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The reproductive ecology of the Antarctic bivalve *Aequiyoldia eightsii* (Protobranchia: Sareptidae) follows neither Antarctic nor taxonomic patterns

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Abstract

The accepted paradigm for reproduction in Antarctic marine species is one where oogenesis takes 18 months to 2 years, and a bimodal egg-size distribution where two cohorts of eggs are present in female gonads throughout the year. These slow gametogenic traits are driven by low temperature and/or the restriction of resource availability because of extreme seasonality in the marine environment. Here we present data on the reproductive ecology of the common Antarctic bivalve *Aequiyoldia eightsii* (Jay, 1839) (Protobranchia: Sarepidae) from monthly samples collected between January 2013 and May 2014 at Hangar Cove, Rothera Point on the West Antarctic Peninsula. These data show that *A. eightsii* is unusual because it does not follow the typical pattern expected for reproduction in Antarctic marine invertebrates, and differs also from closely related nuculanid protobranch bivalves with respect to gametogenic duration and reproductive periodicity. Continuous oogenesis, evidenced by the year-round occurrence of previtellogenic, vitellogenic, and ripe oocytes in female gonads, is supplemented by a seasonal increase in reproductive intensity and spawning in Austral winter (April-May), evidenced by the loss of mature spermatozoa and ripe oocytes from males and females respectively. The simultaneous occurrence of these contrasting traits in individuals is attributed to a flexible feeding strategy (suspension and deposit feeding) in response to seasonal changes in food supply characteristic of the Antarctic marine environment. Asynchrony between individual females is also notable. We hypothesise that the variability may represent a trade-off between somatic and reproductive growth, and previously reported internal interannual cycles in shell growth.

Keywords: Antarctic; marine; invertebrate; bivalve; interannual; reproduction;

Introduction

Marine invertebrate reproductive ecology influences patterns of species biogeography, population persistence, and species survival (Ramirez-Llodra 2002; Lester et al. 2007). Investigating the reproduction of a particular species therefore provides insight into its adaptive capacity and potential resilience to environmental change (Byrne 2011; Sanford and Kelly 2011). As the global ocean is under increasing threat from climate change, especially warming and acidification (Byrne 2011), evaluation of a species' reproductive success is key to understanding vulnerability to future climate scenarios (Grange et al. 2004). In the Southern Ocean, the waters around the West Antarctic Peninsula have experienced pronounced warming relative to the global average (see review by Mayewski et al. 2009), with sea surface summer temperatures in the Bellingshausen Sea on the west of the Peninsula increasing by ~1^{o}C since the 1950s (Meredith and King 2005). Antarctic shallow-water invertebrates are particularly susceptible to the effects of climate change, as warming causes perturbations in sea ice dynamics, which could subsequently lead to ecological regime shifts in benthic systems (Barnes and Conlan 2007; Barnes and Souster 2011; Barnes 2016). Presently, there is a lack of knowledge specific to the recovery potential of the benthos after these disturbance events (Clark et al. 2015). Additionally, many studies have demonstrated the physiological constraints and vulnerability of Antarctic benthic invertebrates to subtle temperature increases (e.g. Peck et al. 2004a; Pörtner et al. 2007; Peck et al. 2010; 2014). Benthic assemblages in Antarctica are taxonomically diverse and abundant, with more than 7137 species identified, which accounts for ~88% of the total number of identified species in the Southern Ocean (De Broyer and Danis 2011). However, the reproductive ecology and related paradigms regarding invertebrate life history and ecology are far from fully understood (Pearse and Lockhart 2004), with details of reproductive biology, especially in terms of variations between the years, or longer term trends, rarely published.

74 The reproductive patterns of Antarctic shallow-water benthos are often characterised by a
75 prolonged reproductive cycle (18-24 months), lecithotrophy, and direct development, low
76 fecundity and seasonal reproductive patterns (Clarke 1979; Brey and Hain 1992; Chiantore
77 et al. 2002; Grange et al. 2004, 2007; Higgs et al. 2009; Pearse et al. 2009; Reed et al.
78 2013a). However, a few species also demonstrate shorter gametogenic periods (12 months
79 or less) (Clarke 1988; Chiantore et al. 2002; Tyler et al. 2003; Grange et al. 2011),
80 planktotrophic larvae (Stanwell-Smith et al. 1999; Bowden et al. 2009), and relatively high
81 fecundity (McClintock and Pearse 1986; Bosch and Pearse 1990; Grange et al. 2004; Orejas
82 et al. 2007). Moreover, the reproductive ecology of Antarctic shallow-water and deep-sea
83 species are similar in several benthic taxa, including asteroids (Bosch and Pearse 1990) and
84 octocorals (Orejas et al. 2012). Several authors have suggested that the abiotic and biotic
85 characteristics shared between the polar and deep-sea environments attribute similarities in
86 reproductive ecology between Antarctic shallow-water and the deep-sea benthos (Bosch and
87 Pearse 1990; Ramirez-Llodra 2002; Orejas et al. 2012). Both realms are characterised by
88 low stable temperatures, low light, and ice scour, and functionally similar benthic
89 communities with slow population turnover rates (Bosch and Pearse 1990; Aronson et al.
90 2007; Clark et al. 2015). Furthermore, the continental shelf in Antarctica is depressed by the
91 weight of the ice-sheet, such that its average depth is around 500 m compared to around 200
92 m elsewhere in the world (Heywood et al. 2014). This feature facilitates the connection
93 between shallow and deep areas of the Southern Ocean across the continental shelf, with
94 submerging Antarctic bottom water and emerging circumpolar deep water that may have
95 enhanced colonisation of shallow fauna to deep waters (and vice versa) during glacial cycles
96 of shelf ice advance and retreat (Berkman et al. 2004; Strugnell et al. 2011). Many Antarctic
97 invertebrate taxa including Bivalvia, Gastropoda, Amphipoda, and Decapoda are reported to
98 have a significantly higher degree of eurybathy compared to their temperate counterparts,
99 often being distributed from surface water to hundreds of meters (Brey et al. 1996).

Protobranchia is a subclass of small deposit feeding bivalves commonly found in soft sediment environments with approximately 750 species distributed globally (see review by Zardus 2002). With a Cambrian origin (Carter et al. 2000; Sharma et al. 2013), this subclass has diversified and colonised the deep sea, representing ~50% and ~90% of bivalve species on the continental slope and abyssal plain, respectively (Allen 1978). Although protobranch bivalves are important bioturbators in the deep sea (Zardus 2002), they remain one of the least studied molluscan groups (Sharma et al. 2013; Reed et al. 2014). Protobranch bivalves are well represented in the Antarctic, but information regarding the ecology of Protobranchia in the Southern Ocean is limited as most species are found only in deeper water (Reed et al. 2013b). One exception is the common shallow-water species *Aequiyoldia eightsii* (Jay 1939) (previously *Yoldia eightsii*), which has been used as a model bivalve species in several investigations. While studies have examined its abundance and ecophysiology (described below), the reproductive ecology and gametogenic cycles in this species are poorly understood, constrained by the problems associated with seasonal sampling of organisms in the Southern Ocean.

