

Growth and longevity of the Antarctic scallop *Adamussium colbecki* under annual and multiannual sea ice

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Abstract: Ecosystem engineers such as the Antarctic scallop (*Adamussium colbecki*) shape marine communities. Thus, changes to their lifespan and growth could have far-reaching effects on other organisms. Sea ice is critical to polar marine ecosystem function, attenuating light and thereby affecting nutrient availability. Sea ice could therefore impact longevity and growth in polar bivalves unless temperature is the overriding factor. Here, we compare the longevity and growth of *A. colbecki* from two Antarctic sites: Explorers Cove and Bay of Sails, which differ by sea-ice cover, but share similar seawater temperatures, the coldest on Earth (−1.97°C). We hypothesize that scallops from the multiannual sea-ice site will have slower growth and greater longevity. We found maximum ages to be similar at both sites (18–19 years). Growth was slower, with higher inter-individual variability, under multiannual sea ice than under annual sea ice, which we attribute to patchier nutrient availability under multiannual sea ice. Contrary to expectations, *A. colbecki* growth, but not longevity, is affected by sea-ice duration when temperatures are comparable. Recent dramatic reductions in Antarctic sea ice and predicted temperature increases may irrevocably alter the life histories of this ecosystem engineer and other polar organisms.

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Introduction

Ecosystem engineers, such as epibenthic bivalves (e.g. oysters, mussels and scallops), not only support fisheries and enhance water clarity, but also increase habitat complexity, leading to increased biotic diversity (Gutiérrez *et al.* 2003). Environmental perturbations and climate change alter the growth of ecosystem engineers (e.g. Menge *et al.* 2008), which can cause cascading effects through biotic communities (Wild *et al.* 2013). The response of polar ecosystem engineers to changing environments remains unclear, as most studies have focused on temperate and tropical regions. Polar regions are particularly vulnerable to the effects of climate change (Turner *et al.* 2014), and recent studies show strong shifts in community composition in response to changing ice dynamics (Dayton *et al.* 2019, Kim *et al.* 2019); therefore, additional understanding of the growth and lifespan of these vital organisms is critical to predicting their response, and thus the response of polar ecosystems, to future environmental change.

The Antarctic scallop (*Adamussium colbecki*) helps structure coastal Antarctic ecosystems. Their shells are often the only hard substrate in soft-sediment

environments, hosting a diverse array of biotic communities and providing major contributions of calcium carbonate biomass to the Antarctic regions where *A. colbecki* occurs (Cummings *et al.* 2006, Cerrano *et al.* 2009, Hancock *et al.* 2015). Circumpolar in distribution and locally abundant (sometimes reaching densities of over 90 individuals m^{−2}), *A. colbecki* also plays an integral role in pelagic-benthic nutrient coupling by filter feeding, bio-depositing and re-suspending organic-rich detritus when phytoplankton production is insufficient to generate nutrients (Stockton 1984, Cattaneo-Vietti *et al.* 1997, Chiantore *et al.* 1998, Heilmayer *et al.* 2003, Schiaparelli & Linse 2006, Norkko *et al.* 2007).

Despite its ecological importance, the maximum lifespan of *A. colbecki* is not well constrained. Maximum lifespan estimates range from 6 years to over a century (Ralph & Maxwell 1977, Berkman 1990, Heilmayer *et al.* 2003). In general, high-latitude bivalves have slower growth and live longer than temperate bivalves. Nevertheless, a century-long lifespan would make *A. colbecki* the longest-lived scallop by far. Furthermore, the highest growth estimates (*K*) derived from von Bertalanffy growth models (VBGMs) for this

species are nearly triple the lowest growth estimates (Berkman 1990, Chiantore *et al.* 2003, Heilmayer *et al.* 2003, Schiaparelli & Aliani 2019). Variation in estimates of lifespan and growth could result from a variety of factors, such as differences in age determination methods, environment (water temperature, primary production related to sea-ice conditions) and latitude (Stockton 1984, Heilmayer *et al.* 2003, Hancock *et al.* 2015).

Sea ice is critical in structuring polar ecosystems (Eicken 1992, Clark *et al.* 2015), and bivalve growth reflects changes in sea-ice extent and duration in the Arctic (Sejr *et al.* 2009). The type of sea ice in an area (annual or multiannual) has important implications for primary production and therefore nutrient availability for Antarctic benthic organisms. Annual sea ice is thinner than multiannual sea ice, allowing more light penetration into the water column that facilitates phytoplankton blooms under the ice (Arrigo *et al.* 2012). Break out of annual sea ice also allows yet more light to penetrate the water column, further increasing primary productivity (Dayton 1990, Clark *et al.* 2015), whereas multiannual sea ice dampens productivity (Norkko *et al.* 2007, Clark *et al.* 2015). Additionally, primary productivity of sea-ice algae is higher under annual sea ice than under multiannual sea ice in Antarctica (Arrigo *et al.* 1997). *Adamussium colbecki* populations consume more detritus and less phytoplankton at sites with multiannual sea ice and more phytoplankton at annual sea-ice sites (Norkko *et al.* 2007). Nutrient limitation and low temperatures reduce metabolism and are thought to drive increased longevity and decreased growth rates in high-latitude bivalves (Moss *et al.* 2016), and caloric restriction, specifically, increases longevity across a wide range of animals (Fontana *et al.* 2010). Thus, *A. colbecki* living under multiannual sea ice may be longer lived and slower growing than their counterparts under annual sea ice when seawater temperatures are similar.

