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Thermal responses and climate change implications of spring and autumn spawning Patagonian squid (*Doryteuthis gahi*) embryos

Jesse M.A. van der Grient [a,b,*], Barend Stander [c], Paul Brickle [a,d], Simon A. Morley [e]

[a] South Atlantic Environmental Research Institute, Stanley, Falkland Islands
[b] Royal Netherlands Institute for Sea Research, t' Horntje, Texel, Netherlands
[c] Falklands Fish Farming (Ltd), Stanley, Falkland Islands
[d] School of Biological Sciences, University of Aberdeen, Aberdeen, United Kingdom
[e] British Antarctic Survey, National Environment Research Council, Cambridge, United Kingdom

ABSTRACT

Ocean warming affects ectotherm physiological and phenological processes, potentially creating mismatches between early life stages and their prey. Seasonal spawning cohorts are thought to provide flexibility in responding to environmental variability, but if there is seasonal adaptation between these cohorts, then they may respond to ocean warming differently, affecting species resilience and potentially impacting the wider food web. We tested the response to warming of egg masses and paralarvae from two spawning cohorts (autumn and spring) of the Patagonian squid (*Doryteuthis gahi*). Treated egg masses were exposed to a strict warming regime while control eggs were exposed to air temperature-driven temperature changes. Egg mass respiration estimates demonstrated that higher temperatures resulted in higher respiration rates (metabolic processes), although no additional influence of the rate and magnitude of warming was detected. There were differences in paralarvae size and weight, with the treated autumn cohort containing smaller and lighter paralarvae, which could affect larval duration, especially if early hatching times and smaller hatchlings cause mismatches with their prey or increased predation. This suggests that temperature could influence survival and recruitment success. Greater understanding is required of how temperature changes influence squid phenology (e.g., from timing of egg laying to paralarvae growth and survival) and its likely influence on biomass at adult feeding grounds, which are also important fishing grounds. Further targeted studies could improve the prediction of future impacts on marine food webs, indicating if, for example, changing the timing of fishing seasons, in response to environmental cues would be a useful climate adaptation strategy for the Falkland Islands.

1. Introduction

Climate change is having wide ranging effects on aquatic ecosystems, especially via changes in temperature. The majority of marine organisms are ectotherms and therefore changes in sea temperature are altering the rates of all their physiological processes (Dell et al., 2011). When temperature affects the development and growth rates of invertebrate embryos and larvae, there can be additional impacts on their dispersal, population connectivity and species persistence (Kendall et al., 2016). These differences are expected to have further cascading impacts through marine food webs (Yang and Rudolf, 2010), altering marine ecosystems and the ecosystem services they provide. However, the effect of temperature changes on phenology, the sequence and timing of life history stages, is inconsistent across species, leading to trophic mismatches which can be important for species ontogeny (Visser and Both, 2005; Yang and Rudolf, 2010). Any such mismatches between larvae, their predators, and prey have long been thought to be one of the main drivers for recruitment variation (Cushing, 1990; Illing et al., 2018) and will only be exacerbated through climate change. In most temperate and polar environments, marine species spawn to ensure that hatching is timed so that larvae feed and develop during the more productive seasons, which are usually spring and summer (Clarke, 1987; Friedland et al., 2018). There are, however, some species that spawn multiple times in the year, for example spring and autumn herring spawning cohorts (dos Santos Schmidt et al., 2021), chinook salmon (Atlas et al., 2023) and Patagonian squid (Patterson, 1988). Such spawning patterns are often thought to relate to species portfolio effects, strategies which increase the variability in the timing or location of spawning to reduce risk of recruitment failure and buffer population responses to environmental variability (Schindler et al., 2010; Wilson et al., 2021). Seasonal temperature change provides different spawning cues for the different spawning cohorts, such as increasing warm temperatures for spring, and cold temperatures for autumn spawners (Pankhurst and Munday, 2011). These opposite seasonal temperature profiles result in different development rates of embryos and larvae of the different spawning cohorts. Eggs spawned in the autumn typically develop more slowly, in the

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* Corresponding author.
E-mail address: jesse.van.der.grient@nioz.nl (J.M.A. van der Grient).

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colder temperatures over the winter before experiencing warming temperatures in early spring, whereas the eggs spawned in spring develop in warming conditions only, so that both autumn and spring spawned eggs hatch to take advantage of the spring and summer productivity (Arkhipkin and Middleton, 2003; Sinclair and Tremblay, 1984). With general expectations that climate change will lead to phase-shifting of seasonal temperature profiles, as well as greater and more frequent extremes (Pankhurst and Munday, 2011), climate change could have markedly different effects between cohorts that spawn in different seasons (dos Santos Schmidt et al., 2021; Rosa et al., 2014).