Here, we investigated the reproductive ecology of an Antarctic shallow-water protobranch bivalve *A. eightsii*, which is one of the most abundant benthic species in the maritime Antarctic. Previous records show densities of *A. eightsii* of up to 1540 m^{-2} at Signy Island (Peck and Bullough 1993), and biomass contributions equivalent to 56.6% of the total macrofaunal biomass at Faro station in Potter Cove (Pasotti et al. 2015a). The geographical distribution of *A. eightsii* is patchy around the Antarctic continent (Dell 1990), but is extended to sub-Antarctic regions including King George Island (62º 10'S) and the Magellan Strait (53º 28'S) (González-Wevar et al. 2012). With a bathymetric distribution ranging from intertidal sand flats to deep waters (824 m), *A. eightsii* is most commonly found at depths shallower than 100 m (Dell 1990; Peck and Bullough 1993). *Aequiyoldia eightsii* has an opportunistic feeding strategy, which typically exhibits deposit feeding but can alternate to a suspension feeding mode when phytoplankton is present in the water column (Davenport 1988). Deposit

feeding and burrowing in *A. eightsii* involve intensive locomotion, where this species is one of the fastest burrowing of all Antarctic marine benthic groups (Peck et al. 2004b). Previous observations have also shown a single specimen can expel sediment up to 13 times its dry tissue mass within 24 hours (Davenport 1988). Given its high abundance and wide distribution within Antarctica, *A. eightsii* is likely to be one of the major bioturbators among the Antarctic shallow-water benthic communities. Moreover, *A. eightsii* has frequently featured in physiological studies as a comparative species with other Antarctic benthos (Peck and Conway 2000; Peck et al. 2004b, 2014; Fattorini et al. 2010; Román-González et al. 2017), and as a model species in studies designed to analyse the impact of climate change on Antarctic seafloor communities (McClintock et al. 2009; Peck et al. 2009, 2010; Clark et al. 2016). A recent study identified an innate endogenous growth rhythm in this species and suggested the pattern may be attributed to the reallocation of energy resources between cycles of somatic and reproductive investment (Román-González et al. 2017). Owing to the use of *A. eightsii* in a range of Antarctic ecological studies, the reproductive data reported here should inform future studies focused on interpreting the biological and ecological role of the species, and the ecological processes of the Protobranchia and Antarctic benthos as a whole.

The objectives of this study were to: (1) describe the reproductive ecology and general anatomy of *A. eightsii* from a shallow-water site at Rothera Point off the West Antarctic Peninsula using wax histology, (2) to compare the reproductive condition of *A. eightsii* with other Antarctic shallow water benthos and protobranch bivalves, and (3) to evaluate, where possible, what may be driving these reproductive patterns.

Materials and Methods

Sample collection

Monthly samples of *A. eightsii* were scuba diver-collected between January 2013 and May 2014 at 13 to 16 m depths in Hangar Cove, adjacent to the British Antarctic Survey's Rothera Research Station on Rothera Point, Adelaide Island, off the West Antarctic Peninsula (67º 33'

52 S, 68º 07’ 43 W) (Fig. 1). Fifteen to 20 individuals were collected per month and fixed in 4% buffered formaldehyde in the field. Formaldehyde-preserved samples were then transported to the University of Southampton, UK for storage. Poor ice conditions and inclement weather prevented field sampling in February and June 2013.

Histological preparation

For each specimen, maximum shell length, height, and width were measured using a digital caliper (± 0.01 mm) and the soft tissue separated from the shell using a scalpel. Photographs of specimens before and after shell removal were taken for anatomical study.

Aequiyoldia eightsii with shell length > 20 mm have been reported to be reproductively mature (Peck et al. 2000). In an effort to maintain consistency, only individuals with a shell length between 20 and 25 mm were selected for processing. None of the bivalves collected in March or August 2013 measured between 20 and 25 mm and were therefore discounted from further study. A total of 95 individuals were selected for histological analysis. Sex of individuals was determined from histological sections.

The gonad of *A. eightsii* is not a discrete organ and the germinal tissues are infiltrated in the visceral mass. Therefore, whole specimens were examined using standard wax histology techniques following the protocol outlined in Higgs et al. (2009). Preliminary studies demonstrated the denser foot muscle to be more sensitive to the process of clearing when compared to other soft tissues. This tissue was therefore dissected and processed separately. Bivalves were dissected in a longitudinal direction through the body just below the digestive gland, removing the foot muscle from the main body.

Both dissected parts of soft tissue were dehydrated in a graded series of isopropanol, cleared in three washes of histoclear (CellPath, UK) and embedded in wax blocks. Serial sections of 7µm thick were mounted and stained with Haematoxylin Z (CellPath, UK) and Eosin Y (CellPath, UK), and immediately cover-slipped using a DPX mounting medium

(Sigma-Aldrich, UK). Note that the gonads of six female individuals were damaged during histological preparation and were therefore excluded from reproductive analysis.

Data analysis

Gonad morphology

General anatomical observations of *A. eightsii* were made with respect to gonad morphology from the serial sectioning of both dissected parts of animals under a light microscope (Olympus BHS (BH-2), and the macrophotography images of soft tissues after shell removal.

Female reproductive analysis

Preliminary analysis indicated that a sexually mature female could simultaneously carry in excess of 3000 oocytes. Therefore, only eight histological sections, evenly distributed across the gonad-digestive complex per specimen (around 1.5 mm apart), were taken for image analysis. Thin tissue sections were photographed using a Nikon D5000 digital camera mounted on a light microscope (Olympus BHS (BH-2)). Oocyte size, measured as Equivalent Circular Diameter (ECD), of individual females was quantified using the 'Area' tool in ImageJ v1.48 (Rasband 1997-2016). ECD assumes the best-fit spherical size of each oocyte and is equivalent to Oocyte Feret Diameter (OFD) used in previous studies (e.g. Reed et al. 2013a, 2014). Only oocytes with a visible nucleus were measured to ensure the size of each oocyte was approximated at, or very close to its maximum cross-sectional area. The equation used for calculating ECD from the traced area of each oocyte was:

$$ECD = 2\sqrt{\frac{A}{\pi}} \quad (1)$$

where ECD is Equivalent Circular Diameter (µm), and A is the area of an individual oocyte (μm^2).

Female maturity was evaluated based on the overall oocyte cellular appearance and description of marine bivalve ovary development outlined in Morse and Zardus (1997). Oocytes < 50 µm ECD, with basophilic cytoplasm and a large nucleus were defined as previtellogenic. Oocytes between 50 and 80 µm ECD, with eosinophilic cytoplasm and yolk

droplets were identified as vitellogenic, whereas oocytes > 80 µm ECD with an outer vitelline envelope and jelly coat were defined as ripe oocytes (Fig. 1 in Online Resource 1).