Our study compares the growth and longevity of *A. colbecki* from two sites located within western McMurdo Sound, Antarctica, which vary in sea-ice duration but not seawater temperature. We postulate that scallops from the multiannual sea-ice site will have a longer maximum lifespan and slower growth than scallops from the annual sea-ice site. However, if growth and lifespan estimates are similar at both sites, then some other environmental variable (i.e. temperature; Menge *et al.* 2008) must be the overriding factor affecting their growth and, ultimately, their lifespan. Additionally, we compared our age estimates with results from previous studies that used alternative age estimates for *A. colbecki* to determine whether the age estimation method also influences lifespan estimates.

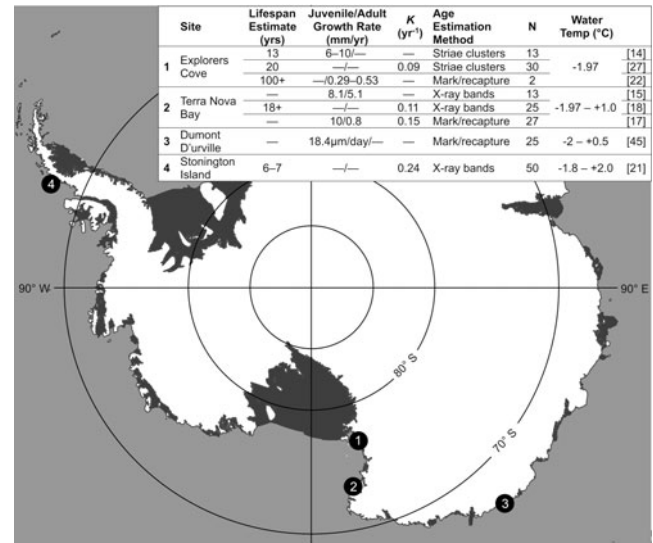


Fig. 1. Growth and lifespan estimates for *Adamussium colbecki* in Antarctica. Previous studies of *A. colbecki* longevity and growth from four Antarctic sites (Explorers Cove, Terra Nova Bay, Dumont d'Urville Station and Stonington Island) resulted in a range of lifespan and growth estimates. Study sites are indicated with numbered circles; numbers correspond to results in the table inset; N refers to sample size; water temperatures are from Stockton (1984), Heilmayer & Brey (2003), Lartaud *et al.* (2010), Hancock *et al.* (2015) and Cziko (personal communication 2018).

Methods

Background: longevity and growth in *A. colbecki*

Adamussium colbecki is endemic to the Southern Ocean, and its distribution is primarily restricted to coastal Antarctica (Schiaparelli & Linse 2006). Sites where its growth and lifespan were examined span ~12 degrees of latitude within a seawater temperature range of ~4°C (Fig. 1). Nevertheless, growth and lifespan estimates have varied widely for this species (Ralph & Maxwell 1977, Stockton 1984, Berkman 1990, Heilmayer *et al.* 2003, Berkman *et al.* 2004), which is possibly attributable to latitudinal differences among populations, the use of various methods to analyse growth and longevity in *A. colbecki* or other environmental factors not considered here (e.g. differences in pH, salinity, carbonate concentration, etc.).

Estimates of *A. colbecki* growth and lifespan were previously made at three sites: Explorers Cove (EC) at the southern end of western McMurdo Sound; Stonington Island, located off the west coast of the Antarctic Peninsula; and Terra Nova Bay, a polynya at the northern end of western McMurdo Sound (Fig. 1). Additionally, juvenile summer growth rates were measured at Dumont d'Urville Station, though lifespan was not estimated. Explorers Cove, the highest-latitude

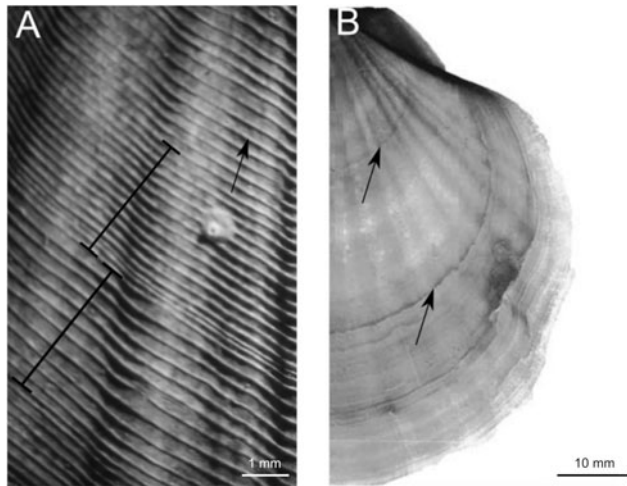


Fig. 2. Age estimation in *Adamussium colbecki*. Striae (small raised co-marginal ridges on valve surfaces) and X-ray bands are used for age estimation in *A. colbecki*. **a.** Grouped striae: 1 year is thought to represent a group of widely spaced striae coupled with a group of narrowly spaced striae (Stockton 1984, Berkman 1990). Black brackets span one widely spaced group and also one narrowly spaced group; a single stria is indicated by the arrow. **b.** X-ray bands: bands visible in X-ray are used as yearly markers (Ralph & Maxwell 1977, Cattaneo-Vietti *et al.* 1997, Heilmayer *et al.* 2003). Arrows point to X-ray bands.

and coldest site, maintains temperatures near the freezing point of seawater (-1.97°C), and *A. colbecki* at that locality have the slowest growth and greatest lifespan estimates (Brody growth constant, $K = 0.09 \text{ yr}^{-1}$; 100+ yr lifespan; Berkman 1990, Berkman *et al.* 2004). Stonington Island, the lowest-latitude and warmest site, had the second highest growth estimate and the shortest lifespan ($K = 0.24 \text{ yr}^{-1}$; 6–7 yr lifespan; Ralph & Maxwell 1977). Lastly, Terra Nova Bay is intermediate between EC and Stonington Island in both latitude and temperature, as well as growth and lifespan estimates ($K = 0.11\text{--}0.26 \text{ yr}^{-1}$; 18+ yr lifespan; Chiantore *et al.* 2003, Heilmayer *et al.* 2003, Schiaparelli & Aliani 2019). At all of the sites, *A. colbecki* growth slows through ontogeny, but multiple authors have remarked upon the high inter-individual variability in growth rates (Chiantore *et al.* 2003, Lartaud *et al.* 2010, Trevisiol *et al.* 2013).