The Falkland Islands are a cold temperate archipelago on the southwest Atlantic Ocean. While over the wider Patagonian Shelf sea surface temperature has already warmed (Oliver et al., 2018; Xu et al., 2022), warming for Falkland Islands offshore areas is predicted to be much less, likely due to the buffering effect of the cold Falklands current flowing north (Franco et al., 2022; Oliver et al., 2018; Palma et al., 2021). However, as many species in offshore Falkland Islands waters, including commercially important species, use coastal habitats as spawning and nursery habitats (van der Grient et al., 2023), it is important to understand if negative impacts of warming in coastal waters could be carried over to offshore waters. While specific data on Falkland Islands coastal seawater temperature change is not available, other correlated factors, such as air temperature show an increase in warming (Lister and Jones, 2015), and globally, variation in seawater warming between coastal and offshore areas is common (Varela et al., 2018) and an expected outcome of climate change (Schlegel et al., 2017).

One of the key commercially exploited species in the Falkland Islands that uses coastal environments as spawning area is the Patagonian squid, *Doryteuthis gahi* (Arkhipkin et al., 2015), which is also an important species in the continental shelf food web (Büring et al., 2024). *D. gahi* is an annual species with a semelparous reproductive strategy (McKeown et al., 2019). While this species spawns year-round, there are two large seasonal peaks in spawning, referred to as the Spring and Autumn Spawning Cohort (SSC and ASC respectively)(Arkhipkin and Middleton, 2003). Changing seasonal conditions could have different impacts on the spawning cohorts (dos Santos Schmidt et al., 2021), ultimately with consequences for the structure of the wider food web and the Loligo fishery in the Falkland Islands. Survival experiments, using squid eggs collected at Nuevo Gulf, Argentina – closer to the northern edge of *D. gahi* distribution (Vega et al., 2002), showed strong declines in egg survival rates at temperatures below 5 and above 20 °C (Cinti et al., 2004), although they did not explore potential differences between the different spawning cohorts. Further, population responses can depend on whether they are from cold or warm regions (Levy et al., 2016), and since the Nuevo Gulf is more influenced by the warm southward-flowing Brazil Current, these results may not be representative for *D. gahi* from the Falkland Islands which may have a lower temperature tolerance. Therefore, understanding the differential sensitivity of Falklands spawning cohorts to changing temperature is key to predict the impact of the complex changes in climate on species resilience.

This study collected and incubated fertilised Patagonian squid egg masses from both spawning cohorts under a rising and naturally varying temperature scenario to test for differences in developmental sensitivities to temperature. Squid egg masses respiration rates as well as paralarvae morphometrics were used to assess the developmental sensitivities. We hypothesize that, given the influence of environmental cues during natural development periods, the spawning cohorts would differ in their thermal sensitivities, influenced by how close to the maximum of their temperature performance response curves they were, with the ASC having lower temperature thresholds and potentially responding more strongly to temperature increases than the SSC egg masses. Such threshold development is important for ecosystem management.

2. Materials and methods

Squid egg masses were collected by SCUBA divers from depths between 10 and 20 m around the northside of Tussock Island in Port William, east Falkland Islands. Egg masses were taken from defoliated kelp fronds by cutting the fronds from the stipe and collected in meshed bags. Egg masses were collected on a single dive trip in July 2023 (ASC, 2023) and one in November 2023 (SSC, 2023). The egg masses were transported to the aquaculture facility located in Moody Brook, the only facility available with a seawater flow-through system in the Falkland Islands. Seawater from Stanley Harbour was pumped to the facility and treated with UV light, ozone, and filters to remove large particles (e.g., sand) and used to supply the experimental setup. The experimental system consisted of a header tank that supplied the control and experimental tanks with seawater, with water from the control tanks flowing back to a sub-tank where the water went through an UV filter, protein skimmer, and particle filter. Water from experimental tanks flowed down a drain. Roughly 10 % of the seawater in the experimental system was replaced each day to prevent the build up of waste products in the system. Squid eggs were kept in labelled floating permeable pots to aid the tracking of separate egg masses. Ethical approval for using the squid egg masses in the experiments was obtained under research license number R08/2022 from the Falklands Islands Government review board, and experiments were performed in accordance with these guidelines.