Male reproductive analysis

Eight histological sections evenly distributed across the gonad-digestive complex of each male *A. eightsii* were photographed for image analysis. Five stages of gonad maturity were identified according to the rationale for the overall development and distribution of spermatozoa in marine bivalve testes development described in Morse and Zardus (1997) (Fig. 2 in Online Resource 1).

Stage I (early developing stage): Spermatogonia develop along the follicle wall.

Stage II (mid developing stage): Spermatogonia divide into spermatocytes and move away from the follicle wall. The spermatocytes have increased in number and occur in clusters.

Stage III (late developing stage): Spermatocytes divide into spermatids, which then differentiate into spermatozoa. The division and differentiation process leads to spermatozoa being placed in the centre of the lumen in chained form.

Stage IV (ripe stage): Spermatozoa increase in number and occupy the entire lumen. Testes expand in size and are fully developed.

Stage V (spent stage): Spawned spermatozoa; testes are reduced in size with empty spaces visible in follicles.

Statistical analysis

A *chi-square test of independence* was conducted between both month using pooled females and individual females within each month, and oocyte size frequency distribution to determine whether there was a statistically significant association between these variables. For instances where expected cell frequencies were less than five, neighbouring oocyte size bin ranges were collapsed and the procedure re-run until this assumption was met. Statistical significance is reported at $p < 0.05$. For instances where a statistically significant association was reported, the strength of association between variables was evaluated using *Cramer's V*

231 (Cohen 1988), with a value of 0 and 1 indicating “no association” and “complete association”,
232 respectively (i.e. small association = 0.1, moderate association = 0.3 and large association =
233 0.5). In addition, the deviation of individual cells from independence was reported using
234 adjusted standardised residuals according to Agresti (2007), where values > 3 were deemed
235 indicative of cells that significantly deviate from independence.
236 All statistical analyses were performed using IBM SPSS Statistics version 24 for Mac OS X.
237 **Results**
238 **Gonad morphology**
239 The overall anatomy of *A. eightsii* is presented in Fig. 2. The gonad envelops the centre of
240 the alimentary canal. A thin layer of gonadal tissue (up to 3-4 cells thick) covers the outer
241 layer of the digestive gland and envelops the stomach where the gonad tissue thins to
242 approximately 1 cell thick. A strip of gonadal cells is located within the anterior adductor in
243 the upper body (Fig. 2b and d; Fig. 3a).

244 While the diameter of the stomach reduces as it penetrates the centre of the foot muscle, the
245 gonadal tissue layer around the stomach thickens (up to 10-12 cells thick; Fig. 3b). The
246 adjacent section of hindgut in the foot muscle is also surrounded by gonadal tissue, but fewer
247 cells are present (around 5-6 cells thick). No gonadal cells are found near the base of the
248 half gut loop in the foot muscle.

249 **Sex ratio**
250 All specimens (n = 95) selected for histological analysis had distinguishable gonads and
251 were separately sexed. Of the 95 individuals, 48 (50.5%) were female and 47 (49.5%) were
252 male.

253 **Female reproductive analysis**
254 Qualitative assessment of the female gonad revealed the presence of oocytes of all
255 developing stages throughout the study period. Previtellogenic oocytes (and other smaller
256 oocytes) were observed developing along the follicle walls next to both vitellogenic and ripe
257 oocytes throughout all months, and in 39 of the 42 females sampled between January 2013

and May 2014 (Fig. 4). The absence of ripe oocytes was observed in the gonad of only three females, comprising single specimens from July 2013 (shell length = 20.95 mm), October 2013 (shell length = 20.40 mm) and May 2014 (shell length = 24.62 mm). The measured oocyte diameters ranged from 12.5 to 176.7 µm. A spawning event occurred between April and May in 2013 and 2014, indicated by a reduction in average oocyte size (±SD), from 97.4 ± 23.4 µm, n = 3549 to 59.3 ±14.3 µm, n = 740, and from 93.0 ± 28.7 µm, n = 2164 to 54.2 ± 14.5 µm, n = 208, respectively.

Although oocytes of all maturity stages were observed in the gonad throughout the study period, the distribution of oocyte sizes varied between months (Fig. 5). *A chi-square test of independence* was conducted between month, using pooled females, and oocyte size frequency distribution. All expected cell frequencies were greater than five. There was a statistically significant association between month and the frequencies of oocytes distributed across the range of oocyte size (χ^2 *= 8156.288, df = 36, p <0.0001*). The association was moderately strong (Cohen, 1988), *Cramer's V = 0.349*, and 46 of 52 cells had adjusted standardised residuals > 3 (Table 1) indicating a significant deviation from independence.

Statistically significant associations between individual females, sampled in the same month, and their oocyte size frequency distributions were also recorded, where the strength of associations was generally moderate (*p < 0.05*; see Table 1 in Online Resource 2).

Male reproductive analysis

Seasonal changes in male maturity stage were interpreted to show a spawning event in April-May, as indicated by spent testicular acini (stage V) in 2013 and newly developed spermatogonia (stage I) in 2014 (Fig. 6). Testes matured from an early developmental (stage I) to mature stage (stage IV) between July 2013 and April 2014, and from a late developmental (stage III) to mature stage (stage IV) between January and April 2013.

Discussion

284 The present study of the reproductive ecology of the Antarctic shallow-water protobranch
285 bivalve, *A. eightsii* demonstrates a reproductive mode that differs from previously described
286 protobranch species and other Antarctic shallow-water invertebrates. Our results indicate
287 that the Hangar Cove population of *A. eightsii* exhibits continuous oogenesis, with a period of
288 increased reproductive intensity and spawning between April and May, with asynchrony in
289 oocyte development among females. Although we acknowledge reduced sample sizes in
290 some months, this was to ensure all samples were comparable with respect to shell lengths
291 and therefore sexual maturity, based on previous studies (Peck et al. 2010). Of those
292 specimens which fit our selection criteria, there was no control over gender at the point of
293 collection. Within the individual females measured, efforts were made to measure in excess
294 of 1000 oocytes where possible to reduce the weighting of inherent variability. All specimens
295 in this study were dioecious with an overall female to male ratio approximating unity, and with
296 no evidence of hermaphroditism found.

