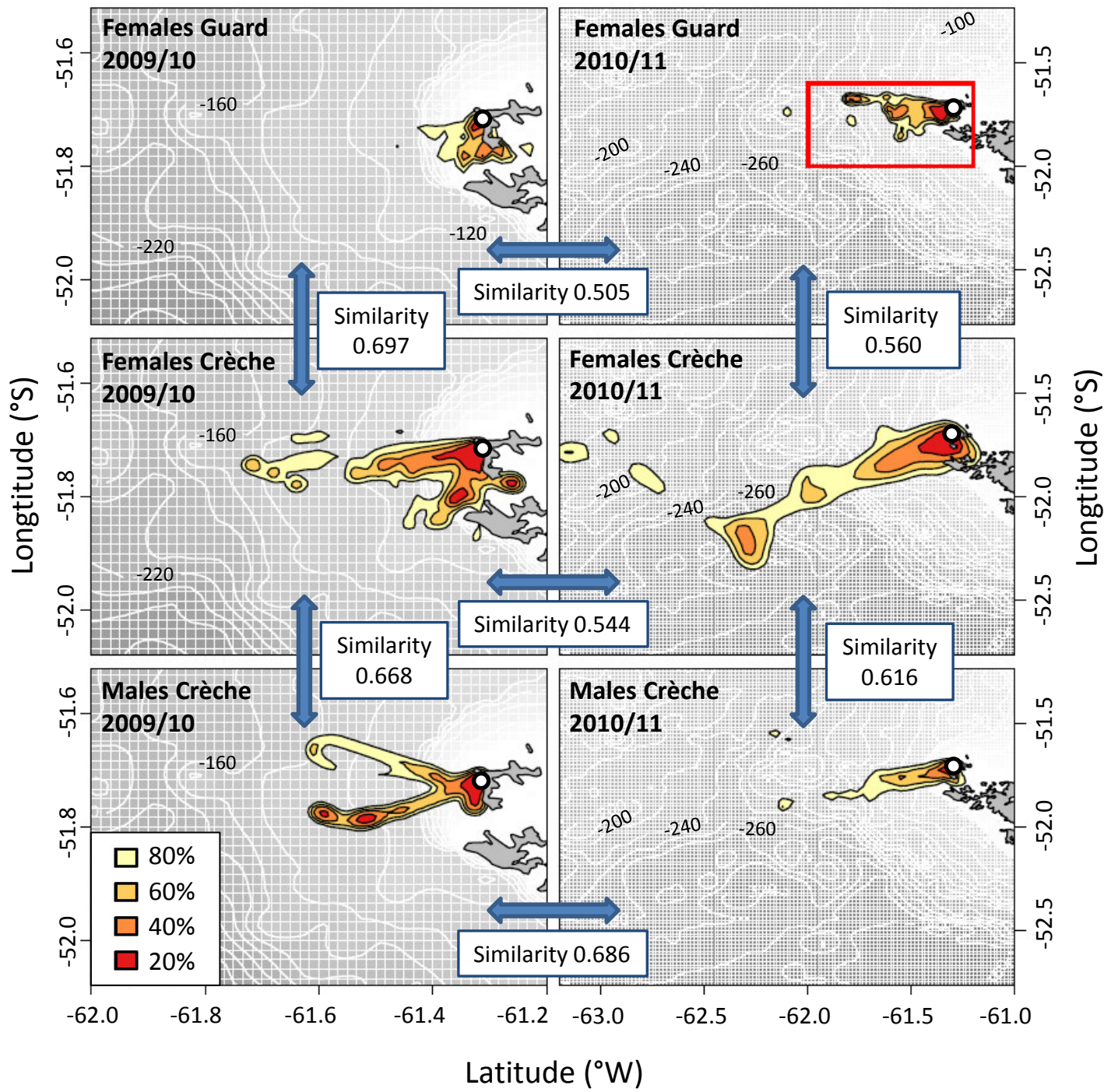


Figure 2

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