The treatment involved either a warming (Treated) or ambient (Control) regime. Treated tanks were heated by heaters (0.1 °C precision) via a digital thermostat. To ensure that temperature could be raised to projected upper limits (around 20 °C; Cinti et al., 2004) within the duration of embryo development, temperatures in treated tanks were raised by 1 °C per day for 3 days (following the medium rate of warming used in van der Grient et al. (2025)), followed by 2 days at temperature to allow physiology to adjust to these temperatures, after which the respiration rate of the egg masses were determined. After respiration rate was measured, tanks were heated by another 3 °C, following the same regime. Control tanks were not heated, but as there was no temperature-controlled room available in the facility, temperature checks showed that the ambient temperature in the control tanks varied by a maximum absolute difference of $\sim$ 4 (SSC) and 7 (ASC) °C over the duration of the respective experiments (Supplementary Materials A, Fig. S1), corresponding loosely to changes in air temperature (Supplementary Materials A, Fig. S2). Note the uptick in temperature for the ASC control tank, which matches with temperature increases in the beginning of spring. Control tanks were monitored to check for any adverse effects of culture conditions, which were not observed. The respiration rates of squid egg masses in the control tanks were measured following the same schedule as the treated eggs. Number of squid egg masses (repeated respiration measurements and total sample size for the treatment group) were as follows: ASC treated $n = 9$ egg masses (5–6 repeated measurements; 48 total measurements), SSC treated $n = 7$ (3–4 repeated measurements; 27 total measurements), ASC control $n = 3$ (13 repeated measurements; 39 total measurements), and SSC control $n = 2$ (5–7 repeated measurements; 12 total measurements). See Supplementary Materials B for details.

Respiration rates were measured by placing squid egg masses in glass Kilner jars with PSt3-NAU oxygen sensor spots (Presens, Germany). The jars containing the squid egg masses were placed in their original tanks for the duration of the measurements. Repeated measurements at different time points were taken to determine the reduction in oxygen concentration, as measured by the phase angle using a Witrox 4 oxygen Meter (Loligo Systems, Denmark). Blanks (closed containers containing only water from the tanks) were included for each tank and measured at interval for as long as all egg masses were measured. Respiration rates were estimated using phase angles, water temperatures, time, and atmospheric pressure, corrected using the blank estimates, and standardised using egg wet mass (measured at the end of each respiration measurement session (Watson et al., 2014);). The volume of the egg mass was measured by displacement and was subtracted from the volume of the chamber to calculate the volume of water in each measurement chamber. Prior to each measurement session, the sensors were calibrated for 0 and 100 % oxygen concentration in the water.

Paralarvae were collected upon hatching. Hatching occurred over several days, and measurements finished when the majority of eggs had hatched, given the influence of reduced embryo numbers on egg mass respiration. Development time varied between egg masses, especially between the control and experimental tanks, with the treated tanks hatching much earlier compared to the eggs in the control tanks. Several morphometric data from paralarvae were estimated (Gowland et al., 2002). Paralarvae were caught in the aquaculture facilities and immediately transported to the Department of Agriculture in Stanley. Squid paralarvae ventral sides were photographed using a Leica M80 dissecting microscope with a Leica IC90 camera. Photos were used to obtain morphometric data using ImageJ (Schneider et al., 2012), including mantle and head length, width, surface area, and chromatophore numbers. Sample sizes for the morphometric data for each cohort and treatment combination are as follows: ASC treated n = 51; ASC control n = 60; SSC treated n = 68; SSC control n = 60. No distinction was made between the different colours of chromatophores, and their densities were standardised using the surface areas. Photographs were taken over several days depending on the availability of the hatchlings. Paralarvae were weighed, using 5 individuals at the time and the average value was taken as an independent observation. Prior to weighing, hatchlings were briefly placed on paper to draw off excess seawater. Sample sizes (for the independent observations for weight) for each cohort and treatment combination are as follows: ASC treated n = 5; ASC control n = 9; SSC treated n = 9; SSC control n = 9.

Squid egg mass respiration rates were analysed using a generalised linear mixed effect model using the *glmmTMB* package (Brooks et al., 2017) in R (R Core Team, 2024). The respiration data followed an exponential increase with temperature (regardless of treatment), and to better account for the mean-variance relationship, which led to overdispersion under a Gamma model, a Tweedie distribution with a log link was used in the model. To meet model assumptions and model fit, Cohort and Treatment variables could not be modelled separately with an interaction between them. Therefore, these two variables were combined, resulting in a variable (CohortTreatement) with four unique levels. Temperature and CohortTreatment were used as fixed effects, and an interaction was specified between these two factors. Squid egg ID (SquidID) was used as a random variable to control for repeated measurements. Time was not included in the model as temperature is highly collinear with time, not just for the treated conditions (correlation = 0.99), but also in the control ASC condition (>0.70; Supplementary Materials A, Fig. S1), and these two factors had high Variance Inflation Factor values (>5; *car* package (Fox and Weisberg, 2019)). The remaining factors were not collinear. The full model tested was as follows (equation (1); as per Zuur and Ieno (2016)):