297 Continuous investment in oogenesis was evidenced by the simultaneous, year-round
298 occurrence of previtellogenic, vitellogenic, and ripe oocytes in the female gonads. This
299 reproductive trait contrasts with observations of seasonal oogenic development reported in
300 most shallow-water Antarctic marine invertebrates studied to date (e.g. Chiantore et al. 2001;
301 Ahn et al. 2003; Tyler et al. 2003; Grange et al. 2004, 2007, 2011; Kang et al. 2009; Reed
302 2013a), and other closely related protobranch bivalves including the cold water *Yoldia*
303 *hyperborea* (Jaramillo and Thompson 2008), where cohorts of oocytes distinguishable in
304 their maturity stage dominate the gonad at different times of year. Continuous oogenesis is
305 observed however in some deep-sea protobranch bivalves (Tyler et al. 1992; Zardus 2002;
306 Scheltema and Williams 2009; Reed et al. 2014). Significant associations between individual
307 females and their oocyte size frequency distribution were also observed indicating
308 asynchrony in oogenesis between individuals sampled in the same month. This asynchrony
309 could be attributed to an aseasonal reproductive rhythm. However, we did not observe any
310 evidence for aseasonality in the form of multiple spawning events in the females (Fig. 6), nor

male maturity stage (Fig. 2 in Online Resource 1). Instead, we observed a seasonal periodicity in the reproduction of both male and female *A. eightsii* (described below). In the case of the females studied, this seasonal periodicity was observed simultaneously to the continuous investment in oocyte development described above. We therefore propose that the asynchrony observed between individual females is consistent with an innate, long-term multi-year reproductive cycle, related to the partitioning of energetic resources between somatic and reproductive investment (as hypothesised in Román-González et al. 2017 and discussed below).

Observed simultaneously to the continuous oocyte development described above was a seasonal increase in reproductive intensity (spawning) during early Austral winter. This was demonstrated by an investment in the size and presence of ripe oocytes and their subsequent loss from the gonad, and a statistically significant association between month and oocyte size frequency distribution. Despite this observation, previous studies have identified very few bivalve veligers or larvae in winter in shallow waters adjacent to Rothera Research Station (Bowden et al. 2009). However, the pericalymma larva of protobranchs differs from the typical veliger larva of most bivalves in identifying features, being barrel-shaped and cloaked with an outer test enveloping the larva (Zardus and Morse 1998). This atypical appearance and the well-established difficulties associated with field identification of larvae, render this larval type susceptible to misidentification, underestimation and/ or being missed entirely in plankton samples. Winter spawning events have been previously reported for other Antarctic shallow benthic invertebrates, including the seastar *Odontaster validus* (Pearse 1965), the ascidian *Cnemidocarpa verrucosa* (Sahade et al. 2004), and the octocoral *Malacobelemnon daytoni* (Servetto and Sahade 2016), and confirmed in some cases by the presence of larval stages in the water column (e.g. for *O. validus*; Bowden et al. 2009). These events have been attributed to flexible feeding, energy storage, and/or extended gametogenic periods. In the case of *A. eightsii*, based on observations in this study, there is no evidence of energy storage or an extended gametogenic period, however flexible feeding in the form of both suspension and deposit feeding has been reported (Davenport

1988), and we speculate that the peculiar reproductive ecology of the bivalve is underpinned by a long-term internal cycle related to energy allocation.

Feeding plasticity may overcome the food limitation that characterises shallow Antarctic waters and poses resource limits for many species during winter, and may also facilitate the continuous oogenesis observed in *A.eightsii. Aequiyoldia eightsii* exploits phytoplankton in the summer by suspension feeding, and deposit feeds on organic material in the sediment, mostly composed of microphytobenthos and macroalgal fragments all year round (Davenport 1988; Corbisier et al. 2004, Pasotti et al. 2015b). Fragments of phytoplankton/algae were observed in the stomach and hindgut of all specimens in the current study, supporting continuous feeding throughout the year. These findings are consistent with previous laboratory experiments where specimens aged younger than 24 years fed primarily on phytoplankton < 20 µm in diameter (Chris and Priddle 1995). As the *A. eightsii* specimens analysed in the current study had shell lengths between 20 – 25 mm, representative of 10 – 33 years of age (Peck and Bullough 1993), it is likely that the phytobenthos is the primary food source. Nanoplankton concentrations in the waters around Rothera Research Station peak in the late summer (~March), and are suggested to have an important influence on the ecology of benthic grazers in the area (Clarke et al. 2008). The settlement and subsequent deposit feeding on nanoplankton in sediment therefore could trigger a reproductive response in *A. eightsii*, such as spawning in the Hangar Cove population, which could explain the increased reproductive intensity and spawning detected in April and May.

While feeding plasticity enables *A. eightsii* to sustain continuous oogenesis, and the seasonal availability of food, i.e. nanoplankton production, acts as a selective pressure driving a superimposed seasonal reproduction, recent evidence of a multi-year cycle in shell growth of the protobranch bivalve (Román-González et al. 2017) suggests the reproductive asynchrony observed in females is not underpinned by environmental factors. Nor can this reproductive pattern be explained by the accepted paradigm of an 18-24 month period needed for oogenesis in several other Antarctic invertebrates (Peck et al. 2005; for examples see Grange et al. 2004, 2007; Brockington et al. 2007; Orejas et al. 2007). The reproductive

ecology of *A. eightsii* also differs from other shallow-water and deep-sea nuculanid protobranch bivalves that have a 12-month gametogenic cycle, often with seasonal investment in reproduction (Tyler et al. 1992; Nakaoka 1994; Jaramillo and Thompson 2008; Scheltema and Williams 2009). Instead the asynchrony observed here may be linked to an innate, endogenous growth rhythm (e.g 9.06 year) that is asynchronous between individuals, not keyed with environmental variability, and attributable to cycles in reproductive output (Román-González et al. 2017).

The maximum egg size of *A. eightsii* measured in this study was 176.7 µm. In marine invertebrates, larval development mode is often inferred from egg size (Moran and McAlister 2009). However, in Protobranchia, egg sizes can vary extensively within individual modes of development and even within closely related species (Gustafson and Reid 1986; Scheltema and Williams 2009). This subclass is known to only exhibit two modes of larval development to date; pelagic lecithotrophy and brooding (Zardus 2002; Scheltema and Williams 2009). Since gametogenesis of *A. eightsii* shows synchrony in seasonality between males and females, the loss of a relatively large proportion of gametes between April and May, and the absence of brooded embryos suggests this bivalve is a broadcast spawner with lecithotrophic larvae. Winter spawning of lecithotrophic larvae may facilitate the avoidance of predators feeding on larvae associated with the summer bloom (Sahade et al. 2004), ice-mediataed disturbance (Barnes and Souster 2011), and a greater availability of free substratum for larval settlement (Bowden 2005). As adult *A. eightsii* can inhibit larval settlement via density-dependent control (Peck and Bullough 1993), larvae spawned during periods with more available habitat could increase the chance of settlement.

The reproductive ecology of *A. eightsii* exhibits continuous oogenesis, with a period of increased reproductive intensity and spawning between April and May, and asynchrony between females. These characteristics contrast with the short-term, seasonal reproductive traits reported for many shallow-water Antarctic invertebrates and closely related protobranch bivalves. We hypothesise that the asynchrony documented between females is underpinned

by a multi-year periodicity attributed to an innate, endogenous rhythm related to energetic allocation between somatic and reproductive investment. Whereas the ability to switch between suspension and deposit feeding modes, according to the quality and quantity of food available, facilitates a continuous investment into oogenesis, whilst being responsive to the seasonal pulse in primary production. This study provides key information on a scientifically important species of bivalve that has been commonly used for baseline ecological investigations in Antarctica. Knowledge of its reproduction provides insight into the biological flexibility of the species and contributes to our wider understanding of adaptations in polar marine environments.

