



Striae in the Antarctic scallop *Adamussium colbecki* provide environmental insights but not reliable age increments

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Abstract

Subannual growth increments in bivalves provide insight into past seasonal seawater conditions at high temporal resolution. The Antarctic scallop *Adamussium colbecki* (Smith 1902) accretes putatively fortnightly surficial growth lines (striae) and interstrial growth increments have the potential to archive sea ice variations. Cycles of paired groups of wide and narrow striae are sometimes used to determine ontogenetic age in these scallops, but previous quantitative work describing strial grouping and formation is limited to a few months of juvenile growth. Here, we analyze striae patterns in *A. colbecki* collected from two sites on western McMurdo Sound, Antarctica that differ by sea ice duration: Explorers Cove with multi-annual sea ice and Bay of Sails with annual sea ice. At both sites, visual analysis of striae groups and cycles (using the methods of previous authors) and wavelet analysis of interstrial increments suggest that striae groups are too variable to age *A. colbecki*. Only ~40% of striae groups and cycles conformed to expectations from annual cycles of fortnightly growth increments (~26 striae per cycle). Moreover, only one scallop from each study site displayed consistent periodicity at ~26 striae throughout juvenile growth in wavelet analysis. Though striae grouping was inconsistent, analysis of concurrent growth of juvenile scallops from Explorers Cove suggested strong environmental control on interstrial increment size and thus that strial increments are suitable for further analysis as sea ice proxies. Finally, the multi-annual sea ice site had smaller interstrial growth increments and less valve wear than the annual sea ice site, indicating overall slower growth and possibly lower metabolic activity.

Keywords *Adamussium colbecki* · Scallop · Antarctica · Sea ice · Growth increments · Wavelet analysis

Introduction

The Antarctic scallop *Adamussium colbecki* is a potentially important high-resolution proxy for seawater conditions in the Southern Ocean (Lartaud et al. 2010). Though patchy, the modern distribution of *A. colbecki* is circum-Antarctic (Schiaparelli and Linse 2006) and the genus *Adamussium* has a fossil record extending back to the Oligocene (Quaglio et al. 2010). Valves provide a hard substrate for encrusting organisms, thereby increasing local diversity (Berkman 1994; Cummings et al. 2006; Cerrano et al. 2009; Hancock

et al. 2015) and the living scallops play a vital role in benthic-pelagic nutrient coupling (Stockton 1984; Cattaneo-Vietti et al. 1997; Chiantore et al. 2000; Norkko et al. 2007). Furthermore, *A. colbecki* growth is affected by sea ice duration at the annual scale (Cronin et al. 2020), thus a more complete understanding of subannual growth patterns could make *A. colbecki* a powerful paleoenvironmental proxy for sea ice variability.

Adamussium colbecki form striae, small commarginal growth ridges on valve surfaces. Striae are common to several scallop species, and growth increments between adjacent striae (interstrial growth increments; ISIs) correspond with environmental and metabolic conditions (Chauvaud et al. 1998, 2005; Owen et al. 2002; Aguirre Velarde et al. 2015). Previous work suggests that patterns in ISI on *A. colbecki* valves indicate seasonality: Groups of widely spaced striae (putative faster summer growth) alternate with groups of narrowly spaced striae (putative slower winter growth) throughout ontogeny (Stockton 1984; Berkman 1990; Lartaud et al. 2010). Adjacent wide and narrow groups are

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thought to be yearly cycles (hereafter, striae cycles) and are used to ontogenetically age *A. colbecki* (Stockton 1984; Berkman 1990). The striae cycles contain $\sim 28 (\pm 2)$ striae (Lartaud et al. 2010). Moreover, mark-recapture evidence suggests that striae in *A. colbecki* form fortnightly and coincident with spring tides (Lartaud et al. 2010). If striae form approximately fortnightly and if the ISIs between adjacent striae vary seasonally, striae on *A. colbecki* valves could provide unparalleled temporal resolution for Antarctic paleoenvironmental investigations.

