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Development observed in the field of the Antarctic bivalve mollusc *Aequiyoldia eightsii* at Signy Island, South Orkney Islands

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ABSTRACT

The embryonic development of marine ectotherms has been shown to be strongly temperature dependent across the world's oceans. However, at the coldest sites, in the polar regions, development is even slower than would be predicted on the basis of the temperature dependence of development in warmer waters, and this is thought to be a consequence of changes in physical characteristics of cytoplasm near 0 °C—such as viscosity and osmolyte packing that slow protein folding and increase the likelihood of interference by charged particles, and their effect on protein synthesis. The overwhelming majority of studies of rates of embryonic development have been laboratory-based, with animals either collected directly from the sea and spawned in the laboratory or held first in the laboratory and preconditioned to set environments before spawning. Few studies have assessed development from regularly collected samples and assessed field development, especially from polar latitudes. Here we present data for the Antarctic bivalve mollusc *Aequiyoldia eightsii*, tracking its development from spawning on 25/26 May to hatching of pelagic veligers on 12 June and the disappearance of pediveliger larvae from the water column at the end of September or early October, 108–114 days later. Larval dry mass was constant at 16.7 μg (SE = 0.19) across the pelagic phase, except for the initial few days after hatching when it was 9.55 μg (SE = 0.60). The difference was likely the calcification of the larval shell. The development time to trochophore was 189 h, and this was in line with previous studies showing larval development at temperatures around 0 °C is around 4–22 times slower than would be predicted from the general effect of temperature on development rates.

INTRODUCTION

The polar regions are characterized by environments with extreme seasonality of light and biological productivity. The combination of this extreme seasonality with low temperature in Antarctic marine environments has had a strong effect on the physiologies of the species present (Peck, Convey & Barnes, 2006b). Feeding in many species is restricted to summer months, and there can be long periods of aestivation, or dormancy, in winter that have been noted for many decades (e.g. Gruzov, 1977; Clarke, 1988; Campbell *et al.*, 2008), and very large seasonal changes in metabolic rate have been identified in a wide range of species from primary consumers to obligate predators (Morley *et al.*, 2016; Souster, Morley & Peck, 2018). Seasonal availability of resources is a clear area where resources are limited to support other functions, such as growth and development, and there has been strong discussion on the importance of both to the observed slowing of the rates of these processes by up to an order of magnitude or more observed in Antarctic marine species (Peck, 2018; Clarke & Peat, 2022), and there appears to be a strong difference between benthic and pelagic species in the processes entrained (Clarke & Peck, 1991; Clarke & Peat, 2022). Many studies have demonstrated slow or very slow growth and early-stage development of ectotherms in the Southern Ocean (e.g. Peck, 2018; Reed *et al.*, 2021). This includes oogenesis, which in most of the species studied takes between 18 and 24 months compared to 3–6 months in temperate species (e.g. Pearse & Cameron, 1991; Grange *et al.*, 2004; Grange, Tyler & Peck, 2007; Grange, Peck & Tyler, 2011; Hanchet *et al.*, 2015; De Leij, Peck & Grange, 2021). Recent research has shown that the slowing of growth and embryo development in Antarctic species is greater than might be expected on the basis of the temperature dependence of development in warmer water species (Peck, 2016). This is likely linked to the observed problems making functional proteins at temperatures near 0 °C, where high viscosity and increased molecular packing from osmolytes and other molecules used to reduce the likelihood of freezing affect the

correct folding of newly synthesized proteins (Fraser, Clarke & Peck, 2007; Peck, 2018; Fraser *et al.*, 2022).

Of the studies showing that embryonic and larval development in polar marine ectotherms living close to 0 °C is slow or very slow compared to temperate and tropical species, the vast majority have been laboratory-based (e.g. Pearse, 1969; Bosch *et al.*, 1987; Hain, 1991; Pearse, McClintock & Bosch, 1991; Peck, 1993; Stanwell-Smith & Peck, 1998; Peck, Clarke & Chapman, 2006a; Peck, Powell & Tyler, 2007; Peck, Heiser & Clark, 2016), and recently Moran *et al.* (2019) showed that embryo development in broods of the Antarctic neogastropod *Antarctodomus thielei* (Powell, 1958) requires an astonishing 8 years to complete. In the Moran *et al.* (2019) study, *Antarctodomus thielei* broods developed at temperatures around or below –1 °C, which suggests that the temperature effect below zero is very large indeed. Studies involving observations of field spawning and then tracking development to hatching and subsequent regular observation of larvae in pelagic phases are rare or absent.