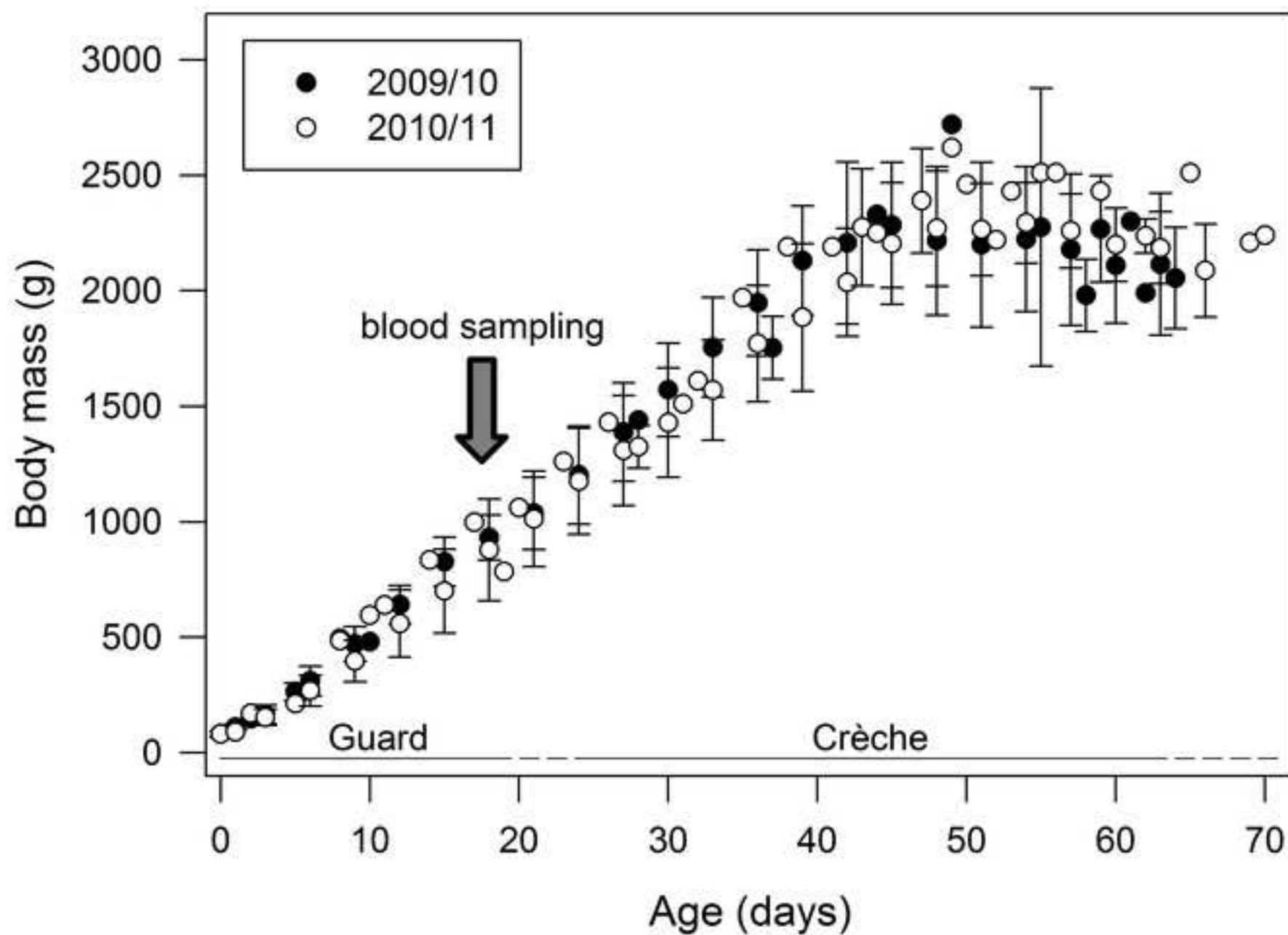


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