Fortnightly periodicity in striae formation may be unique among scallops. Daily periodicity is suggested for several species (Antoine 1978; Broom and Mason 1978; Helm and Malouf 1983; Chauvaud et al. 1998), although two-day periodicity is also recorded (Thébault et al. 2006). Though studies that establish the timing of striae formation usually only examine a truncated portion of juvenile growth (Johnson et al. 2000; Lartaud et al. 2010; Aguirre Velarde et al. 2015), the timing of striae formation can change throughout the year (Broom and Mason 1978; Gruffydd 1981; Joll 1988; Owen et al. 2002) or throughout ontogeny (Antoine 1978; Berkman et al. 2004).

Timing of striae formation and the number of striae in striae cycles remains poorly understood in *A. colbecki* except for a portion of juvenile growth during summer (Lartaud et al. 2010) and in late adulthood, where striae formation appears to be infrequent and irregular (Berkman et al. 2004). Despite irregularities, ISIs can still be used as a high-resolution sclerochronological tool when striae are well understood for a particular species (Chauvaud et al. 2005).

Our study tests whether striae on *A. colbecki* have consistent periodicity throughout juvenile growth (≤ 50 mm; Cattaneo-Vietti et al. 1997) and whether sea ice duration affects striae formation in this ecosystem engineer at two sites that have similar environmental conditions except that they differ in sea ice duration. We analyzed two aspects of striae growth patterns to determine if they are consistent with fortnightly formation. First, we determined the number of striae per summer and winter group as well as the yearly cycle among individuals. Second, we examined the periodicity in ISIs. We then assessed the similarity in ISI patterns among concurrent growth in juveniles to parse out whether ISI primarily reflects endogenous or environmental controls. Finally, we examined if sea ice duration affects striae formation.

Methods

Study sites and sample collection

Scallops were collected from two sites in western McMurdo Sound, Ross Sea, Antarctica: Explorers Cove (EC) and Bay of Sails (BOS) share similar, topography, currents, and water

temperature, but EC has fine silty sands with a modal grain size of 125–300 μm and BOS has coarser sediment with very fine sands and a modal grain size of 63–125 μm ; crucially, sea ice melts annually at BOS and persists for multiple years at EC (Fig. 1; Bernhard 1987; Barry and Dayton 1988; Bowser and Bernhard 1993; Thrush et al. 2010; Radford et al. 2014; Hancock et al. 2015). In 2008, 11 adult (> 70 -mm shell height) scallops were collected live from EC and seven adult scallops were collected live from BOS (> 70 -mm shell height). An additional five juveniles (four juveniles < 20 -mm shell height; one juvenile < 50 -mm shell height) were collected live after a recruitment event in 2016. Their contemporaneous growth can be compared to evaluate whether ISIs are predominantly controlled by the environment or individual biology during summer juvenile growth, when striae formation timing is known (\sim fortnightly; Lartaud et al. 2010).

Valves are predominantly calcite, but layers of aragonite are present in some valve areas, notably near the myostracum (Barrera et al. 1990; A. Pérez-Huerta pers. comm.). Based on studies of gonad development, *A. colbecki* reach