$$\mathit{Respiration\ rate}_{ij} \sim \mathit{Tweedie}\left(\mu_{ij}, \phi, p\right)$$

$$\log\left(\mu_{ij}\right) = \mathit{Temperature}_{ij} + \mathit{CohortTreatment}_{ij} + \mathit{Temperature}_{ij} \times \mathit{CohortTreatment}_{ij} + \mathit{SquidID}_i$$

$$\mathit{SquidID}_i \sim N\left(0, \sigma^2\right) \qquad \text{(equation 1)}$$

where *Respiration rate*$_{ij}$ is the *j*th observation of squid egg mass *i*; ϕ is the dispersion parameter, and *p* is the Tweedie power parameter. SquidID$_i$ was used as the random intercept. The model was analysed using log-likelihood ratio tests and AICc (*AICcmodavg* package (Mazerolle, 2023)) to select the most parsimonious model for fixed effects. The final model was inspected for diagnostics including normality and homogeneity in residuals against different factors and dispersion (supplementary materials C) using the *DHARMa* package (Hartig, 2024). Visualisation were created using *ggplot2* (Wickham, 2016).

Paralarvae morphometric data were analysed using linear models. While egg mass ID would ideally have been included as a random variable, paralarvae could not be reliably be connected to egg masses. Linear models were constructed to test whether there were differences in paralarvae mantle and head length and width (mm), mantle and head surface area (mm^2), mantle and head chromatophore total number (#) and density (# chromatophore mm^{-2}), and weight (g) between the two spawning cohorts and treatments (control and treated). In the case of the paralarvae, Treatment and Cohort could be modelled separately (each two levels). To investigate interactive effects between these two variables, an interaction was specified. Each model followed the following structure:

$$\mathit{Morphometric\ variable}_i \sim N\left(\mu_i, \sigma^2\right) \qquad \text{(equation 2)}$$

$$\mathit{Morphometric\ variable}_i = \mathit{Cohort}_i + \mathit{Treatment}_i + \mathit{Cohort}_i \times \mathit{Treatment}_i$$

where *Morphometric variable*$_i$ is the *i*th observation for the morphometric variable used in the model. Each model was checked to determine whether the assumptions of normality and equal variance were met (supplementary materials C). For pairwise comparisons between the different treatments, Tukey's Honestly Significant Difference tests were used with a Bonferroni correction to control for multiple comparisons.

3. Results

3.1. Squid egg mass respiration

Respiration of squid egg masses from the different treatments and cohorts responded in a similar way to temperature as demonstrated by the non-significance of the interaction between temperature and CohortTreatment ($X^2 = 1.13$, $p = 0.77$). The interaction between temperature and CohortTreatment was dropped, and the simplified model met the assumptions of normality and equal variance and was non-significant for dispersion (Supplementary Materials C). There was a significant effect of temperature on respiration rate (mean = 1.160 μmol h^{-1} g^{-1}; $X^2 = 85.85$, $p < 2.2 \times 10^{-16}$), with respiration rate positively and exponentially increasing with increasing temperature (Fig. 1). The four levels within CohortTreatment differed from each other ($X^2 = 25.37$, $p = 1.29 \times 10^{-5}$), with higher intercept values for the control groups compared to the treated groups, and higher intercept values for the ASC egg masses compared to the SSC egg masses (ASC control: mean = 0.066 μmol h^{-1} g^{-1}; SSC control: mean = 0.052 μmol h^{-1} g^{-1}; ASC treated: mean = 0.032 μmol h^{-1} g^{-1}; SSC treated = 0.021 μmol h^{-1} g^{-1}). Note that the intercept differences are likely an artefact of age (indicated by Day; Fig. 1). Older egg masses were exposed to colder and warmer temperatures in control treatments, while only to warmer temperatures in the treated conditions, which affects the intercept value estimates. As the intercept is, therefore, potentially an artefact of the experimental design, the remainder of this study will focus on the slope estimates for the squid egg masses.