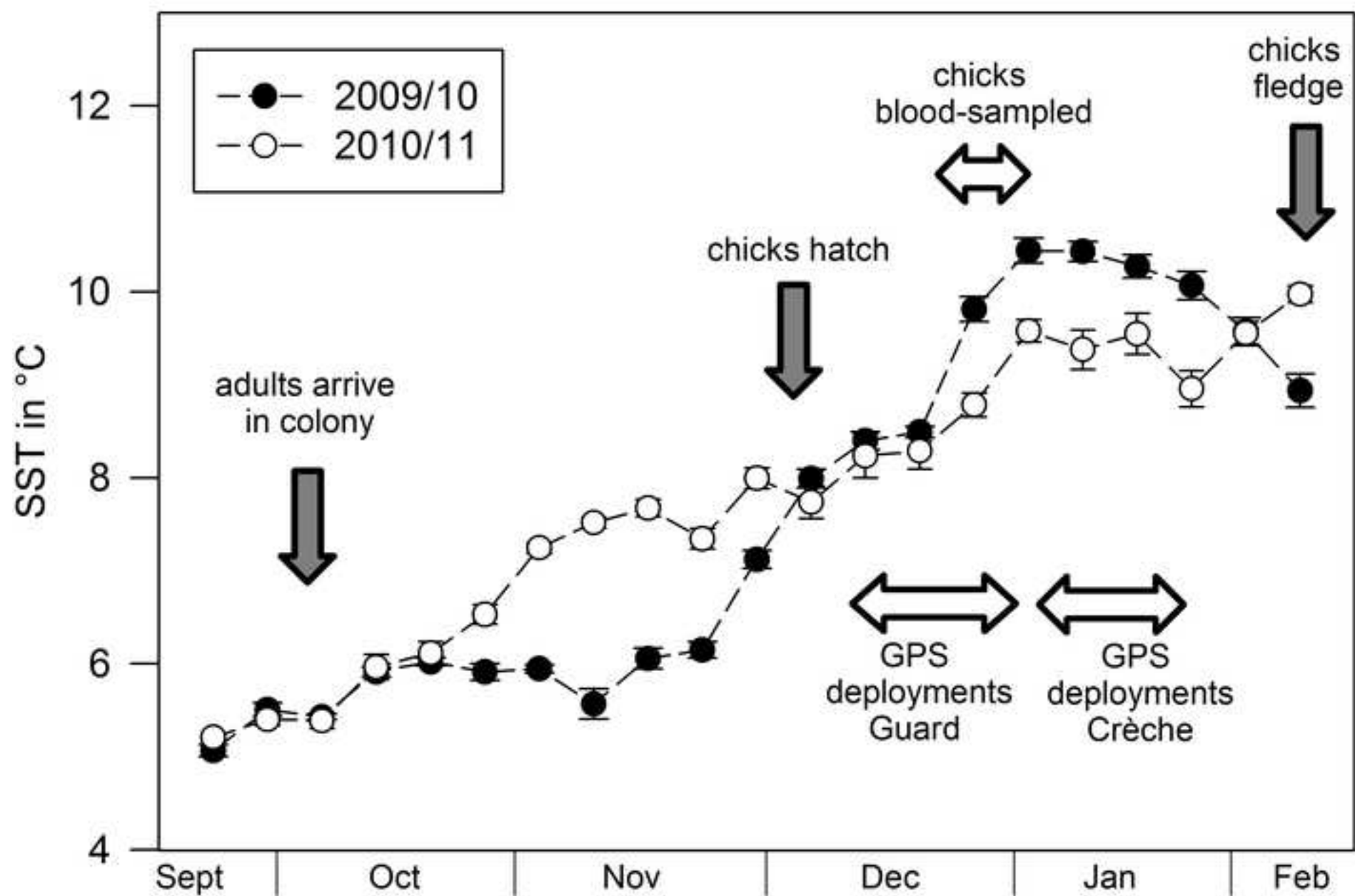