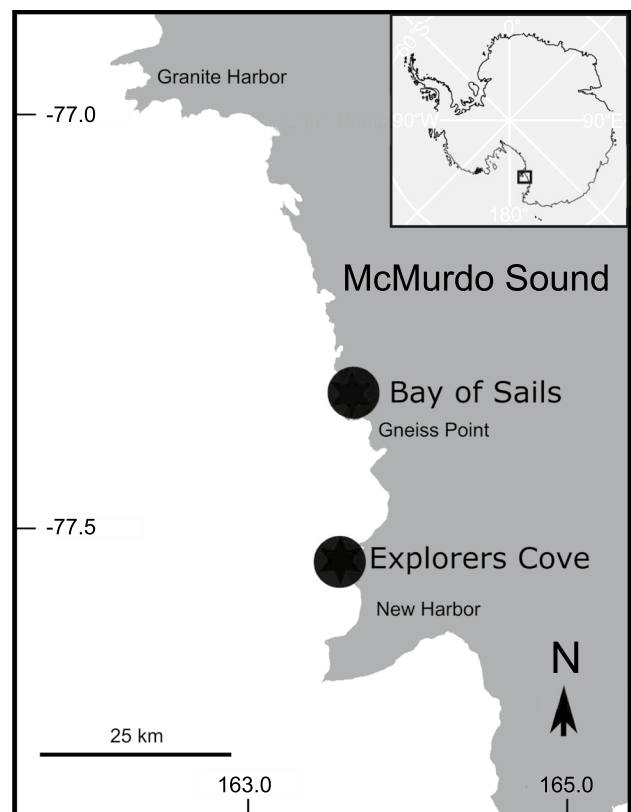


Fig. 1 Study Sites of Explorers Cove (EC) and Bay of Sails (BOS), western McMurdo Sound, Antarctica. EC ($77^{\circ}34.259'S$, $163^{\circ}30.699'E$) is a marine embayment in New Harbor ~ 25 km south of BOS ($77^{\circ}21.911'S$, $163^{\circ}32.594'E$). At BOS, sea ice melts annually, whereas sea ice at EC persists for multiple years

sexual maturity at 50–60 mm valve height (Cattaneo-Vietti et al. 1997). For this study, we defined juvenile growth conservatively, and ended our measurements at 50 mm valve height on the adult valves from EC and BOS. All valves collected in 2016 had < 50 mm valve height and are considered to be in juvenile growth.

Striae digitization

Only right (lower) valves were analyzed for this study. Right valves are less convex than left valves in *A. colbecki* which minimized distortion in digital measurement of photographs. Valves with the least amount of wear were used because lower valves are susceptible to wear from abrasion that can destroy striae. Only the juvenile portion of shell growth—between the umbo and 50-mm shell height (after Cattaneo-Vietti et al. 1997)—was analyzed on the adult scallops (Fig. 2). For the juveniles collected from EC in 2016, the entire right valve was analyzed.

Valves were digitally photographed under 25× magnification and the photos were stitched to create a continuous profile along the central growth axis. All subsequent data were collected from the photos. Each discernable stria was identified and the distance between adjacent striae (ISIs) was measured using ObjectJ in FIJI (Schindelin et al. 2012).



Fig. 2 Striae measurements. Striae on adult *Adamussium colbecki* valves from EC and BOS were counted and measured from the umbo to 50-mm shell height along the central axis, a conservative estimate of juvenile growth. Black line indicates 50 mm from the umbo

Striae group analysis

Groups of widely spaced or narrowly spaced striae were identified on each valve and adjacent wide and narrow groups were classified as yearly striae cycles (after Stockton 1984). Identified groups reflected meaningful differences in interstrial increment size, the mean ISI of each group was calculated and compared to the mean of each adjacent group using Student's *t* tests. Differences between ISI of all striae between BOS and EC were evaluated using means and 95% confidence intervals generated from bootstrap resampling. The number of striae within each wide or narrow striae group and within each yearly cycle were counted. The median number of striae per wide group, narrow group, and yearly cycle was evaluated using the maximum likelihood estimator of the Poisson rate parameter and their 95% confidence intervals. The median number of striae per striae group and cycle were compared between EC and BOS to assess the possible influence of sea ice duration on striae grouping. All statistical analyses were performed in R Statistical Software (R Core Team 2017).

Despite selecting for unworn valves, portions of some lower valves were abraded such that striae were obscured or absent along portions of the central axis. In these cases, the obscured section of the central axis was measured and the total obscured portion for each valve was calculated:

$$\frac{\text{Total abraded valve height}}{50 \text{ mm}} = \text{Worn fraction}$$

Differences between valves from BOS and EC in worn fraction were evaluated using means and 95% confidence intervals generated from bootstrap resampling. The worn portion of each valve is used here as a potential proxy for metabolic activity: higher worn fraction is assumed to indicate more valve movement against the sediment, whereas lower worn fraction is assumed to indicate more sedentary scallops.