Researchers have used two different valve features to analyse growth and lifespan, which may contribute to the disparate longevity and growth estimates. Small sub-annual bands (striae; Fig. 2a) were used either individually or in groups to analyse growth at EC. At that site, individual striae were counted and growth rates ranging from 0.29 to 0.53 mm yr^{-1} were estimated on recaptured scallops, leading the authors to conclude that the largest known *A. colbecki* (108 mm) could be over a century old (Berkman *et al.* 2004). Other studies, using

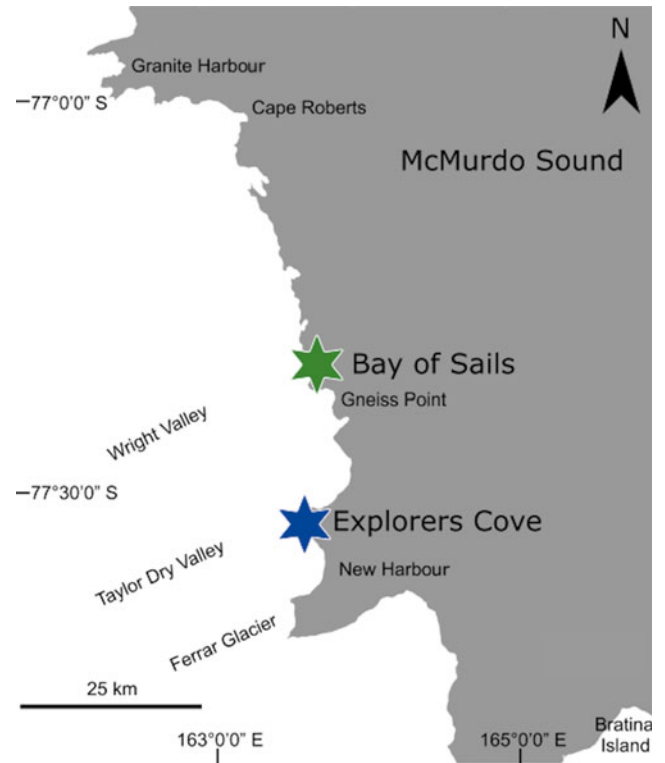


Fig. 3. Study sites of Explorers Cove and Bay of Sails, western McMurdo Sound, Antarctica. Explorers Cove ($77^{\circ}34.259'\text{S}$, $163^{\circ}30.699'\text{E}$) is a marine embayment at the mouth of Taylor Dry Valley and is $\sim 25 \text{ km}$ south of Bay of Sails ($77^{\circ}21.911'\text{S}$, $163^{\circ}32.594'\text{E}$). At Bay of Sails, sea ice melts annually, whereas sea ice at Explorers Cove persists for multiple years.

grouped striae, suggest that *A. colbecki* lives for 13–20 years at EC (Stockton 1984, Berkman 1990). Rather than using striae, bands visible under X-ray (Fig. 2b) were used for *A. colbecki* from Stonington Island and Terra Nova Bay. Using X-ray bands, *A. colbecki*'s lifespan could be 6–18+ years (Ralph & Maxwell 1977, Heilmayer *et al.* 2003, Trevisiol *et al.* 2013, Schiaparelli & Aliani 2019). The disparity in growth and lifespan estimates for *A. colbecki* necessitates a comparison of estimates from various sites using a consistent method.

Study site and collection

Adult scallops were haphazardly collected live by divers in November 2008 from water depths between ~ 9 and 18 m from areas totalling $\sim 300 \text{ m}^2$ from two sites in western McMurdo Sound, Ross Sea, Antarctica (Fig. 3). The sites were chosen based on similarity in water temperature (-1.97°C), proximity to each other and differences in sea-ice persistence. The lower valves of 37 scallops collected from EC and 19 collected from Bay of Sails (BOS) were used in this study. Scallops from EC were slightly smaller than scallops from BOS (EC mean

valve height = 78.7 mm, 95% confidence interval (CI): 76.3–81.0 mm; BOS mean valve height = 80.7, 95% CI: 76.9–84.2 mm).

Both EC and BOS are characterized by gently sloping topography and negligible water currents except for tidal flow ranging from ~ 1.0 to 2.6 cm s^{-1} (Barry & Dayton 1988, Hancock *et al.* 2015). Both sites are considered oligotrophic: organic carbon and diatom fluxes are two orders of magnitude lower than in eastern McMurdo Sound due to current flow under the Ross Ice Shelf (Leventer & Dunbar 1987).

Explorers Cove is an embayment located at the mouth of the Taylor Valley and maintains multiannual to decadal sea-ice cover. Sea ice broke out partially in 1999 and more extensively in 2002, but has otherwise remained intact since 1993. Sea ice at EC during the 1990–2011 field seasons was typically multiyear and ~ 3.25 – 4.00 m thick (Bowser, personal observations 1990–2011). Sediment at EC is composed of polymictic fine silty sands with a modal grain size of 125 – $300 \mu\text{m}$ (Radford *et al.* 2014). Additionally, an ice wall along the shoreline at $\sim 5 \text{ m}$ depth creates a moat containing nutrient-rich brackish water that enters EC periodically (during spring high tides) and supplies nutrients to areas within 100 – 200 m (Dayton *et al.* 2019). Scallops collected for this study were found within the area that would be influenced by the nutrients from the ice wall.