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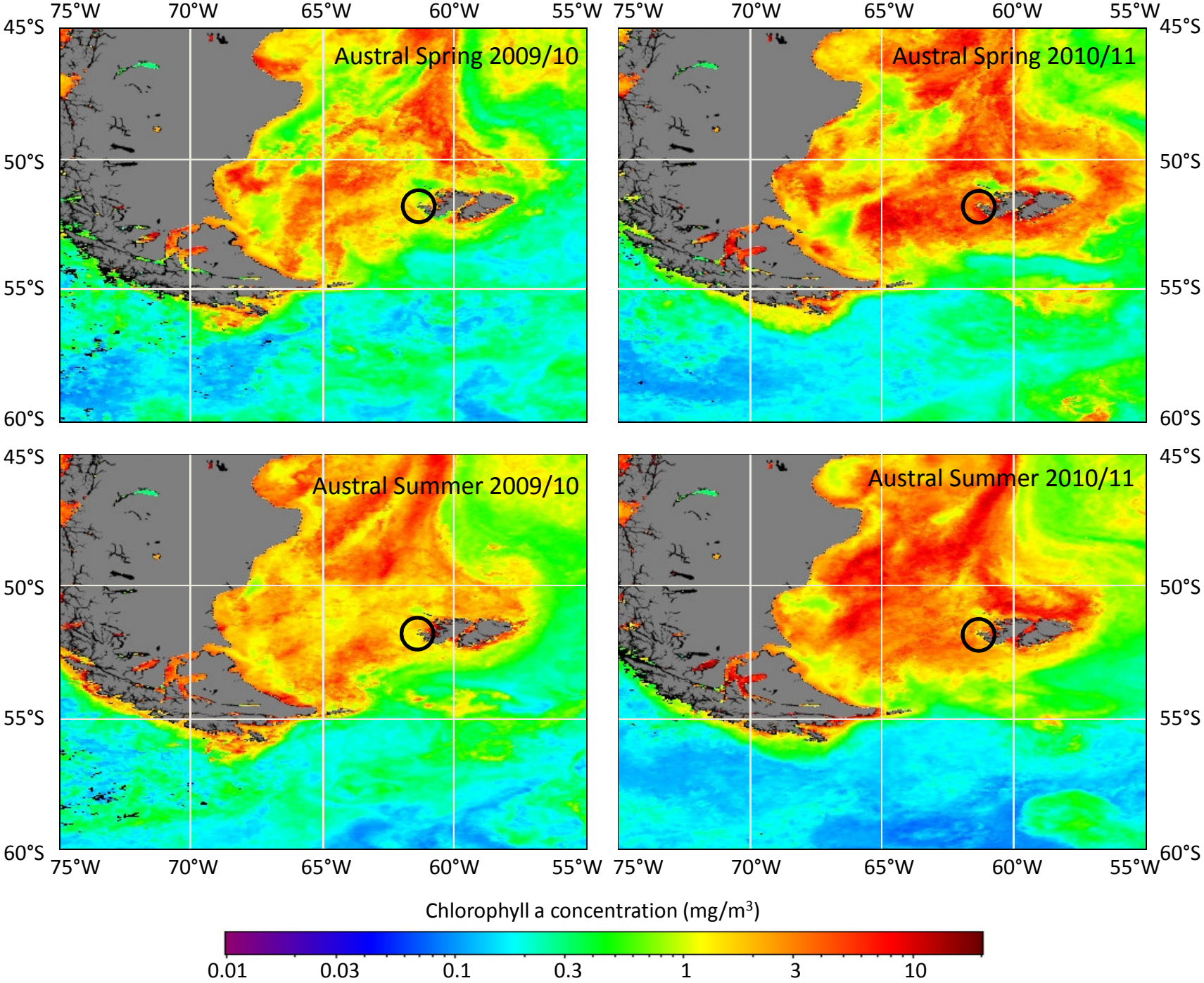