Compliance with Ethical Standards

The authors declare they have no conflict of interest. All applicable institutional and/or national guidelines for the care and use of animals were followed and the necessary permits for collection of Antarctic animals obtained.

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631 **Figures**

632 **Fig. 1** Location of sampling site for *Aequiyoldia eightsii* in Hangar Cove, Adelaide Island,
633 West Antarctic Peninsula (67º 33' 52 S, 68º 07' 43 W).

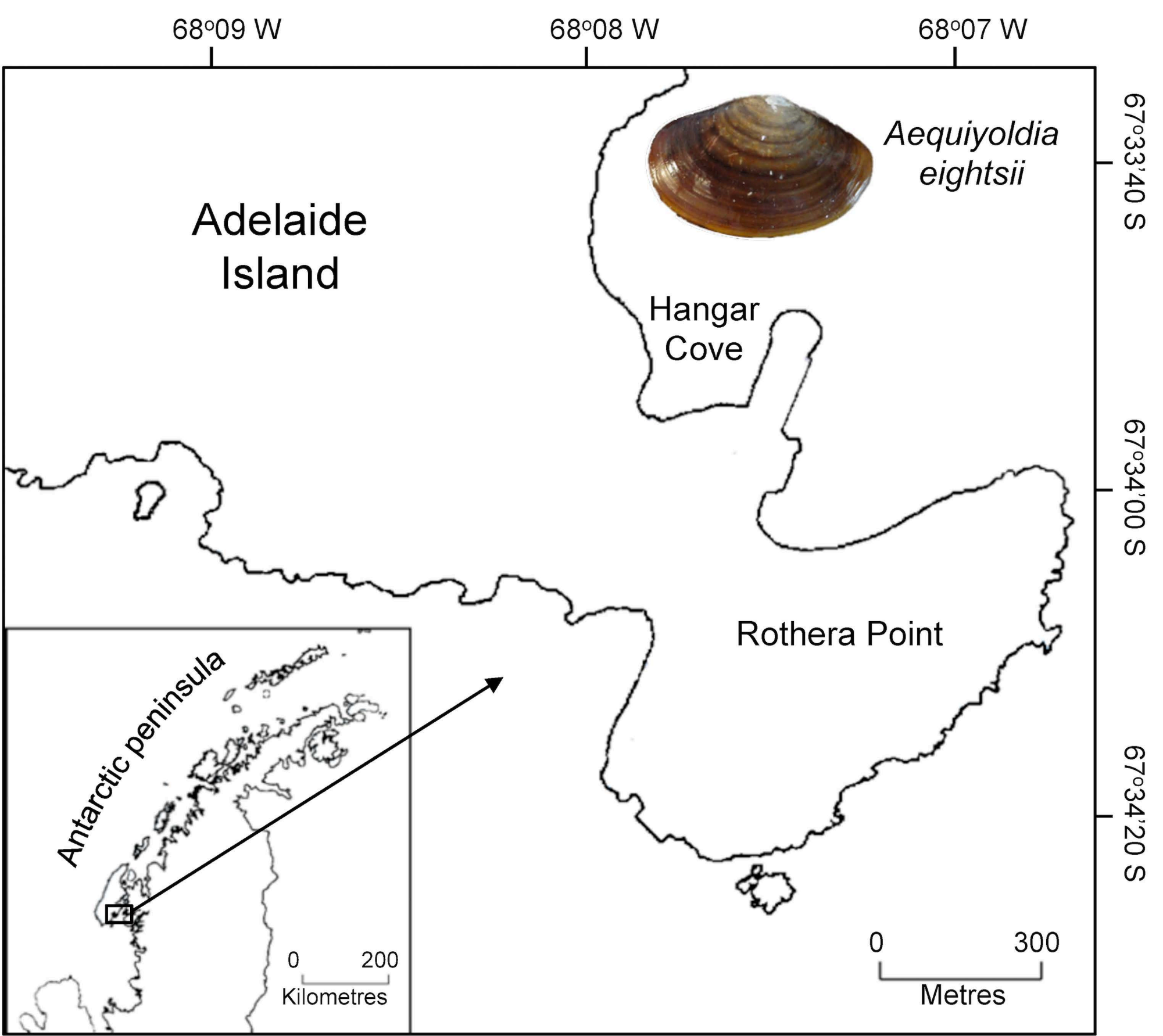
634 **Fig. 2** Anatomy of a female *Aequiyoldia eightsii* collected in April 2013 from Hangar Cove,
635 Adelaide Island, West Antarctic Peninsula (67º 33' 52 S, 68º 07' 43 W). (**a**) Photograph of
636 soft tissue after shell removal (left side); (**b**) General anatomical structure (left side). Gonad
637 envelopes *dg* digestive gland shown in orange; (**c**) Photograph of soft tissue after shell
638 removal (right side). (**d**) Configuration of the alimentary canal and associated gonad (right
639 side). *a* anus, *aa* anterior adductor, *dg* digestive gland, *es* exhalent siphon, *f* foot, *ct*
640 ctenidium, *h* hinge, *hg* hindgut, *is* inhalant siphon, *o* oesophagus (attaches to *pl*), *pa* posterior
641 adductor, *pl* palp lamella, *pp* palp proboscid, *r* rectum, *st* stomach. Scale bar = 1 cm.

642 **Fig. 3** Transverse histological sections of a female *Aequiyoldia eightsii* collected in April 2013
643 at Hangar Cove, Adelaide Island, West Antarctic Peninsula (67º 33' 52 S, 68º 07' 43 W). (**a**)
644 Horizontal section through the median level of the visceral mass. (**b**) Horizontal section
645 through the top level of foot muscle. *fm* foot muscle, *o* oocytes. Scale bar = 500 µm. For
646 other abbreviations see Fig. 2.

647 **Fig. 4** Oocyte ripening in *Aequiyoldia eightsii* from Hangar Cove, Adelaide Island, West
648 Antarctic Peninsula (67º 33' 52 S, 68º 07' 43 W) between January 2013 and May 2014. *DG*
649 digestive gland, *HG* hindgut, *MO* ripe oocytes, *OG* oogonia, *PVO* previtellogenic oocytes, *VO*
650 vitellogenic oocytes. Scale bar = 200 µm.

651 **Fig. 5** Average monthly oocyte size-frequency distributions measured as Equivalent Circular
652 Diameter (µm) of *Aequiyoldia eightsii* from Hangar Cove, Adelaide Island, West Antarctic
653 Peninsula (67º 33' 52 S, 68º 07' 43 W) between January 2013 and May 2014. Box-whisker
654 plots for each month; diamond = mean, line = median, box = 25th to 75th percentile range,
655 and whiskers = 1.5 times the value of the interquartile range. Oocyte diameter = equivalent
656 circular diameter. N = number of females, n = number of oocytes measured. Error bars = ±
657 1SE.