3.2. Squid paralarvae

All tested morphometric traits contained significant interactions between cohort and treatment, and there were differences in the effect of both cohort and treatment as separate variables (Fig. 2; Supplementary materials C). Apart from mantle width, morphometric traits significantly differed between the two cohorts, while only mantle length, head width and weight were significantly different between treated and control treatments (see supplementary materials C for ANOVA tables). The smallest values for mantle and head length, width, surface area, and weight were observed in the treated ASC paralarvae (Fig. 2), while the largest values for these traits were predominately observed in the

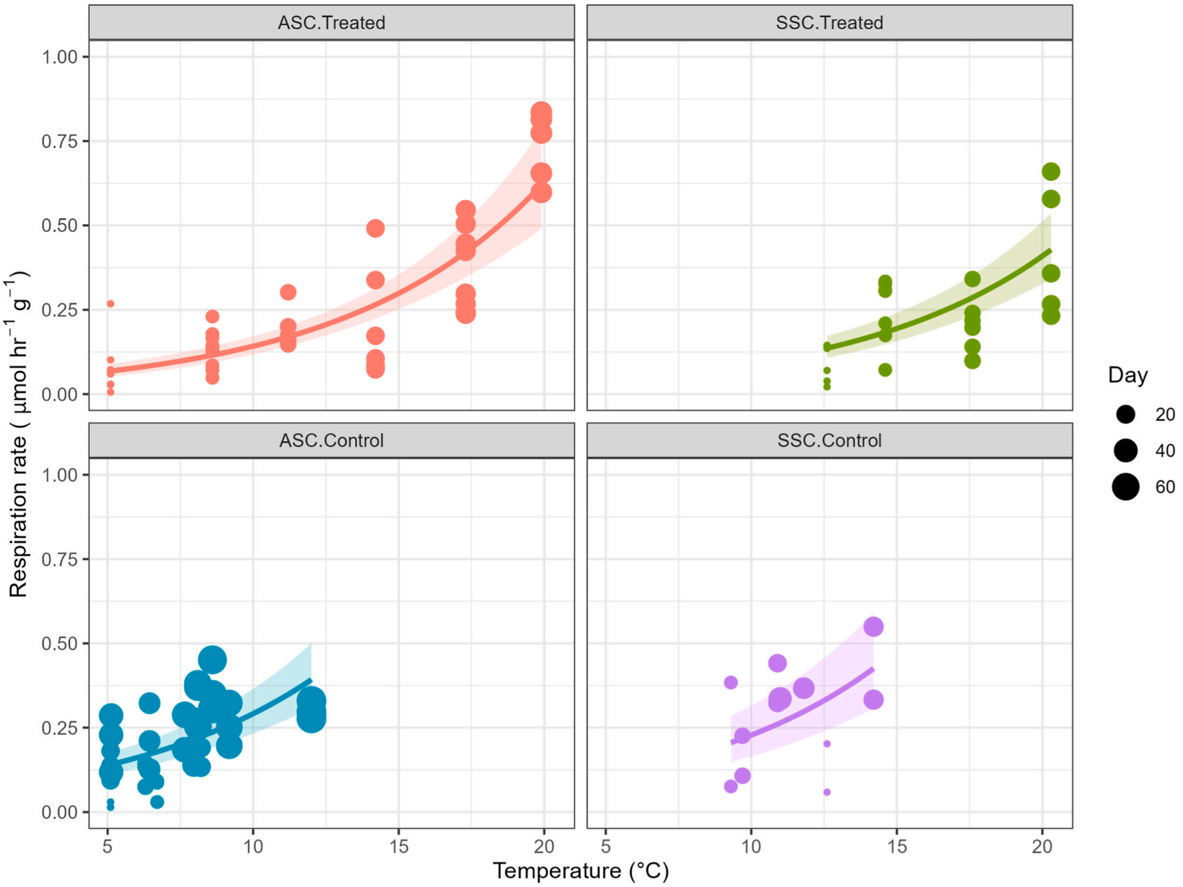

Fig. 1. The relationship between temperature and respiration rate for each cohort and treatment (CohortTreatment) combination. The size of the circles indicates the time (by day) from the start of the experiment.

treated SSC, except for mantle length (control SSC) and mantle width and weight (control ASC). Treated SSC paralarvae had similar weights to treated ASC paralarvae. The highest chromatophore densities in both mantle and head were observed for treated ASC paralarvae, while the lowest values were present in the treated SSC paralarvae.