Bay of Sails is located $\sim 25 \text{ km}$ north of EC, offshore of Wilson Piedmont Glacier. Sea ice breaks out annually at BOS and iceberg disturbance is probably higher at BOS than at EC (Hancock *et al.* 2015). Sediment at BOS is comprised of polymictic very fine sands with a modal grain size of 63 – $125 \mu\text{m}$ (Radford *et al.* 2014).

Annuli identification and growth increment measurement

We used annual bands visible on shell surfaces (annuli) to compare growth and lifespan at EC and BOS (after Merrill *et al.* 1966) for three reasons. First, though X-ray bands in *A. colbecki* valves have been validated as annual using $\delta^{18}\text{O}$ (Heilmayer *et al.* 2003), Heilmayer *et al.* (2003) also identified annuli on valve surfaces and found $\sim 90\%$ agreement between the numbers of X-ray bands and annuli per valve. Therefore, counts of X-ray bands and annuli should result in comparable lifespan estimates for *A. colbecki*. Second, we had difficulties interpreting X-ray bands in *A. colbecki*'s thin shells, difficulties also encountered by a previous author (Stockton, 1984). We found annual X-ray bands were impossible to distinguish from other irregularities in growth that produced similar rings, possibly shock rings (Merrill *et al.* 1966). Third, annuli are commonly employed to age scallops in fisheries studies, making results from this method comparable to other scallop research.

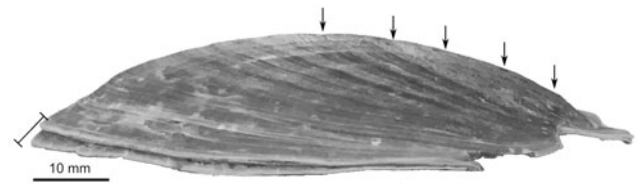


Fig. 4. Annuli identification on *Adamussium colbecki* valves. Annuli (indicated by arrows) appear as whitish rings in concave depressions against the brown, convex shell surface. Shingled annuli representing late adult growth are indicated by brackets.

Annuli were recognized by changes in valve colour and curvature. These annuli represent annual slowing or cessation in growth (Merrill *et al.* 1966). We found that *A. colbecki* had two distinct annuli types (Fig. 4). The first type of annuli appear as whitish rings in slight concave depressions against the brown surface colour of the shell, which we interpret as slower growth, but not growth cessation. The second type of annuli are still whitish rings, but also have a shingled appearance and occur during late adult growth (near valve margins). We interpret the second annuli type as growth cessation; the shingled appearance results from new growth beginning under, then growing past, the previous shell margin.

The age of each valve was determined by counting discernible annuli. Median ages and 95% CIs for each site were calculated using bootstrap resampling and compared to determine whether sea-ice duration affected age.

The distance from the umbo to each annulus along the central axis of each valve was measured using electronic callipers (accuracy: $\pm 0.01 \text{ mm}$) yielding height-at-age measurements. Yearly growth increments (yearly growth rates) were calculated by subtracting the height at age t from the height at age $t + 1$.

Shell height-at-age measurements were also used to model *A. colbecki* growth using the VBGM. We used the typical von Bertalanffy growth equation in Eq. (1):

$$L_t = L_\infty(1 - e^{-K(t - t_0)}) \quad (1)$$

where L_t is the shell height at time t , L_∞ is the asymptotic average height (the theoretical maximum height of the average individual in a population and the asymptote that the curve approaches), the Brody growth constant (K) describes how quickly valve height approaches L_∞ and t_0 represents the time at which the valve would have a height of zero. Curves were fitted to height-at-age data using non-linear least square regression (R Core Team 2017, <https://github.com/droglenc/FSA>).

The VBGM characterizes the average growth at each site and the typical VBGM equation is commonly used in *A. colbecki* studies (Ralph & Maxwell 1977, Berkman

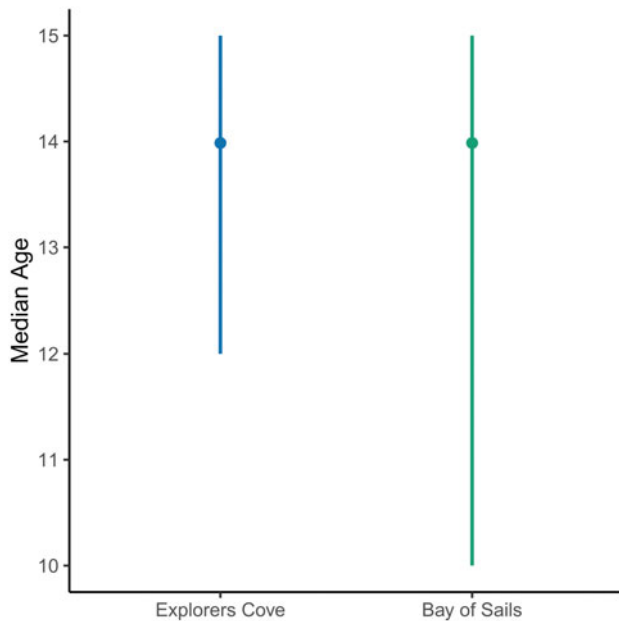


Fig. 5. Median valve ages by site. Points indicate median ages; lines delineate 95% confidence intervals on the medians.