Time series analysis of interstrial growth increments

Visual assignment of striae to wide or narrow groups and the identification of widening and narrowing patterns are somewhat subjective. We therefore used time series analysis to uncover patterns in ISIs that could be overlooked even by a careful observer. The time series analysis was used to assess the periodicity of ISI for consistency with yearly striae cycles based on fortnightly-forming striae. For this time series, we used wavelet analysis, which allows evaluation of important frequencies through time and accommodates non-stationary time series (Torrence and Compo 1988). Wavelet analysis permits assessment of any changes

in periodic behavior of interstrial increments throughout juvenile ontogeny. One continuous sequence of striae was analyzed for each valve: from the first visible striae after the umbo to either 50 mm valve height or to the first portion of the valve obscured by wear (including all identifiable striae grouped and ungrouped). Each adult valve had a continuous sequence of at least 48 striae. Wavelet analysis was performed using the R package WaveletComp1.1 (Roesch and Schmidbauer 2018).

Comparison of interstrial growth increments on EC juveniles

Striae increment measurements from the five 2016 EC juveniles were compared to each other to evaluate the suitability of striae measurements for environmental analysis. The adult valves cannot be compared to one another in this way because their juvenile portions grew during different years. Thus, a direct comparison of ISI sequences is only possible with the 2016 juveniles, which grew concurrently. Similar striae patterns among several individuals over a concurrent growth period provides evidence of an external or environmental control on ISI, making striae suitable for seasonal or environmental analysis. In contrast, different patterns in ISI among several individuals from the same location over the same time period suggests strong endogenous or biological control, making ISI unsuitable for environmental analysis.

Results

Striae as age indicators

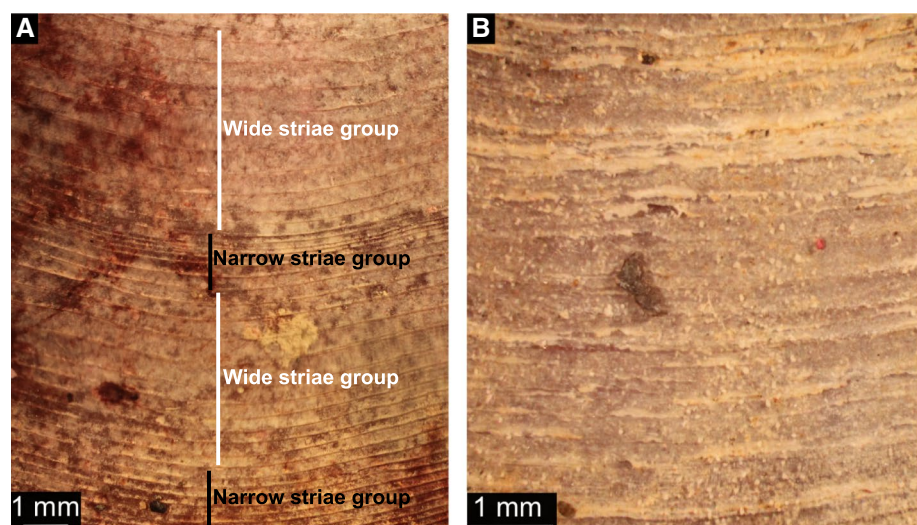
Striae groups and cycles

Alternating groups of wide and narrow striae (striae cycles) were obvious on all valves from both sites (Fig. 3a). Moreover, the groups that we visually defined were statistically distinct from one another and represented meaningful differences in ISI; 98% of adjacent striae groups had mean ISIs that were statistically significantly different than means of adjacent groups (Supplemental Information).

Beginning at the first striae after the umbo, at least two complete striae cycles were observed on the juvenile portion of all adult valves at both sites, but on some valves, some striae were either not in recognizable groups (ungrouped striae) or were affected by valve wear. Approximately 40% of the valves from both sites (EC: 45%: 5/11; BOS 42%: 3/7 valves) contained striae that could not be visually assigned to wide or narrow groups. Ungrouped striae had sequences of striae that did not meet the minimum requirements of three widely spaced or narrowly spaced striae per group, but instead alternated between 1–3 wide striae followed by 1–3 narrow striae without ever forming a visually identifiable group (Fig. 3b). The ISIs of ungrouped striae were measured and they were included in time series analyses but were excluded from analyses of striae groups and cycles.