In this study, we observed the spawning of the common Antarctic infaunal protobranch bivalve mollusc *Aequiyoldia eightsii* (Jay, 1839) (Sareptidae) at Signy Island, South Orkney Islands, and then, using approximately biweekly collections of veliger larvae from the water column, followed development to settlement. *Aequiyoldia eightsii* lives in the surface layers of sediments to water depths of around 100 m and has a circum-Antarctic distribution (Dell, 1990), which extends into the sub-Antarctic as far as the Magellan Strait (González-Wevar, Díaz & Gerard, 2012). It has been reported to occur at densities up to 1,540 m^{-2} (Peck & Bullough, 1993) and accounts for over 50% of the macrofaunal biomass in Potter Cove, King George Island (Pasotti, Manini & Giovannelli, 2015). *Aequiyoldia eightsii* is mainly a deposit feeder, but it can also consume suspended material during phytoplankton blooms (Davenport, 1988). It reburies relatively rapidly when removed from sediment (Peck *et al.*, 2004), and it can live for as long as 60 years (Peck & Bullough, 1993; Román-González *et al.*, 2017).

MATERIAL AND METHODS

Aequiyoldia eightsii were observed spawning and samples of fertilized eggs, embryos and pelagic veligers were collected from a site at 6–8 m depth in Factory Cove, Signy Island (60°43′S, 45°36′W) in May–September 1990 (Fig. 1). Initial observations of spawning individuals were made directly by SCUBA divers (J.G. Colman, personal observation). Collections of fertilized and developing eggs were made by divers using 10 cm diameter hand-held corers with closing bungs at each end and a 100 μm mesh plankton net, taking the surface 0.5–1.0 cm of sediment, and this was done daily from 25 May until 4 June.

Veliger larvae were collected using small plankton nets with a 100-μm mesh towed from an inflatable boat during periods of open water and hauled vertically through holes cut in sea ice using a chain saw when there was strong ice cover. Samples returned to the laboratory were initially filtered through a 180-μm sieve, and veliger larvae were isolated and linear dimensions measured using a calibrated eyepiece graticule in a WILD M5 binocular field microscope with ×50 magnification, with maximum shell dimension being the longest dimension of the larval shell. Samples were collected individually and transferred to preashed and preweighed aluminium boats to obtain dry mass. Because of their small size, dry mass was measured on groups of larvae between 8 and 39, but predominantly between 15 and 20. After placing in weighing boats, larvae were rinsed rapidly in reverse osmosis freshwater to remove salt, and excess water was removed with a pipette. Samples were dried to constant mass at 60 °C to obtain dry mass values.

Across the duration of this study, sea-ice thickness was measured between daily and twice-weekly intervals by the station marine assistant using an auger to drill through the sea ice and measure its thickness directly. Sea-ice duration between 1900 and 2010 was obtained from daily observations logged in the South Orkney fast ice record (https://ramadda.data.bas.ac.uk/repository/entry/show/?entryid=f9e983e6-d2d8-4988-9c56-ca040b51ee39). Data are a combination of observations on two islands in the South Orkney group, Signy Island and Laurie Island. The earlier part of the set is from Laurie Island, and the most recent 50 years are from Signy Island (Murphy *et al.*, 1995, 2014).

RESULTS

Eggs collected from surface sediments during the time when adults were observed spawning (25/26 May 1990) showed strong fertilization reactions, with clear separation of the vitelline membrane from the egg surface (Fig. 2). Spawning was observed at the same time in the previous year (1989), but representative sampling was not made. Eggs were pale orange and 180–200 μm in diameter, and collections included embryos in the 2, 4 and 8 cell stage. Later developmental stages (blastula, gastrula and trochophore) were passed through during the daily sediment samplings between 25 May and 4 June. The time for 50% of the embryos to reach trochophore stage was 189 h. The first early veliger larvae were identified on 5 June, and these veligers were still intracapsular, within the egg membrane. Fully developed veligers were first observed on 8 June, and in 1989 they were first observed on 10 June. The time taken to reach the early veliger stage from fertilisation was estimated at 13–14 days, from a spawning date of 25/26 May to 8 June.

The first free-swimming pelagic veligers were observed and collected on 12 June, 18 days after the first spawning was observed. The maximum shell dimension of the larvae on 12 June was 350 μm. By the second sampling on 16 June, this had increased to 360 μm, and it stayed at that value throughout the full period when veliger larvae were present in the water column to 30 September, 116 days later. After this time, extensive sediment sampling was conducted, but no settled juveniles or settling pediveligers were collected. Throughout the pelagic phase, larvae did not recognisably change their morphology or structure, and they appeared as pediveligers with an obvious foot and velum (Fig. 3).

At hatching on 12 June, and in the earliest part of the pelagic phase, mean larval dry mass was 9.55 μg (SE = 0.60); this rose to values between 13 and 22 μg for the rest of the pelagic phase, with a mean value of 16.7 μg (SE = 0.19) (Fig. 4). Throughout most of the pelagic phase, larvae had a large yolk mass visible under a light microscope. However, from 21 September samples of larvae began to appear with no yolk mass, and by 30 September the proportion of larvae lacking a yolk mass had reached 36%. There were no *Aequiyoldia eightsii* larvae in extensive sampling efforts taken on 5 and 10 October, and settlement was therefore between 30 September and 5 October. The pelagic phase was therefore between 108 and 114 days.