1990, Chiantore *et al.* 2003, but see Heilmayer *et al.* 2003, Schiaparelli & Aliani 2019). We therefore use the typical VBGM to compare our results to previous work. We fit VBGM curves to the height-at-age data for EC and BOS valves to compare average growth.

The similarity of the VBGM curves fitted to the EC and BOS height-at-age data was compared with maximum likelihood methods (Nelson 2017). First, four hypothetical curves were fitted to the EC and BOS data. Three of the hypothetical curves have identical values for a single VBGM parameter (K , L_{∞} , t_0), positing that EC and BOS share a VBGM parameter in common. The fourth hypothetical curve has equal values for all three VBGM parameters, in essence positing that the growth at EC and BOS is indistinguishable. Second, the residual sum of squares is then calculated for the fit of all four hypothetical curves and for the actual curves fitted to the height-at-age data for each site. The curve, whether hypothetical or actual, with the smallest residual sum of squares is said to have the best fit, and support for each model was represented using the Akaike information criterion (ΔAIC), such that the lowest ΔAIC indicates the curve that best fits the data (Nelson 2017, R Core Team 2017).

We analysed individual variation in growth (K and L_{∞}) using Ford-Walford plots for each valve. Ford-Walford plots are used to model individual growth when there is variability in K and L_{∞} within a population (Hart & Chute 2018). In a Ford-Walford plot, height at age t is plotted against height at $t + 1$, and both K and L_{∞} can be calculated from a linear

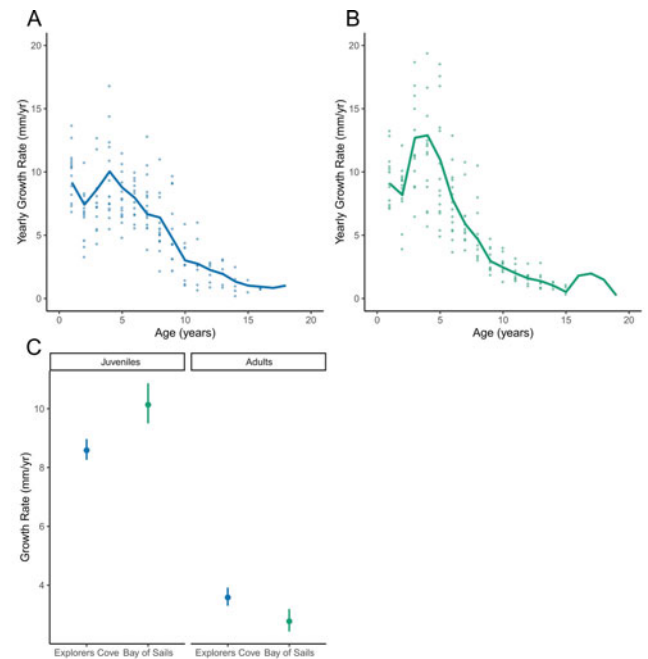


Fig. 6. Growth rates by site. **a.** Mean yearly growth rates at Explorers Cove. **b.** Mean yearly growth rates at Bay of Sails. Open circles indicate the yearly growth rates for each individual and the line indicates the mean yearly growth rate. **c.** Mean juvenile and adult growth rates by site. Juveniles include valve growth rates for ages ≤ 6 years. Adult growth rates include growth rates for ages > 6 years. Points indicate mean growth rates; lines delineate 95% confidence intervals on the means.

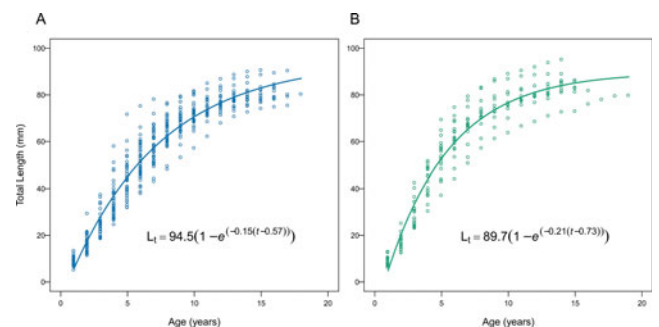


Fig. 7. von Bertalanffy growth models for *Adamussium colbecki* by site. **a.** Explorers Cove; **b.** Bay of Sails. Circles indicate individual height-at-age data points and solid lines indicate the von Bertalanffy growth models.

regression using Eqs (2) and (3):

$$K = -\ln \beta \quad (2)$$

$$L_{\infty} = \alpha / 1 - \beta \quad (3)$$

where β is the slope and α is the y -intercept of the Ford-Walford linear regression (Walford 1946). To alleviate

Table I. Likelihood ratio tests of von Bertalanffy models for *Adamussium colbecki* by site.

Hypothesis	AIC	Δ AIC
No parameters are equal	189.37	1.14
$L_{\infty\text{VBGM}} = L_{\infty\text{FW}}$	191.62	3.39
$K_{\text{VBGM}} = K_{\text{FW}}$	201.62	13.39
$t_0 = t_0$	188.23	0
All parameters are equal	208.82	20.59

Bold Δ AIC values indicate the models with the strongest support (lowest Δ AIC).

AIC = Akaike information criterion.

ambiguity in reporting K and L_{∞} derived from two different methods, K_{VBGM} and $L_{\infty\text{VBGM}}$ will denote results from VBGM models and K_{FW} and $L_{\infty\text{FW}}$ will denote results from Ford-Walford plots. The means and 95% CIs of K_{FW} and $L_{\infty\text{FW}}$ for scallops from each site were calculated using bootstrap resampling. The coefficients of variation of K_{FW} and $L_{\infty\text{FW}}$ were calculated to evaluate the amount of individual variability for each site. Valves ≤ 70 mm in height were excluded from individual Ford-Walford analyses; therefore, 31 valves from EC and 14 valves from BOS were included.