Fig. 6 Testes maturation in *Aequiyoldia eightsii* from Hangar Cove, Adelaide Island, West Antarctic Peninsula (67º 33' 52 S, 68º 07' 43 W) between January 2013 and May 2014. *DG* digestive gland, *HG* hindgut, *LM* lumen, *RS* residual sperm, *SC* spermatocytes, *SG* spermatogonia, *SS* spent acini, *SZ* spermatozoa. Scale bar = 200 μm.


68°09 W
68°08 W
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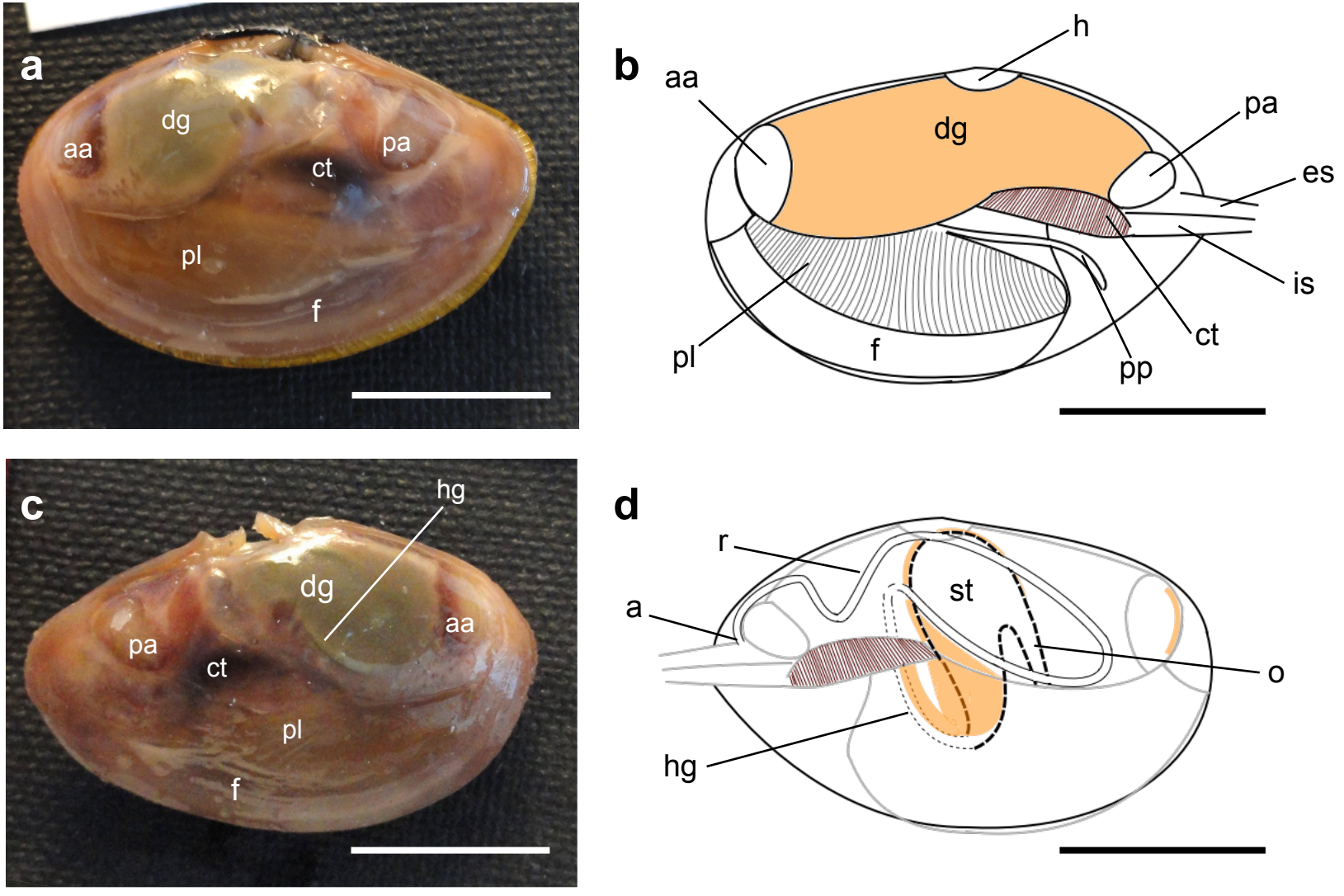
Aequiyoldia eightsii