Aequiyoldia eightsii spawns in early winter, and development occurs across June to October, with settlement in very late winter. This winter period is characterized by the presence of sea ice, and in 1990, there was strong sea ice for most of the winter, with it breaking up and disappearing around the same time as larvae settled from the water column (Fig. 4). Sea ice stabilises the water column and reduces wind-induced mixing, as well as light levels. As a result, there is very little chlorophyll in the water column when fast ice is present (Clarke, Holmes & White, 1988). At Signy Island, annual sea-ice duration ranged from 10 to 278 days between 1900 and 2010 (Fig. 5). There was also a clear decline in annual sea-ice extent over the 110-year period, from an average of 175 days in 1900 to 124 days in 2010, a reduction of 29%. There was great variation between years, with 1990 being below average but not extreme.

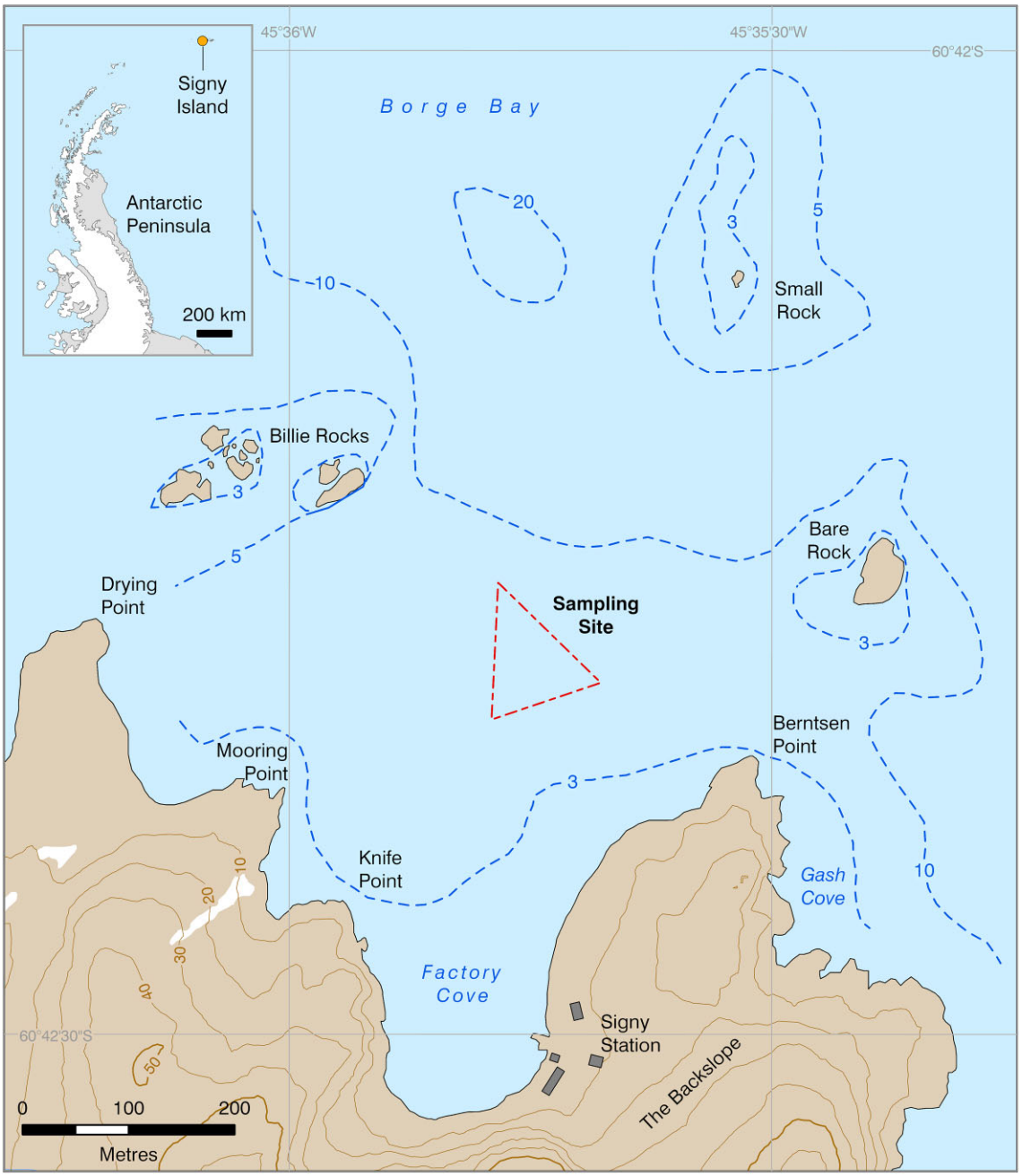

Figure 1. Map showing the sampling site where *Aequiyoldia eightsii* were observed spawning, and later collections were made of eggs from surface sediments and subsequently larvae from the water column.