Results

Lifespan estimates

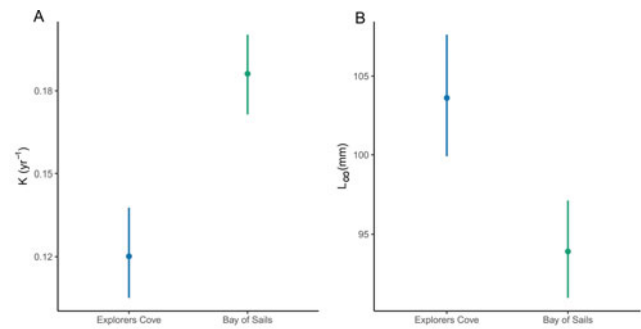
Adult *A. colbecki* from EC and BOS had identical median ages of 14 years (Fig. 5), though BOS scallops had a greater maximum age (19 years) than EC scallops (18 years).

Yearly growth rate estimates for *A. colbecki* at EC and BOS

As with other bivalves, *A. colbecki* yearly growth is fastest in juveniles and slows throughout ontogeny. At both sites, mean growth rates were fastest at 4 years of age and declined thereafter (Fig. 6a & b). Juvenile (≤ 6 years of age) mean yearly growth rate was slower at EC (8.6 mm yr⁻¹) than at BOS (10.2 mm yr⁻¹), but adult growth was faster at EC (3.6 mm yr⁻¹) than at BOS (2.8 mm yr⁻¹) (Fig. 6c).

von Bertalanffy growth models

Growth parameters calculated from fitted VBGM equations indicated that EC scallops have slower growth rates and greater maximum heights than BOS scallops (EC $K_{\text{VBGM}} = 0.15$; BOS $K_{\text{VBGM}} = 0.21$; EC $L_{\infty\text{VBGM}} = 94.5$ mm; BOS $L_{\infty\text{VBGM}} = 89.7$) (Fig. 7). Comparisons of VBGMs using likelihood methods suggested growth at EC and BOS is indeed dissimilar. Of the four hypothetical VBGMs, the model that posited EC and BOS share an identical t_0 best fit the data, but the

**Fig. 8.** Mean K and L_{∞} derived from Ford-Walford plots for individual valves. **a.** K comparison by site. **b.** L_{∞} comparison by site. Points indicate mean K and L_{∞} values; lines delineate 95% confidence intervals on the means.

model positing that no parameters were equal between the sites also had strong support (Table I). The hypothetical model with the weakest support posited that $L_{\infty\text{VBGM}}$ or K_{VBGM} are equal for EC and BOS (Table I).

Among individual valves, K_{FW} and $L_{\infty\text{FW}}$ were both more variable at EC than BOS, suggesting that there may be more inter-individual variability in growth at EC than BOS. The coefficient of variation for K_{FW} was higher at EC (0.32) than at BOS (0.13). Similarly, the coefficient of variation for $L_{\infty\text{FW}}$ was higher at EC (0.11) than at BOS (0.07). Furthermore, the range of K_{FW} was larger at EC (0.07–0.23 yr⁻¹) than at BOS (0.14–0.22 yr⁻¹), and the range of $L_{\infty\text{FW}}$ was also higher at EC (86–135 mm) than at BOS (86–106 mm). Finally, the mean of individual K_{FW} values was lower and the mean of individual $L_{\infty\text{FW}}$ values was higher at EC than at BOS, supporting the results from the fitted von Bertalanffy equations indicating that EC scallops grow more slowly than BOS scallops (Fig. 8).

Discussion

Effects of sea-ice persistence on lifespan

Sea-ice condition appears to have no effect on *A. colbecki* lifespan; the median age of individuals living under primarily multiannual sea ice (EC) was indistinguishable from that of those living under annual sea ice (BOS). If sea-ice condition is irrelevant, some other factor must control lifespan. The comparable water temperatures at BOS and EC are consistent with longevity being controlled by temperature.

Theoretical maximum lifespan

We found no direct evidence of extreme longevity in *A. colbecki*. Instead, we found < 20 year maximum ages at both western McMurdo sites of EC and BOS. Our maximum ages agree well with the 18+ year longevity

estimate from Terra Nova Bay (Heilmayer *et al.* 2003), but are considerably lower than the highest estimate from EC. The century-long age estimation for *A. colbecki* stems from measuring growth rates ($0.24\text{--}0.53\text{ mm yr}^{-1}$) of marked and recaptured individuals at EC, then extrapolating the rates to the largest known *A. colbecki* (108 mm; Berkman 1990, Berkman *et al.* 2004). It should be noted that sea ice at EC was typically multiyear prior to the collection of these two scallops in 1986 (Bowser, personal communication 2018), but extrapolating from these very low growth rates may overestimate the *A. colbecki* maximum lifespan. For instance, if our average scallop (~ 14 years old, ~ 80 mm shell height) grew at 0.53 mm yr^{-1} for 76 years, it would be over 125 mm (> 15 mm larger than the largest known *A. colbecki*) when it reached 100 years old. On the other hand, if we assume the oldest scallop in our study (80 mm at 19 years) grew at its final yearly growth rate (0.24 mm yr^{-1}) for 80 years, it would be just over 100 mm by 100 years of age. It is therefore theoretically possible to have a century-old *A. colbecki*, but this is improbable.