Adelaide Island
Hangar Cove
Rothera Point
Antarctic peninsula
0 200
Kilometres
0 300
Metres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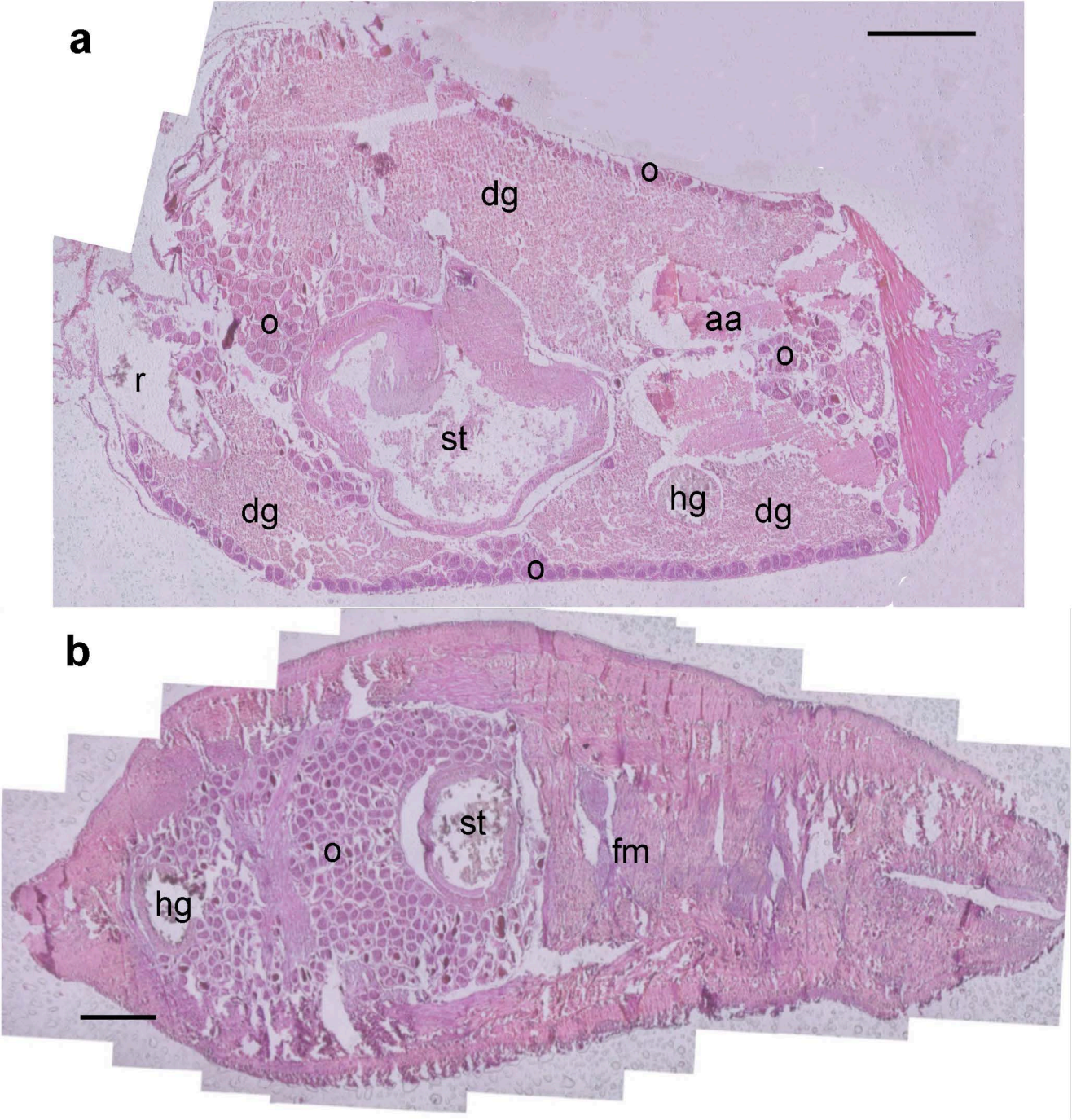
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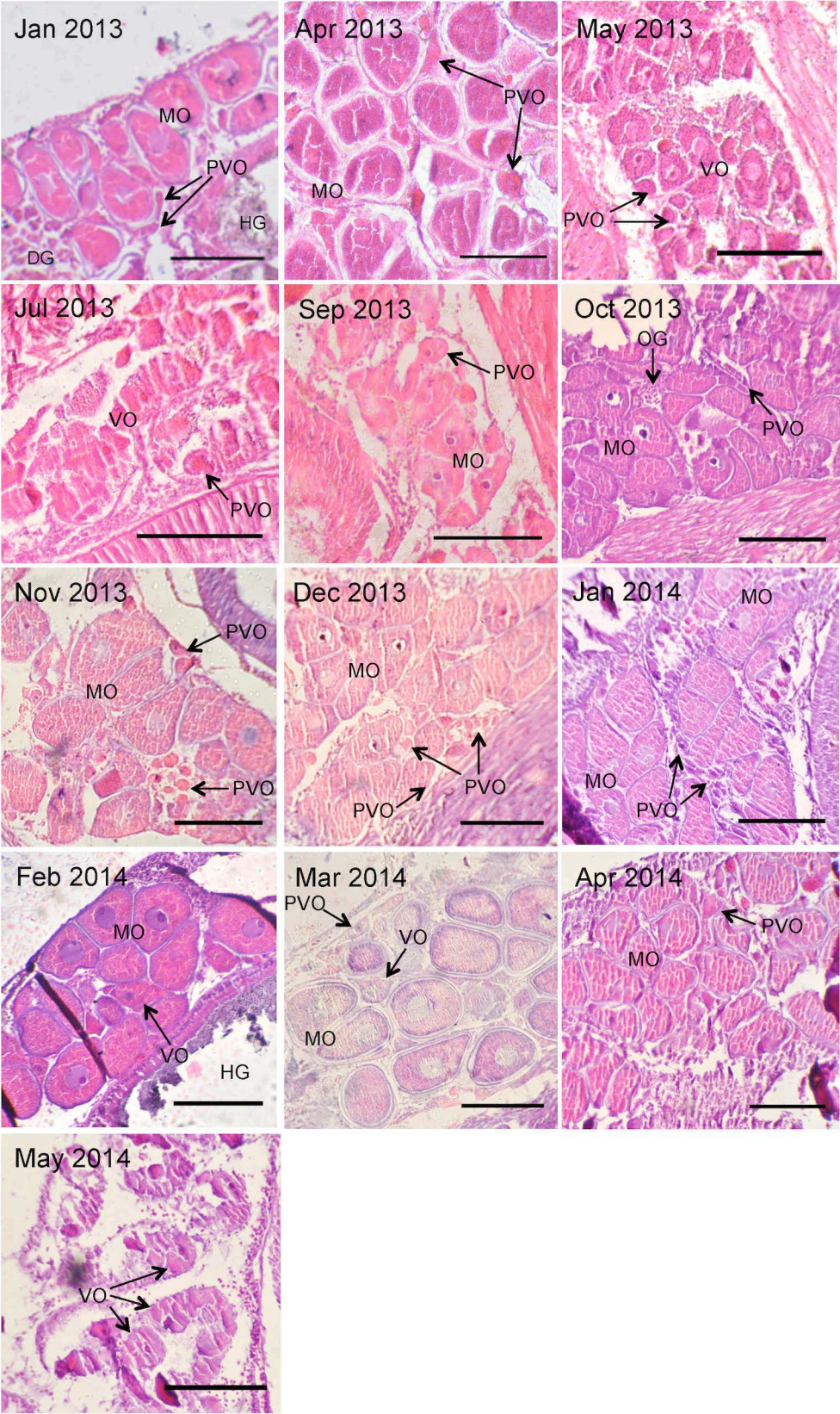
Jan 2013
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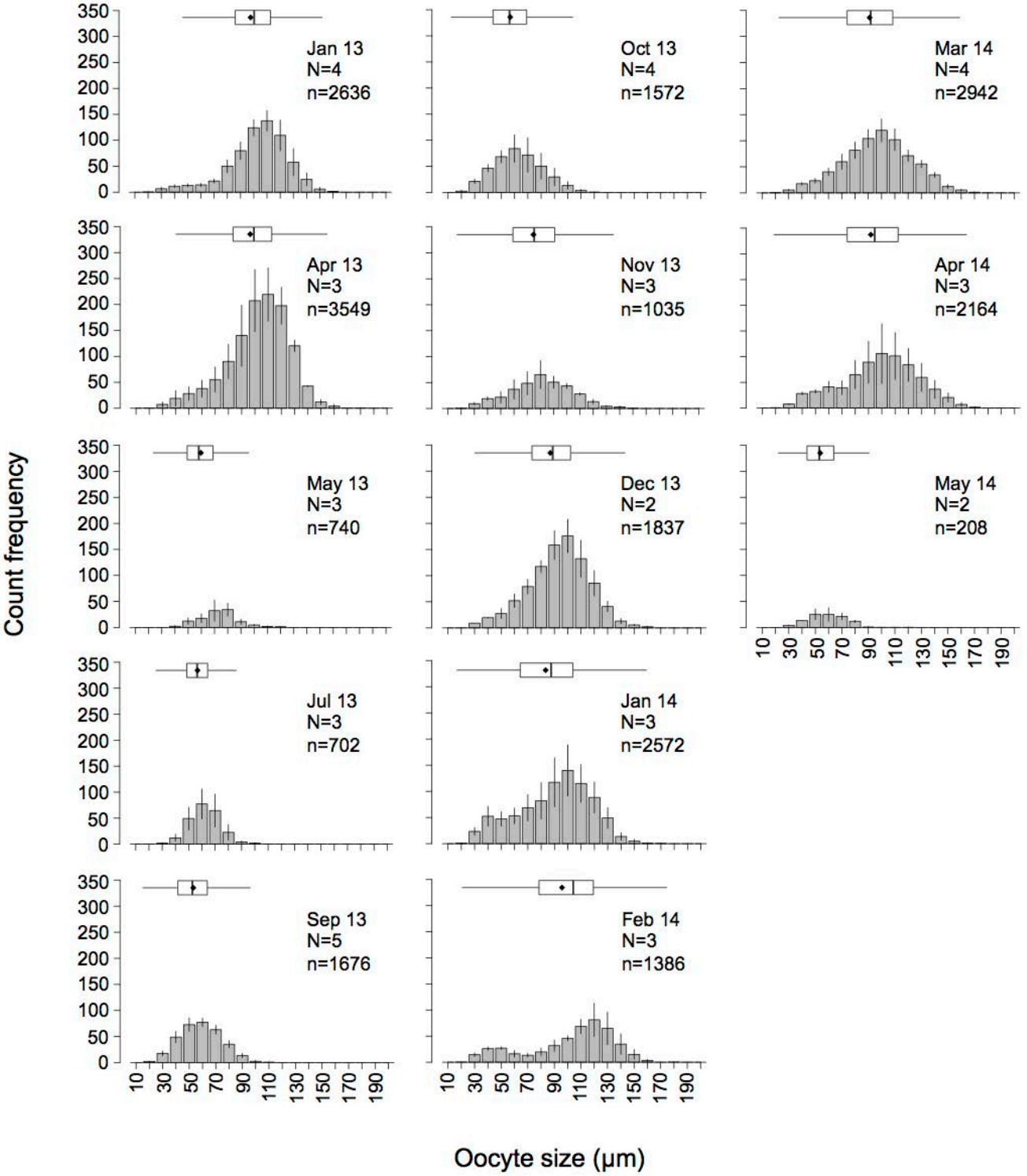
Count frequency
Oocyte size (µm)
Jan 13
N=4
n=2636
Oct 13
N=4
n=1572