DISCUSSION

Field observations from Signy Island, South Orkney Islands, show that *Aequiyoldia eightsii* spawns towards the end of May and develops into free-swimming veliger larvae in 13–14 days. It then remains as a pelagic veliger until the end of September or early October, and the pelagic phase is 108–114 days. At hatching, larvae were 9.55 μg dry mass (SE = 0.60), and this rapidly rose to between 15 and 20 μg (mean 16.7 μg, SE = 0.19). This increase in dry mass was likely due to calcification and thickening of the shell, as the increase only occurred over the first few days of release, and larvae were unlikely feeding because of their early stage and the low levels of available food in winter. There is further evidence that larvae were not feeding during the pelagic phase because their stores of yolk were depleted by the end of winter. Lau *et al.* (2018) investigated reproduction in *A. eightsii* at Rothera Point on the Antarctic Peninsula, which is around 500 miles further south than Signy Island, where the current study was conducted. They documented changes in egg size in gonads from specimens collected at monthly intervals and showed that spawning occurred in late April or early May. This is up to a month earlier than the spawning periods observed here at Signy Island. It is possible that the stronger seasonality further south results in this shift in reproductive timing. Several other Antarctic marine species have been noted to reproduce and have pelagic phases in winter. For invertebrates, these include the starfish *Odontaster validus* (Stanwell-Smith & Clarke, 1998; Pearse & Bosch, 2002; Grange *et al.*, 2007) and the gastropods *Marseniopsis mollis* and *Torellia mirabilis* (Peck *et al.*, 2006a), though both of

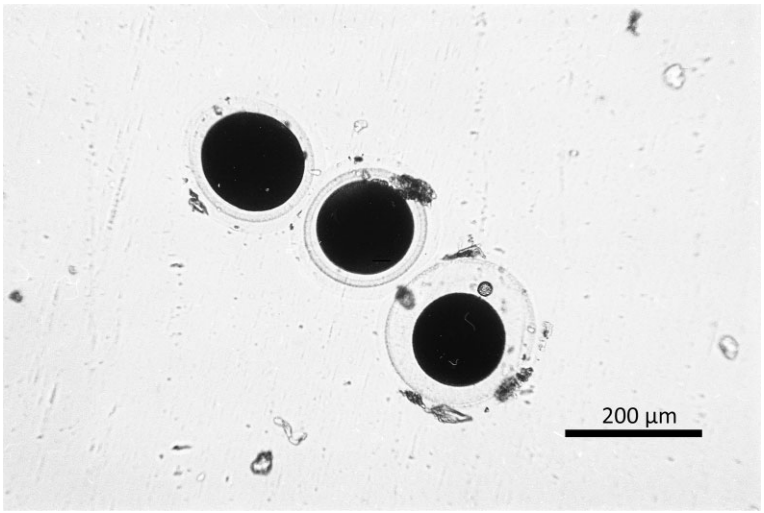

Figure 2. Fertilized *Aequiyoldia eightsii* eggs collected from the sampling site in Factory Cove, Signy Island, during 25/26 May 1990 showing strong fertilisation reactions.