Nevertheless, maximum ages from our study should not be considered an upper limit on *A. colbecki* maximum lifespan for two reasons. First, our largest individual was ~ 12 mm smaller than the largest recorded *A. colbecki*, and this species can sustain very low growth rates over multiple years (Berkman *et al.* 2004, this study). Second, the maximum bivalve lifespan typically increases with latitude (Moss *et al.* 2016), and some species of lower-latitude scallops have higher recorded maximum ages, such as *Chlamys islandica* (35 years from Svalbard; Fevolden 1992). A multi-decadal (≥ 20 year) lifespan for *A. colbecki* is therefore probable, though we did not observe direct evidence for this.

Age estimation methods compared

Age estimation methods appear to strongly affect lifespan estimates for *A. colbecki*. Maximum ages from our study (18–19 years) were more similar to the maximum age from Terra Nova Bay based on X-ray bands (18+ years; Heilmayer *et al.* 2003) than to maximum ages from striae-based EC studies (13–100+ years; Stockton 1984, Berkman 1990, Berkman *et al.* 2004). Moreover, lifespan estimates are more variable for striae methods: maximum lifespans estimated from EC scallops were 13, 20 or 100+ years (Stockton 1984, Berkman 1990, Berkman *et al.* 2004). In contrast, maximum lifespans based on X-ray bands produced estimates of 6 years from Stonington Island (Ralph & Maxwell 1977) and 18+ years from Terra Nova Bay (Heilmayer *et al.* 2003). Counting annuli provides a maximum age estimate of 19+ years (this study). The similarity between our age estimates and those from Terra Nova Bay suggests that discrepancies in age estimation methods might be

contributing to the wide range of lifespans reported for *A. colbecki*.

Annuli- or X-ray-based age estimation methods produce more consistent lifespan estimates than striae-based methods, possibly due to incorrect assumptions about the timing of striae formation in adults. *Adamussium colbecki* striae accrete approximately fortnightly in juveniles (Lartaud *et al.* 2010), but fortnightly striae formation probably does not continue through adulthood. For example, in a mark-recapture study at EC, one adult scallop was recaptured after 8 years and another adult was recaptured after 12 years, but they had accreted 19 and 105 striae, respectively (Berkman *et al.* 2004). Their results suggest that striae do not form at consistent time intervals in adults. Estimating age in *A. colbecki* using the grouped striae method implicitly assumes that striae form at consistent time intervals throughout both juvenile and adult growth. Theoretically, the grouped striae method would underestimate scallop ages if striae form at irregular time intervals. For example, the largest known *A. colbecki* (108 mm) was estimated to be 20 years old based on extrapolation from a VBGM for EC scallops whose ages were determined using the grouped striae method (Berkman 1990); in contrast, our 19 year-old individual was ~ 80 mm. Striae do not appear to be reliable for age estimation in adult *A. colbecki*, and therefore annuli or X-ray bands should be used.

Effects of sea-ice persistence and temperature on growth

Sea-ice duration affects *A. colbecki* growth rates and variability; growth (proxied by K_{VBGM} , K_{FW} and mean juvenile growth rates) is slower and more variable at EC than at BOS. Seawater temperature is comparable at EC and BOS; we therefore postulate that growth differences result from differences in nutrient availability. Sea ice is a critical factor controlling nutrient supply to benthic organisms. Specifically, *A. colbecki* is known to consume more re-suspended detritus under multiannual sea ice at EC where less phytoplankton is available and more phytoplankton at Terra Nova Bay, which has a long open-water period (Norkko *et al.* 2007). Furthermore, phytoplankton consumption by *A. colbecki* decreases with increasing sea-ice duration (Norkko *et al.* 2007). In laboratory experiments, *A. colbecki* metabolism was higher for individuals provided with summer-like nutrient quantities than for individuals provided with winter-like nutrient quantities, even though temperature was held relatively constant (Heilmayer & Brey 2003). Therefore, it is plausible that sea-ice-mediated dietary differences resulting in fewer and more episodic nutrients may explain the slower and more variable growth at EC, our multiannual sea ice site.

Higher individual variability in K_{FW} at EC reinforces our interpretation that overall slower growth at EC is caused by nutrient limitation related to persistent multiannual sea ice. K is negatively correlated with latitude in bivalves, a trend that is attributed to nutrient restriction (Moss *et al.* 2016). Higher individual variability in K_{FW} at the multiannual sea-ice site may result from episodic, unevenly distributed nutrient availability under multiannual sea ice than under annual sea ice. In an overall lower-nutrient environment with episodic and patchily distributed input of sea-ice algae and nutrient-rich waters from behind the ice wall, we posit that some individuals will acquire more nutrients and grow faster than others, resulting in more individual variability in growth. Conversely, annual sea ice break out should supply phytoplankton consistently to an entire population and reduce individual variability in K_{FW} , similarly to the results at BOS.

The slower adult growth rate in *A. colbecki* at BOS is reinforced by the higher K_{VBGM} value at BOS. Though K_{VBGM} is not a growth rate *per se*, it does describe how quickly the population approaches its theoretical maximum size ($L_{\infty VBGM}$). A higher K value indicates that a population reaches its maximum size faster than a population with a lower K value. If the BOS population approaches $L_{\infty VBGM}$ more quickly than the EC population, as indicated by its higher K_{VBGM} , then adult growth rates should be slower at BOS because the BOS scallops are slowing their growth as they approach their theoretical maximum size. Conversely, growth rates are higher at comparable adult ages at EC because the EC scallops included in this study are further from their theoretical maximum height. Based on the VBGM results, it is possible that EC scallops live longer than BOS scallops, but our directly aged samples did not corroborate this.