In total, 143 striae groups and 62 striae cycles were identified across the juvenile portion of 11 EC valves, and 58 striae groups and 27 striae cycles were identified across the juvenile portion of all seven BOS valves. EC and BOS had similar median numbers of striae in each group (EC: 12.6 striae; BOS: 13.6 striae; Fig. 4a) and cycle (EC: 25.7 striae;

Fig. 3 Grouped and ungrouped striae. **a** Grouped striae. Wide striae groups are marked by white lines, narrow striae groups are marked by black lines. The alternating pattern of wide and narrow striae groups was evident on all valves. Photograph from Explorers Cove Valve 6. **b** Ungrouped striae. On some portions of five valves from EC and three valves from BOS, no grouping of wide or narrow striae could be identified. Photograph from Explorers Cove Valve 7



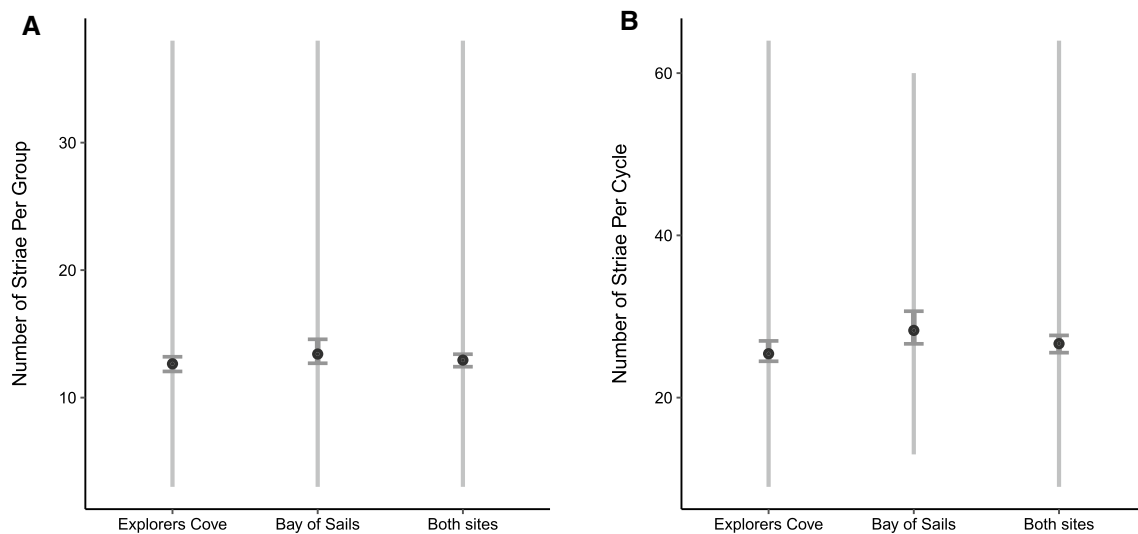


Fig. 4 Striae per group and cycle. **a** Median, 95% CI, and range of striae per group at EC, BOS, and both sites pooled. **b** Median, 95% CI, and range of striae per striae cycle at EC, BOS, and both sites

BOS: 28.5 striae; Fig. 4b) but overlapping confidence intervals suggest that differences between the sites are not statistically significant. For both sites, the median number of striae per group and striae per cycle were close to our expectations for striae that accrete fortnightly in a yearly cycle of wide and narrow ISIs (~13 striae per group and ~26 striae per cycle) and comparable to previous visual findings ($\sim 28 \pm 2$ striae per cycle; Lartaud et al. 2010).

In contrast, the number of striae in any single group or cycle was quite variable. The range of striae per group is large at both sites (3–38 striae), as is the range of striae per yearly cycle (EC: 9–64 striae; BOS: 11–60 striae). More striae groups and cycles deviate from the expected values than conform to them. Only 37% (75/201) of striae groups from both sites had 10–16 striae, while 39% (39/89) of the striae cycles had 20–32 striae. These results indicate that a majority (>60%) of individual striae groups and striae cycles are inconsistent with fortnightly striae formation in a yearly cycle.