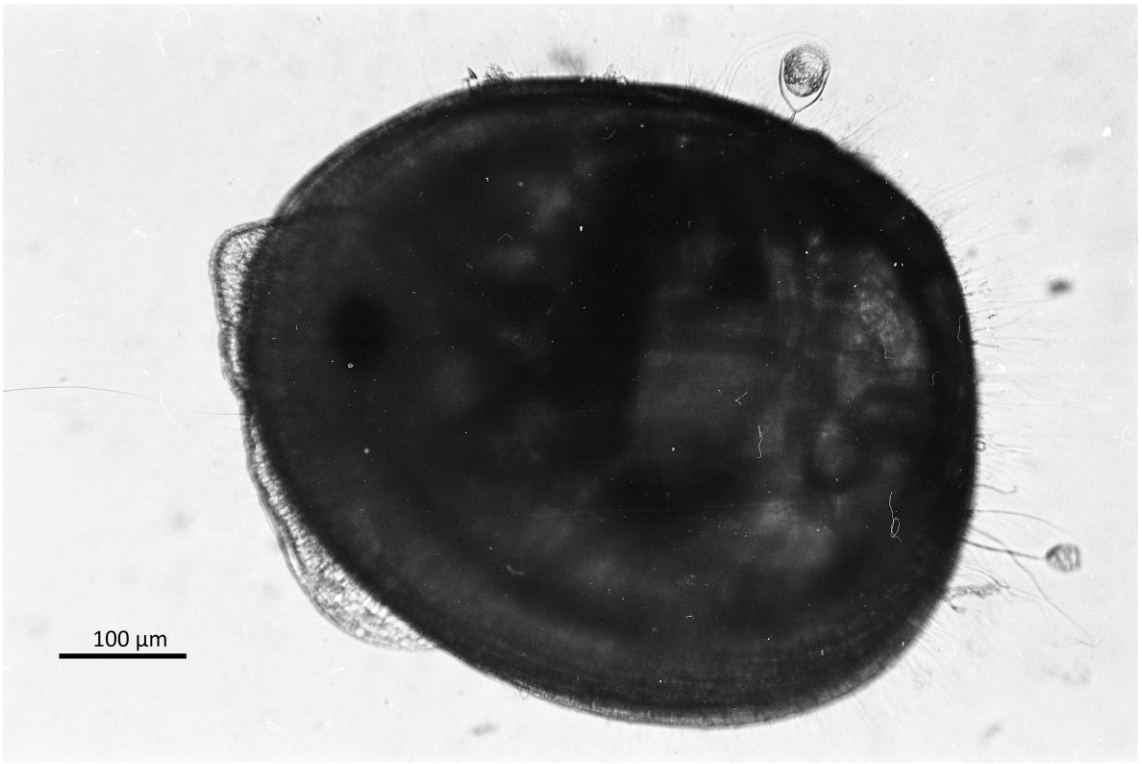

Figure 3. Pelagic *Aequiyoldia eightsii* pediveliger larva with well-developed foot and velum. Note suctorian protists attached to either the mantle or shell edge.

these lay broods in late summer/early winter that hatch and produce pelagic larvae in late winter. Some fish also have pelagic larval phases in winter, and these include the plunderfish *Harpagifer antarcticus* (White & Burren, 1992) and the toothfish *Dissostichus mawsoni* (Parker *et al.*, 2019). Pelagic larvae of many species have also been collected in Antarctica during winter at both Signy Island (Stanwell-Smith *et al.*, 1999) and Rothera Point, Adelaide Island (Bowden, Clarke & Peck, 2009). Winter spawning and development of embryos and larvae is thought to have two potential benefits to match the timing of settlement and metamorphosis to juveniles with the availability of suitable food sources, the settlement timing hypothesis (Todd & Doyle, 1981; Bowden *et al.*, 2009; Burgess *et al.*, 2016); and to reduce the likelihood of predation of early stages by suspension feeders that predominantly feed on the summer phytoplankton bloom (Pechenik, 1999; Pechenik & Levine, 2007; Burgess *et al.*, 2016; Clarke & Peat, 2022).

Sea ice is one of, if not the most defining characteristic of polar marine environments (Peck, 2018). When the sea freezes, it reduces light levels in the water column, reduces phytoplankton production and stabilizes the water column (Montes-Hugo *et al.*, 2009; Meredith & Brandon, 2017). These conditions reduce the feeding activity of most pelagic and benthic herbivores in

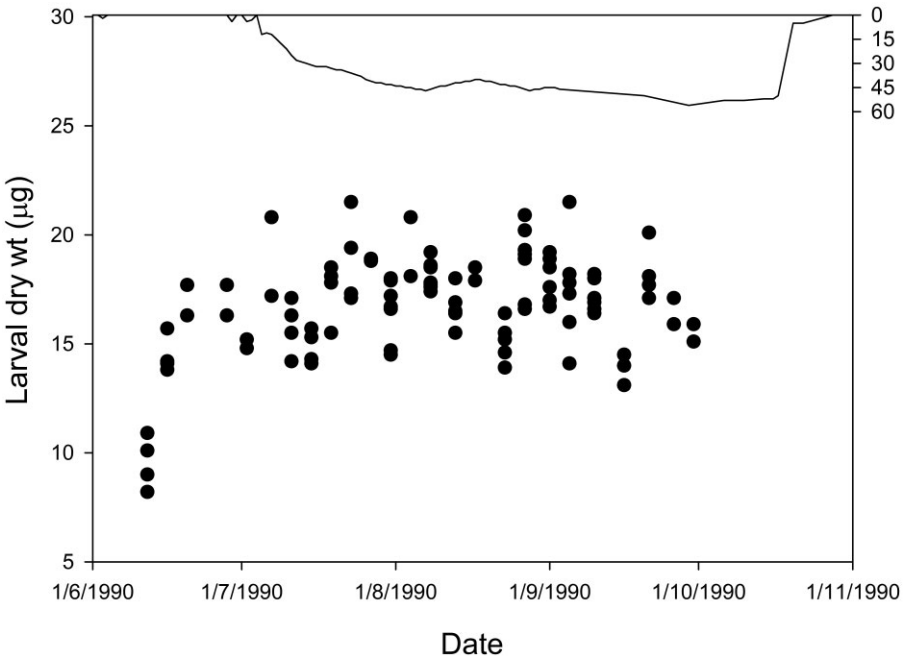

Figure 4. Main pane: dry mass of *Aequiyoldia eightsii* larvae between their first appearance in the plankton on 12 June and their disappearance at the end of September or at the start of October. Upper pane: sea ice cover and thickness for the period of presence of *A. eightsii* pelagic larvae in Factory Cove, Signy Island, note axis scale on right of plot.