Despite generally slower growth at EC, yearly mean growth rates followed similar trajectories over ontogeny at both sites; mean yearly growth rate reached a maximum at year 4 and fell thereafter. Studies based on gonadal analysis and shell morphology from Terra Nova Bay placed *A. colbecki* sexual maturity at 6 or 7 years of age (Cattaneo-Vietti *et al.* 1997). Peak growth rates during year 4 suggest that scallops might start devoting energy to gonad development by as early as year 5 at EC and BOS, but studies of gonadal tissue are needed to confirm this observation.

The effects of temperature on *A. colbecki* growth rates are supported by both laboratory and *in situ* studies. When shell growth was monitored for 1 week in laboratory conditions, juvenile *A. colbecki* kept in 3°C water grew faster than juvenile *A. colbecki* kept at 0°C under the same light and food regimes (Heilmayer *et al.* 2005). Moreover, when compared to temperate scallops, *A. colbecki* metabolism is low but proportional to the

temperature and latitudinal context in which they live (Heilmayer & Brey 2003). Effects of temperature are also evident in growth over the entire lifetime of scallops, proxied by K . Based on previous reports, the shortest estimated lifespan and highest K occurred in *A. colbecki* living in the nearshore waters of Stonington Island, where summer water temperatures can reach 2°C (Ralph & Maxwell 1977). All other reports suggest that *A. colbecki* live longer and grow more slowly in the colder water around mainland Antarctica (Berkman 1990, Heilmayer *et al.* 2003). *Adamussium colbecki* also has a low tolerance for increased water temperature, further supporting temperature effects on growth. For example, laboratory experiments demonstrated that swimming ability in *A. colbecki* declines at water temperatures > 0°C; temperatures of ~4°C resulted in 50% mortality at 19 days (Peck *et al.* 2004). Explorers Cove and BOS maintain *A. colbecki* populations near the freezing point of seawater, and populations can be found as far north as the Antarctic Peninsula, where seawater reaches 2°C during summer.

A combined role for temperature and nutrients determining growth would not be unusual. Temperature and nutrients were implicated as factors that determine growth in other scallop species (e.g. Pilditch 1999). Additionally, a study comparing the strength of factors affecting the growth of the temperate ecosystem engineer *Mytilus* found that temperature accounted for 32.0% of growth variation and nutrients accounted for 12.5% (Menge *et al.* 2008). We posit that nutrient availability through sea-ice persistence affects *A. colbecki* growth, though temperature also plays a role.

Effects of growth estimation methods

Previously recorded *A. colbecki* growth rates for all juvenile growth overlap at EC, BOS and Terra Nova Bay, despite sea-ice, seasonal temperature and methodological differences (Stockton 1984, Cattaneo-Vietti *et al.* 1997, Chiantore *et al.* 2003, Trevisiol *et al.* 2013, Schiaparelli & Aliani 2019). Juvenile growth rates from this study fall within the ranges from these previous studies. In contrast, previously reported adult growth rates vary widely among EC, BOS and Terra Nova Bay, but the differences appear to be driven mainly by the ontogenetic ages of the adult scallops included in each study. Including only young individuals in studies will increase reported adult growth rates, while exclusively using older individuals will decrease them, because *A. colbecki* growth slows over its lifetime. We excluded neither old nor young adults from our calculations, and therefore adult growth rates from our study are higher than those previously reported from an EC study that included only older adults (Berkman *et al.* 2004) and lower than those previously reported from a Terra Nova Bay study that

included only younger adults (Chiantore *et al.* 2003, Trevisiol *et al.* 2013).

Estimates of K allow for more direct comparison among the sites, but VBGMs are modelled from size-at-age data, and size-at-age data depend upon the age determination method. Consequently, comparison among studies of the same species that use various age determination methods should be made carefully. Our K_{VBGM} results from BOS scallops were closer to reported K values from studies using X-ray bands, though the sites (Terra Nova Bay and Stonington Island) are seasonally warmer than EC and BOS (Ralph & Maxwell 1977, Chiantore *et al.* 2003, Schiaparelli & Aliani 2019), and our EC K_{VBGM} results were higher than the reported K values from an EC study (Berkman 1990) using the grouped striae method. The grouped striae method therefore appears to underestimate K compared to annual band methods (annuli or X-ray).

Conclusions

No evidence was found suggesting that sea-ice persistence controls *A. colbecki* lifespan, but growth was slower and more variable for scallops living under multiannual sea ice than for scallops living under annual sea ice. Large discrepancies in age estimates are probably the result of using various and incompatible age estimation methods for this species. Based on counting annuli, the maximum lifespan of *A. colbecki* from our sites is probably 19+ years and is in good agreement with estimates using X-ray bands from Terra Nova Bay. We recommend the use of either annuli or X-ray bands for age estimation in this species, although we found X-ray bands difficult to interpret. Counting groups of striae is a common method for ageing *A. colbecki* at EC, but it may lead to misestimates of lifespan and growth.

A comparison of the growth and lifespan of historical and modern populations on Stonington Island, where climate change-induced temperature increases are more pronounced, is warranted to predict *A. colbecki*'s future in a warmer Antarctica. Warmer water and reduced sea-ice duration would increase primary productivity but may also dramatically alter the life history of this Antarctic ecosystem engineer and the biotic communities that depend on it.

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Author contributions

KEC developed the concepts and approach used for data collection and analysis, performed the analyses and prepared the manuscript. SEW and SSB designed the field sampling and original concept and managed field operations and specimen collection. KEC, SEW, RM, ASC and MCL developed the approach used for scallop age determination. KEC, SEW, RM, ASC and SSB edited the manuscript.

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Details of data deposit

Data and code for analysis will be available at <http://dx.doi.org/10.17632/59h4dxwdzn.1>.

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