4. Discussion

Seasonal spawning cohorts within a species are expected to respond differently to ocean warming given their varying environmental spawning cues (dos Santos Schmidt et al., 2021; Pankhurst and Munday, 2011). The egg masses of the two spawning cohorts of *D. gahi* in the Falkland Islands, however, showed similar responses to ocean warming as indicated by a lack of significant differences in slopes between the two treated cohorts. *D. gahi* spawns year-round, with two large seasonal peaks corresponding to the ASC and SSC, and which also dictates the timing of the two fishing seasons targeting the adult squid at their offshore feeding areas (Arkhipkin and Middleton, 2003). The absence of cohort differences is interesting. While this species spawns year-round (Arkhipkin and Middleton, 2003), ASC peak spawning occurs in March–April while adults are on the offshore feeding ground in October–January, while SSC peak in spawning occurs in October–November and adults are on the offshore feeding grounds in May–June (van der Grient et al., 2023), and some mixing may occur away from the peaks, likely influenced by maturation rates; that is, the earliest maturing adults could potentially overlap with the other cohort. It could thus be possible that egg masses could have been laid by an individual from a different cohort rather than the targeted cohort. It could also be possible that there is some intra-cohorts mating, maintaining gene flow between the cohorts. *D. gahi* from the Falkland Islands waters shows no genetic differentiation between the spawning cohorts, suggesting that the spawning structure is a flexible mechanism in its life history, as an adaption to unpredictable recruitment influenced by environmental conditions (Shaw et al., 2004). While seasonal adaptation may be a useful strategy in a predictable environment, the Falkland Islands has unpredictable environmental variation, experiencing episodic upwelling, as suggested by the thermal physiological responses of other coastal species (van der Grient et al., 2025).

The similarity in slope estimates between the two treatments and spawning cohorts indicates a consistent response to ocean warming, with a predictable change in respiration rate. This is a strong and consistent response, even considering the limited number of egg masses available. The squid egg masses seemed to respond quickly to temperature changes, as indicated by the varying respiration rates in the controls for the different aged egg masses (Fig. 1). One caveat to consider is time. While we could not include time (because of collinearity issues with temperature) in our model, developmental effects can affect respiration rates. That is, older (and larger) embryos respire at a higher rate compared to younger (and smaller) embryos. This effect can be seen in our control conditions when older and younger egg masses are exposed to the same temperature. It is also clear from our results that temperature has a larger effect on respiration rate than age. Associated with this is the consideration that there can be different aged eggs within an egg mass, as female squid can attach their capsules to others that are already attached (Arkhipkin et al., 2000). However, as egg masses were tracked over time as a whole, measured as a whole and egg mass ID was included as a random factor, such effects, if present, would have been accounted for in the model.

Many morphological and behavioural variation in *D. gahi* seems plastic which can be advantageous in the seasonal and changing