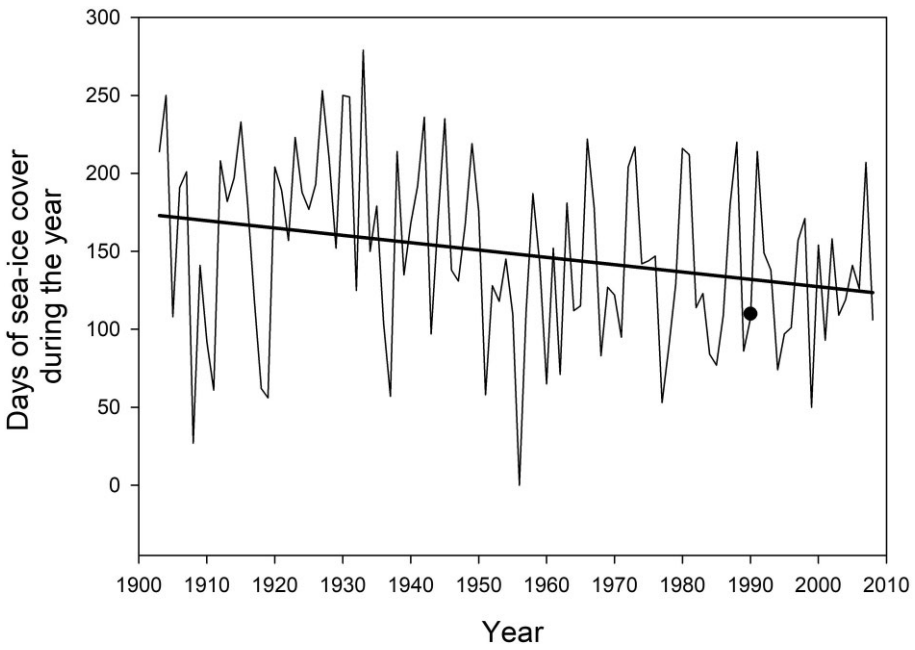

Figure 5. Annual sea-ice duration at Signy Island between 1900 and 2010. Data for 1990 shown as black circle. The regression equation is: duration = 1069.55 − 0.4713 days ($r^2 = 0.06$, $F_{2,104} = 375.5$, $P < 0.0001$). Data used are a composite from records for Lawrie Island and Signy Island, both in the South Orkney Islands (see Murphy *et al.*, 2014).

winter and hence predation on larvae (Clarke & Peat, 2022). From a phenology perspective, the timing and duration of winter sea ice are critical for the successful recruitment of juveniles. In 1990, it seems likely that sea-ice duration fitted well with the requirements of *A. eightsii* because the ice disappeared soon after the larvae settled, which increased the productivity of benthic phytobionts (Peck *et al.*, 2000), at a time when juveniles would have been dependent on such productivity. The year 1990 had a slightly low, but close to average, sea-ice duration for the period between 1950 and 2010 (Fig. 5). Sea-ice trends around the South Orkney Islands have decreased consistently across the 110 years of observations, from an average of 175 days per year in 1900 to around 125 days per year in 2010 (for detailed discussion, see Murphy *et al.*, 2014). At a whole Antarctic scale, it appears that