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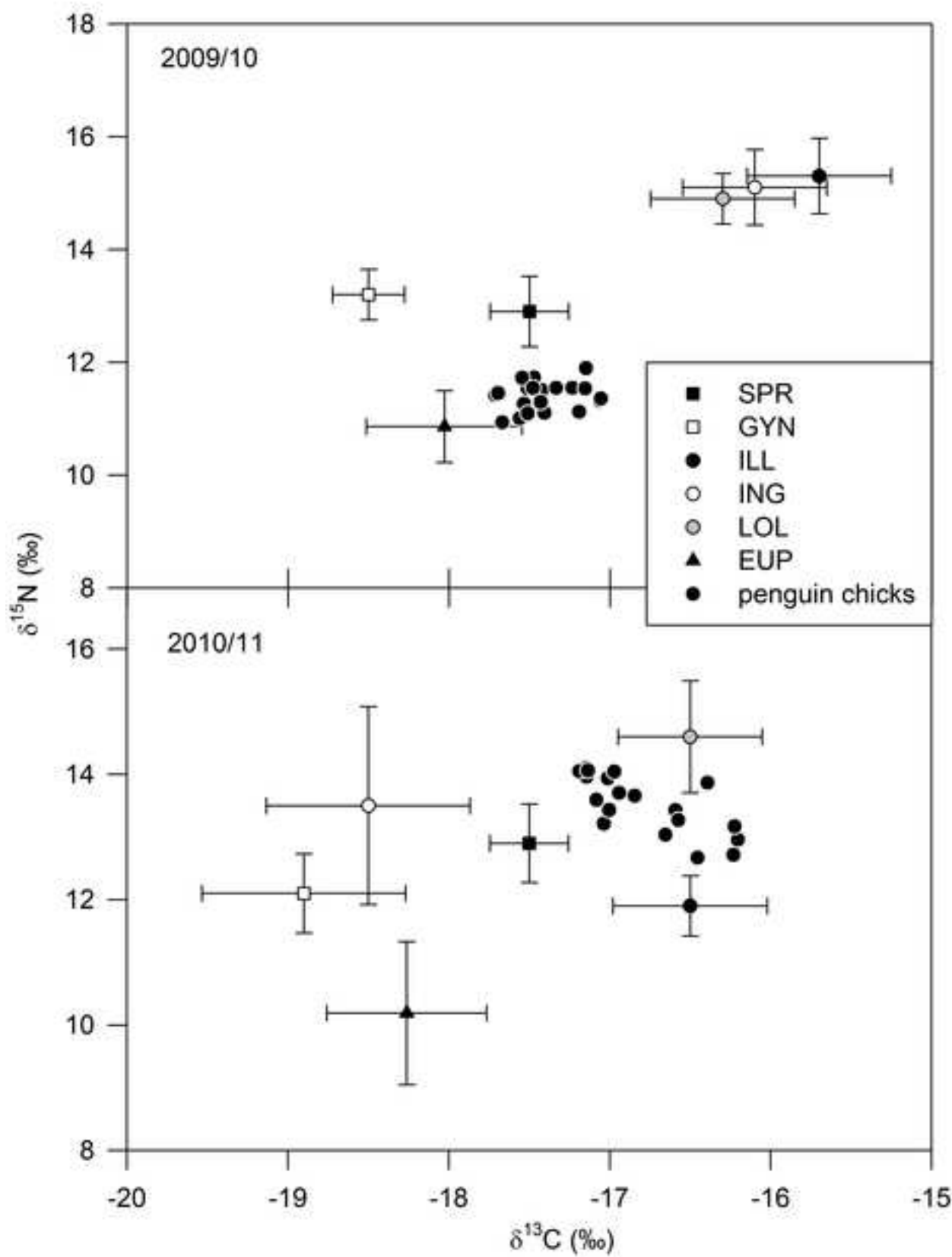