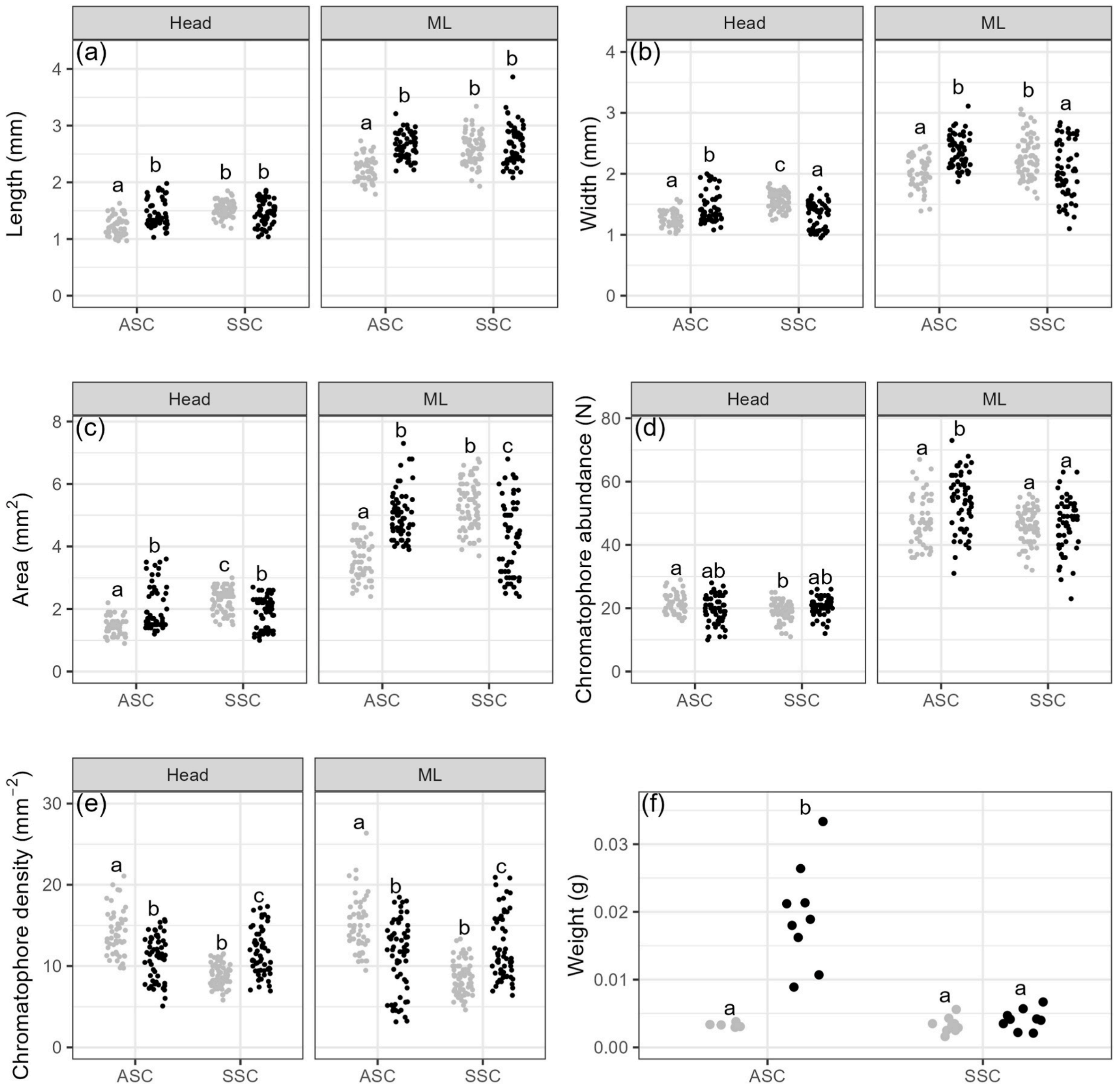

Fig. 2. Paralarvae morphometric and weights for the different spawning cohorts (ASC = autumn spawning cohort; SSC = spring spawning cohort) and treatment groups (grey = treated; black = control). Morphometric data are separately presented for the paralarval head and mantle (ML). Letters above data points indicate statistical group significance. (a) = length, (b) = width, (c) = surface area, (d) = chromatophore abundance, (e) = chromatophore density, and (f) = weight.

environmental conditions (including in response to climate change) present in the Falkland Islands, and it may aid it in its survival in an unpredictable environment. For example, while (adult) *D. gahi* from the Falkland Islands morphologically differ from Chilean *D. gahi* (Vega et al., 2002), genetically there is little difference between squid specimens obtained from these two areas, which likely reflects plasticity in response to environmental heterogeneity (McKeown et al., 2019). Within the Falkland Islands, the extent and distribution of the spawning grounds of *D. gahi* are not known, nor is it known whether the squid select areas based on environmental conditions, although they may select exposed sites, at least for those egg masses attached to kelp styles (Arkhipkin et al., 2000). Egg masses have also been observed attached to rocks at ~ 50 m (personal observation), and they have been trawled up from ~ 70 m (Laptikhovsky, 2008). As deeper rocky habitats and kelp forests differ in environmental conditions, it is likely that squid can flexibly select its habitat which may aid in reducing risk of recruitment failure or buffer population responses to environmental variability (Schindler et al., 2010; Wilson et al., 2021).

While the response to temperature did not vary between the four egg-mass groups, there were differences between the groups in hatching time (longer for control compared to treated groups, longer for ASC compared to SSC groups) and paralarvae morphometric characteristics. Paralarvae morphometric characteristics are especially interesting for understanding survival and recruitment at later life stages. Temperature is known to influence squid development (Gowland et al., 2002), where higher temperatures can result in squid eggs hatching earlier with smaller hatchlings (Pecl and Jackson, 2008). Earlier hatching can result in mismatches with prey, while smaller hatchling sizes could indicate less stored energy and higher vulnerability to predators. The paralarvae from the experiment show differences in various morphometric data and some of these factors could influence survival and growth rates in the hatchlings. For example, the ASC control paralarvae were much heavier than the ASC treated paralarvae, which were similar in weight to SSC paralarvae. It is possible that SSC paralarvae can be naturally lighter, having less internal tissue reserves as their natural hatching times are more likely to occur during high prey availability given the later spring/early summer hatching times. Conversely, ASC egg masses hatch at the beginning of spring, meaning that the paralarvae may need more energy reserves in order to find food at this time. Being larger at those times could mean that they can endure starvation longer, but also that they could explore a larger area to help maximise the chance of finding prey (Doyle et al., 2019; Pimentel et al., 2012; Vidal et al., 2002). Temperature is known to reduce the hatch size of larvae of some species of squid and fish, following the expectations of the temperature body-size rule (Verberk et al., 2021). While it is currently unknown what the *D. gahi* paralarvae may consume as prey, it is likely that prey include small micro- or mesozooplankton organisms, which is a poorly studied group in the Falkland Islands. A better understanding of these trophic links is therefore crucial to predict whether sufficient energy will be available to paralarvae in warmer conditions. Under warmer water temperatures, metabolic rates of ectotherms increase, requiring higher energy intake to survive and reproduce (Pecl and Jackson, 2008). Further, while the treated ASC paralarvae were of similar weight to the SSC paralarvae, the treated ASC paralarvae tended to be smaller (shorter mantle and head length and width). How these factors may influence swimming success, including hunting success and predator avoidance, is unknown. Interestingly, chromatophore head and mantle density was significantly higher for the treated ASC paralarvae compared to the other groups. This contrasts with *Loligo forbesii,* whose chromatophores numbers were strongly reduced by temperature, more so than morphometric features (Gowland et al., 2002). Chromatophores are important organs in intra-specific communication and camouflage. It is possible that the higher chromatophore density could be a compensatory mechanism, leading to improved camouflage, and thereby reduced predation. There could, however, also be an increased metabolic cost for the higher density of chromatophores (Gowland et al., 2002). This could result in negative effects, especially if squid require higher energy intake because of increased water temperatures and this could also reduce the capacity for going without food for prolonged periods (Pecl and Jackson, 2008).