Time series analysis of interstitial growth increments

If striae form fortnightly throughout juvenile growth and if the increments between them vary seasonally, sequences of interstitial increments should conform to two expectations in wavelet analysis. First, there should be a statistically significant period (different from background noise) at around 26 striae, indicating a repeating pattern in interstitial increments every 26 striae (one year of fortnights). Second, the periodic behavior should remain consistent and near 26 throughout juvenile ontogeny without much change over time. Of the 11 adult valves from EC and seven from BOS, only one

pooled. Medians are marked by black points. 95% CIs spanned by dark gray brackets. Ranges spanned by light gray bars

valve from each site met both expectations, with consistent, significant periodicity near 26 striae throughout juvenile ontogeny (EC valve #4 and BOS valve #7; Figs. 5, 6). The remaining valves either had significant, but short-lived periods near 26 striae (i.e., EC valves #2 and #11; BOS valve #4), periods that rose or fell by 4–13 striae through juvenile growth (i.e., EC valves #1, #5, #6, and #7; BOS valves #1, #2 and #5), or periods that persisted through ontogeny (varied by ≤ 2 striae) but were not near 26 striae (i.e., ~40 striae in EC valve #2, ~50 striae in EC valve #3, 21 striae in EC valve #9, and 31 striae in BOS valve #6).

Striae as environmental information

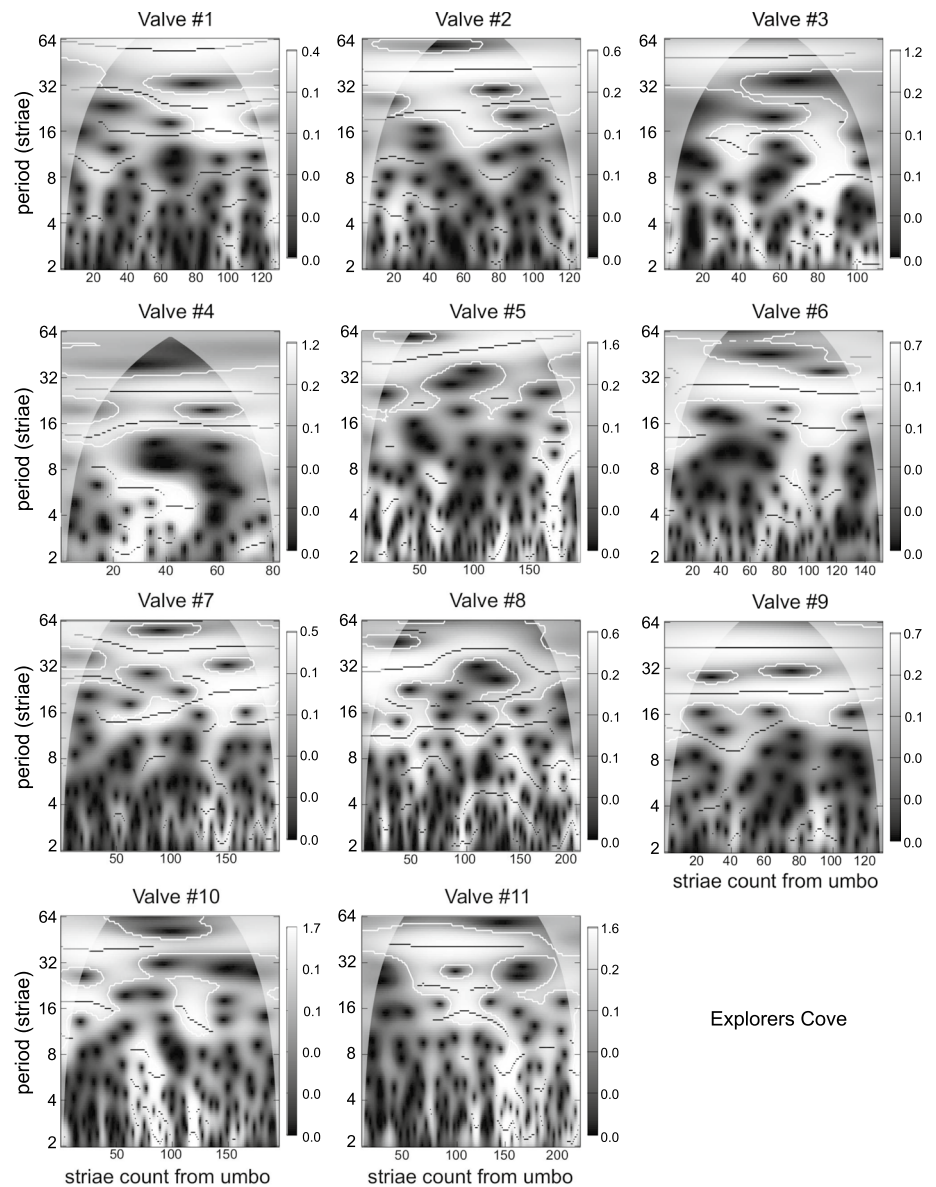
Comparison of interstitial growth increments on EC 2016 juveniles