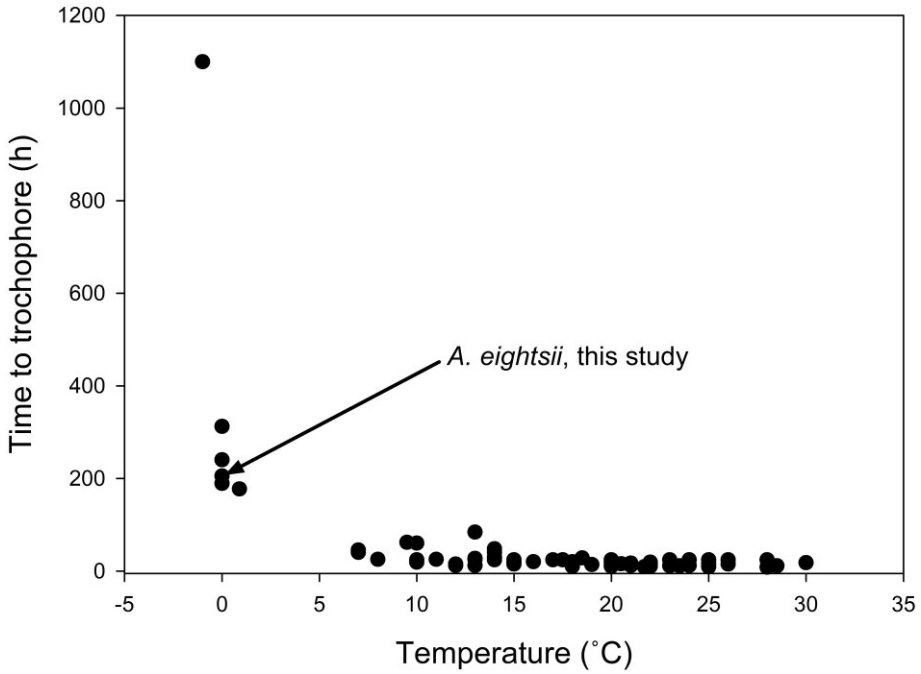

Figure 6. Time taken in hours to reach the trochophore stage for bivalve molluscs from polar to tropical latitudes, in relation to environmental temperature. Updated from Peck *et al.* (2007) with data for the current study and for the nuculoid bivalve *Acila castrensis* (Zardus & Morse, 1998), the solemyid bivalve *Solemya reidi* (Gustafson & Reid, 1986) and the Solenogastre *Wirenia argentea* (Todt & Wanninger, 2010). For *Acila castrensis* and *S. reidi* the time taken to reach the pericalymma larva stage was used instead of trochophore and for *W. argentea* the time taken to develop trochozoan characteristics was used.

a widespread loss of sea ice, similar to that seen in the Arctic in recent decades, might be starting as four of the lowest sea ice minima on record have occurred in the last 6 years (NOAA: https://www.climate.gov/news-features/understanding-climate/understanding-climate-antarctic-sea-ice-extent). This loss of sea ice will not only change productivity dynamics and seabed disturbance from freeing icebergs (Barnes, 2017), but it will also have serious consequences for the phenology of reproductive events for winter spawning species.

The disappearance of larvae from the water column at the end of September was most likely due to the pediveligers reaching maturity and competence to settle. This is supported by the observations that the yolk mass had been used up by over a third of the larvae collected in the last samples taken at the end of September. Previous research at Signy Island showed that levels of benthic chlorophyll in surface sediments at this site increase in October and November, suggesting there is an increasing food supply for newly metamorphosed juveniles (Peck *et al.*, 2000), which also supports the settlement timing hypothesis (Todd & Doyle, 1981; Bowden *et al.*, 2009). Other explanations could include that currents or water movement moved them out of the bay or that they ran out of resources and died. It is unlikely that they were removed by currents because sea ice persisted beyond the time when they disappeared, and Factory Cove is protected from major currents because of its shape and relatively shallow depth. It is also unlikely that they died due to running out of energy stores (yolk) because more than half still had yolk stores at the end of September, and it is very unlikely none would have survived the five days to the next sampling. The most likely explanation is that they settled but died soon after settlement. The vast majority of pelagic larvae die due to predation, and the largest impact is from suspension feeders (Pechenik, 1999; Pechenik & Levine, 2007). However, *A. eightsii* larvae were present in the water column throughout winter when the activity of suspension feeders is low (Morley *et al.*, 2016; Clarke & Peat, 2022), and there was not a noticeable reduction in numbers of larvae when sampling across the winter. A sudden removal of larvae suggests settlement. Previous research has shown that high densities of conspecifics can inhibit recruitment of juveniles by grazing or smothering in gastropods (Peck & Culley, 1990) or by predation by suspension feeding species (David *et al.*, 1997; Pechenik & Levine, 2007).

The time taken to develop to the various stages reported here of 189 h to trochophore and around 250 h to reach early veliger are in line with previous studies on Antarctic bivalve molluscs, and much slower than temperate or tropical species (Fig. 6), where data for species living around 0 °C ranges from 175 h to over 1,000 h, whereas temperate and tropical species require 8–84 h. One Antarctic species, *Lissarca miliaris* (Richardson, 1977), took over 100 h to reach trochophore stage, but at –1 °C, this is the coldest recorded temperature for bivalve mollusc development. It suggests that below 0 °C temperature has a very strong effect on development rates, as also seen in some gastropods that require over 8 years to develop from fertilised eggs in broods to hatched juveniles when development occurs at temperatures around or below –1 °C (Moran *et al.*, 2019). Development rate data have been analysed in the past using Arrhenius plots that are used widely to assess the effect of temperature on biological systems (Clarke, 2017; Peck, 2018). The Arrhenius plot is one of the logarithm of the development rate (1/time) against inverse absolute temperature. When Arrhenius data are plotted for development rates of temperate and tropical bivalve molluscs, a strong significant relationship is obtained (Fig. 7). All the data for polar species living near or below 0 °C are all below the relationship for temperate and tropical species, and their development rate is significantly slower than would be expected for the predicted effect of low temperature. Similar outcomes have been found for development in brooding gastropod molluscs and for growth in echinoderms (Peck, 2018), and it is likely that this slowing beyond normal temperature effects is a general phenomenon for growth and early development.