Mar 14
N=4
n=2942
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n=3549
Nov 13
N=3
n=1035
Apr 14
N=3
n=2164
May 13
N=3
n=740
Dec 13
N=2
n=1837
May 14
N=2
n=208
Jul 13
N=3
n=702
Jan 14
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Sep 13
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Feb 14
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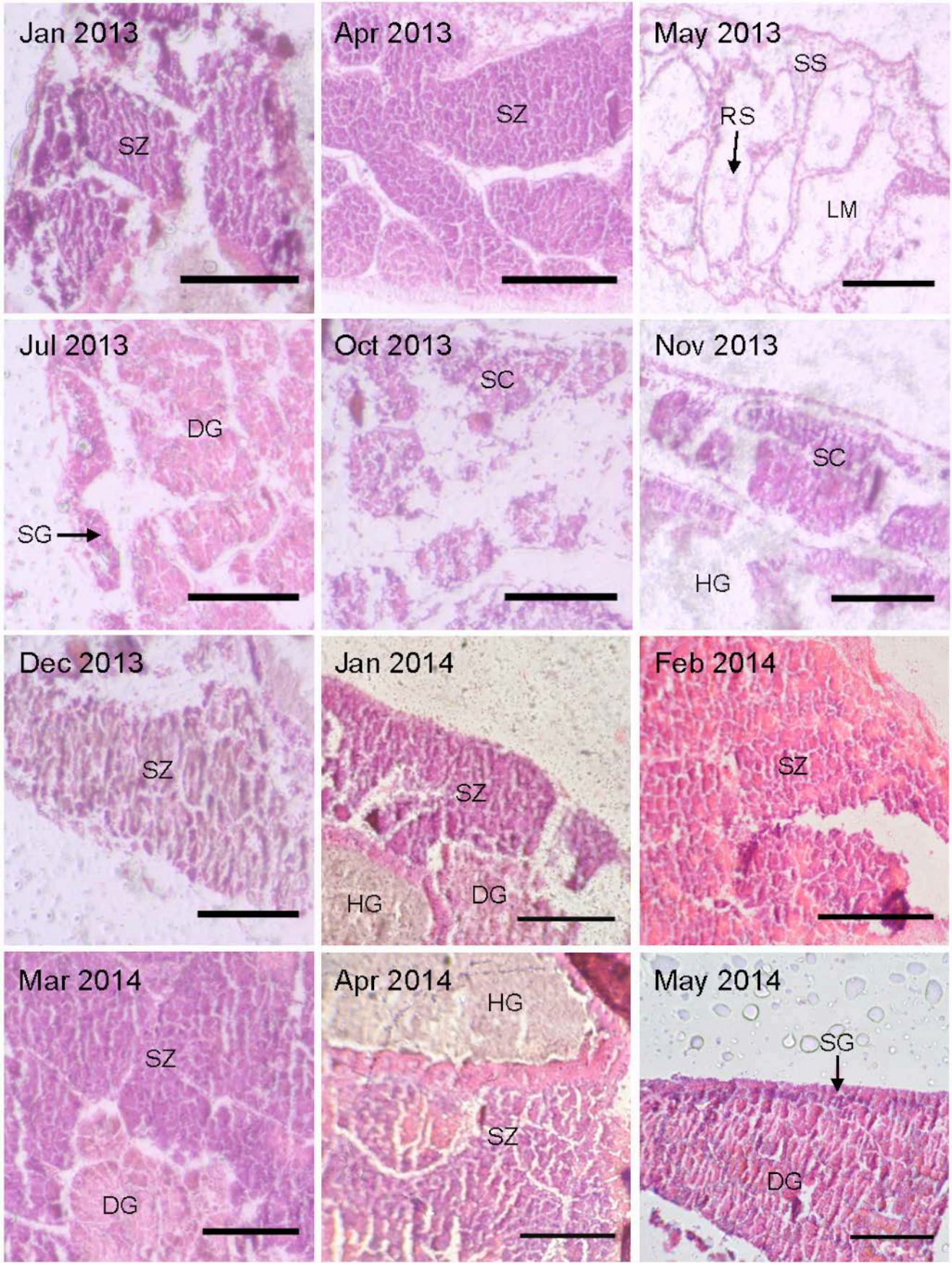
Jan 2013
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