Four of the juveniles collected in 2016 had only one full striae cycle (containing both a wide and narrow group of striae). The two remaining valves had ~1.5 and 3 striae cycles. The portions of valves that represent concurrent growth had very similar patterns in ISI, regardless of the total number of striae cycles present on each valve (Fig. 7), suggesting that ISI is primarily controlled by exogenous (environmental) factors, rather than endogenous (individual biological) factors.

Striae groups and cycles under annual and multi-annual sea ice

ISI and valve wear differed under annual and multi-annual sea ice. The mean ISI of all measured striae was larger at

Fig. 5 Explorers Cove wavelet results. Blue lines demarcate ridges of strongest periodicity. Areas bounded by white lines indicate periodicity that is different from white noise at 95% confidence. Among EC valves, only EC valve # 4 has a period of 24 striae throughout juvenile growth. Other valves (e.g., EC valves #1, 2, 3, 5, 10, 11) display intermittent periods near 26 striae or periods that change over juvenile growth (e.g., EC valves #6, 7, 8). Some valves have strong periodicity that persists throughout juvenile growth, but the period is not near 26 (e.g., EC valves # 9, 11)



BOS than at EC (mean EC 0.22 mm, CI 0.22–0.23 mm; mean BOS 0.26 mm, CI 0.25–0.27). ISI range was also wider at BOS than at EC (EC 0.026–0.70 mm; BOS 0.006–1.15 mm). More BOS valves were abraded such that striae could not be discerned compared to EC valves (EC 4/11 valves; BOS 5/7 valves). Similarly, of the valves that were worn, BOS valves had a higher mean worn fraction than EC valves (EC 0.06, CI 0.03–0.09; BOS 0.29, CI 0.13–0.50).

Despite differences in mean ISI, both sites had approximately equal numbers of striae in their wide groups as in their narrow groups. At EC, narrow striae groups contained 12.2 striae (CI 11.4–13.0 striae) and wide groups contained 12.9 striae (CI 12.1–13.7 striae). At BOS, narrow striae groups contained 13.2 striae (CI 11.9–14.6 striae) and wide striae groups contained 13.9 striae (CI 12.6–15.3 striae).

Discussion

Striae groups and cycles as age indicators

If analyses of striae are restricted to means and medians, then striae groups and cycles appear to match expectations consistent with yearly striae cycles and fortnightly formation. For instance, alternating groups of wide and narrow striae were apparent on all *A. colbecki* valves, consistent with descriptions from previous work (Stockton 1984; Berkman 1990; Lartaud et al. 2010). Additionally, the median number of striae per group and cycle (EC 12.6 striae; BOS 13.6 striae) are roughly equivalent to values expected if striae form fortnightly and in yearly striae cycles (after Lartaud et al. 2010). Nonetheless, when individual valves are examined, the large variation and inconsistency in number

Fig. 6 Bay of sails wavelet results. Blue lines demarcate ridges of strongest periodicity. Areas bounded by white lines indicate periodicity that is different from white noise at 95% confidence. Among BOS valves, only BOS valve # 7 has a period of 26 striae throughout juvenile growth. Other valves (e.g., BOS valves #1, 4) display intermittent periods near 26 striae or periods that change over juvenile growth (e.g., BOS valves #1, 2, 3, 5, 6). One valve has strong periodicity that persists throughout juvenile growth, but the period is not near 26 (BOS valves #4)