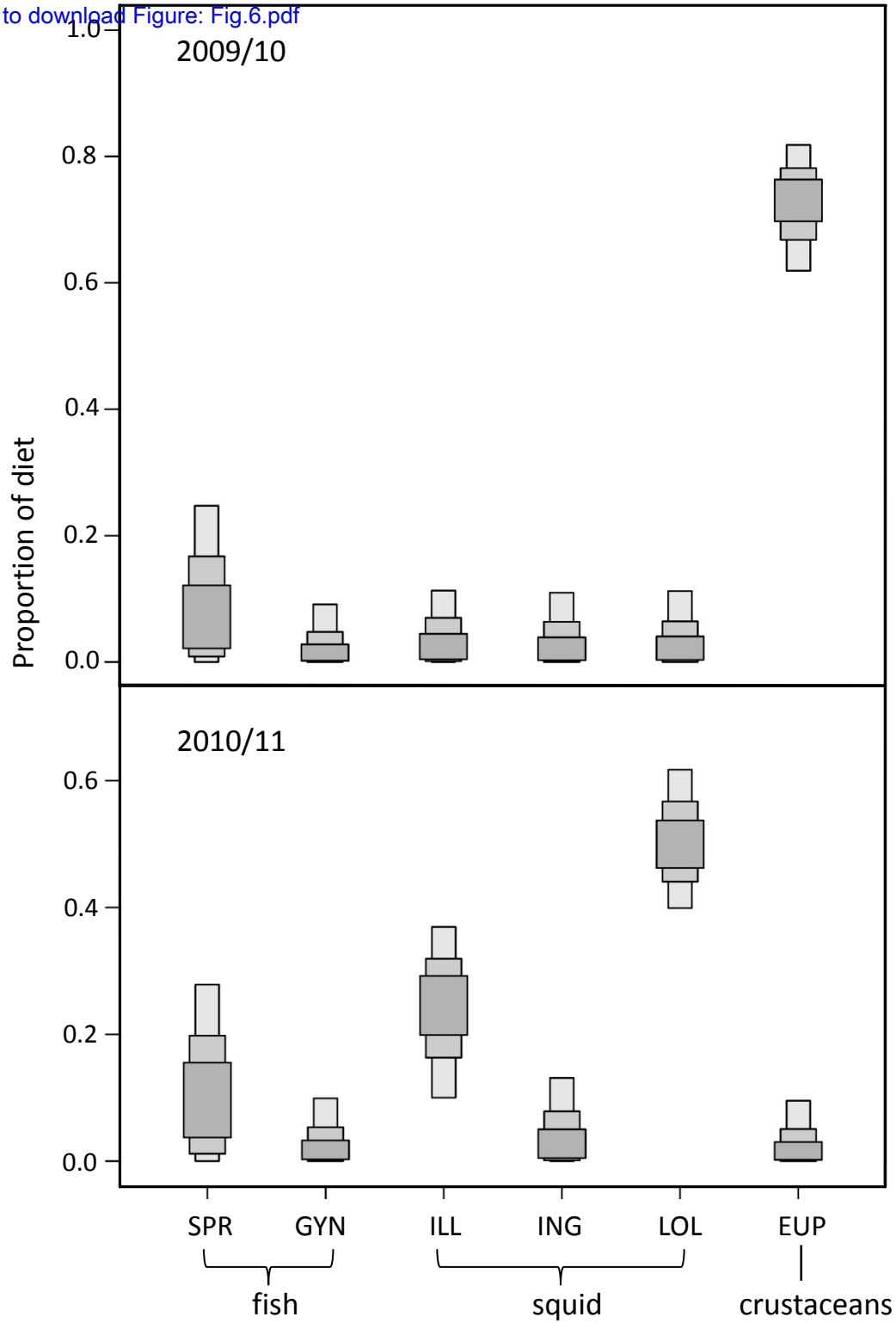


Figure 6
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