D. gahi is a cold-adapted loliginid squid, and it lives in the coldest waters of all loliginids (Arkhipkin and Middleton, 2003). There have been suggestions that the temperature limit of this species is at 5 °C and below this limit, development may be halted and/or survival could be strongly reduced and nearing 0 % (Barón, 2002; Cinti et al., 2004). The water temperatures in the treated and control tanks for the ASC started at 5 °C, and a few times in the experiment, the water temperature in the control tank reached 5 °C (again). While it is difficult to state whether development may have slowed down or halted at this limit (Supplementary Materials A, Fig. S1), it was clear that, if there was any effect, the egg masses recovered quickly and no dead embryos were visible in the egg masses. Further investigation of the effect of this lower temperature limit could provide useful insights, especially as El Niño Southern Oscillation (ENSO) can result in very cold conditions, as observed in 2023. The spring spawning cohort egg masses were found for collection 1.5 months later than expected in 2023. Long-term environmental oscillations, like ENSO, have influenced the habitat use of other southern hemisphere squid species (Abreu et al., 2020), as well as the pelagic ecosystem structure and communities in the southwest Atlantic ecosystem (Morley et al., 2025). Understanding the effects of cold periods as well as warm periods is important when temperature has a significant effect on phenology and development of squid (Márquez et al., 2021). As *D. gahi* is a wasp-waist species in the Falkland Islands (offshore) food web (Büring et al., 2024; van der Grient et al., 2023), there is a risk for knock-on effects via trophic cascades if temperature changes result in changes in squid biomass, including peaks, at different times of the year, resulting in mismatches between them and their predators. Falkland Islands seabird (penguins, black-browed albatross) breeding success was low for the 2023 season, and one suggested reason for this was the effect of ENSO on prey availability (Kuepfer and Stanworth, 2024); *D. gahi* is an important prey for these species (van der Grient et al., 2023). In addition, long-term environmental oscillations could influence fishing success in the Falkland Islands. However, the effect of temperature on phenology of *D. gahi* is not well considered. The second Loligo fishing season in 2023 closed entirely and this season contained the adult recruits from the 2023 SSC - whose eggs were laid potentially 1.5 months late, which may have had knock-on effects with late hatching and migration to the adult feeding grounds, resulting in low pre-season biomass during the survey. Further knowledge on the effect of temperature on squid phenology and potential corresponding trophic cascades can play an important role in fisheries management and specifically provide recommendations for adaptive management. Several studies have demonstrated the usefulness of predicting future adult cephalopod abundance or biomass using environmental factors such as temperature (Büring et al., 2025; Marcout et al., 2024; Sobrino et al., 2020). It is currently unclear if, and how, conditions that influence the timing of egg laying, development time, hatching success and paralarvae growth and survival influence biomass at adult feeding grounds (the fishing grounds). It would, however, be useful to understand, at a minimum, if changing the timing of fishing seasons in response to environmental cues could be a useful climate adaptation strategy for the Falkland Islands.

CRediT authorship contribution statement

Jesse M.A. van der Grient: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Barend Stander:** Writing – review & editing, Resources. **Paul Brickle:** Writing – review & editing, Resources, Funding acquisition. **Simon A. Morley:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.107856.

Data availability

The data are contained in supplementary material B and C

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