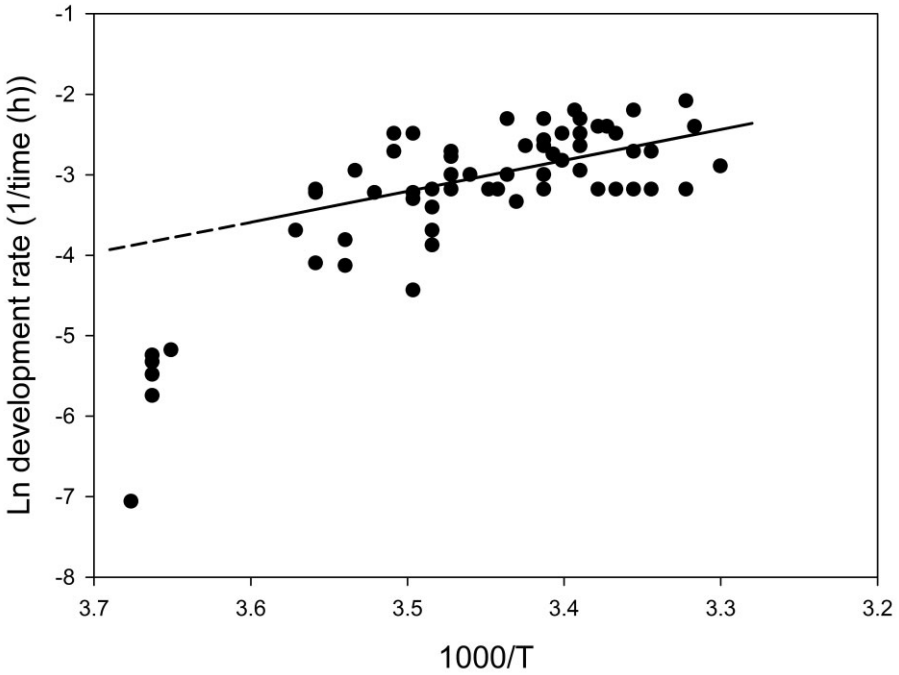

Figure 7. Arrhenius plot of development rates of free-spawning bivalve molluscs from tropical to polar latitudes. Line shown is the relationship for temperate and tropical species living between 5 and 30 °C (Ln development rate = 9.94–3.749(1/T), where development rate = 1/time to trochophore (h) and T = absolute temperature. The dashed line shows the extension of this relationship to polar temperatures. Data for species living at polar latitudes are significantly below the Arrhenius line (paired *t*-test comparing predicted line values with observed polar development rates: $t = 6.80$, $n = 6$, $P = 0.001$). Rates for polar species are 4–22 times slower than the Arrhenius prediction from rates for temperate and tropical species. Updated from Peck *et al.* (2007).

An explanation is that processes associated with freezing, aggregation of water molecules, increased viscosity and processes entrained to resist them, such as increased osmolyte concentrations in cells, likely impede protein folding and protein stability with a strong impact on growth and development (Peck, 2016).

CONCLUSIONS

Aequiyoldia eightsii was observed spawning over two seasons at Signy Island, South Orkney Islands, and in each year, it spawned in the last week of May, in what is one of the first field-based studies of reproduction in an Antarctic marine invertebrate to cover the whole period from spawning to settlement. In 1990, veliger larvae hatched 14–15 days later. They remained in the water column until the end of September, 108–114 days later when they likely settled, but were most likely consumed by the dense infauna at the collection site. In average years over the last century, sea ice broke up around the time or soon after the time that *Aequiyoldia eightsii* larvae settled, enhancing productivity on the seabed for newly settled juveniles. Long-term reductions in sea ice could have large impacts on the timing of reproduction in this species, and in other species with winter spawning and embryo/larval development. The development rate of *A. eightsii* embryos was in line with previous studies showing a substantial slowing at temperatures near or below 0 °C to values significantly lower than would be predicted by Arrhenius considerations. This indicates another factor than just the direct effect of temperature on biological processes becomes entrained at near freezing temperatures. The likely candidates are cytoplasm viscosity, water molecule attraction and aggregation and biological processes to alleviate freezing stresses, such as increased concentrations of osmolytes and the synthesis of molecules to increase cytoplasm fluidity or reduce the likelihood of the formation of ice crystals.

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CONFLICT OF INTEREST

There are no conflicts of interest.

DATA AVAILABILITY

The data for this paper are deposited with the Polar Data Centre: https://doi.org/10.5285/2790409c-e8e3-40a9-a189-792c3c853f5b.

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