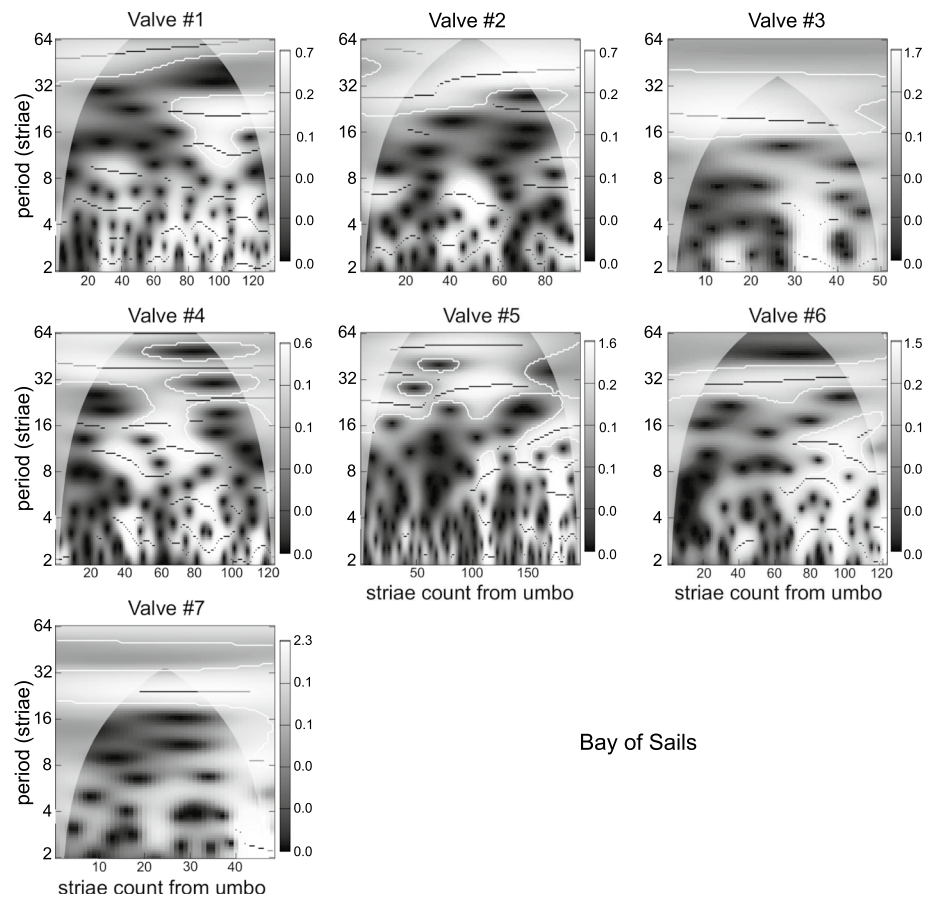
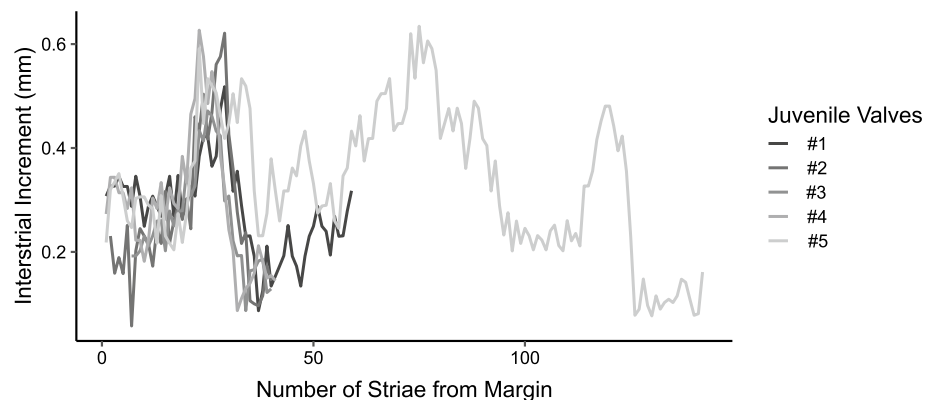


Fig. 7 Interstrial growth increments of EC juveniles collected in 2016. Interstrial increments for the five juveniles collected from EC in 2016 show good agreement in growth patterns during times of overlapping growth. Growth direction proceeds right to left; striae 0 is at the margin of each valve



of striae in any individual group or cycle, combined with the occurrence of ungrouped striae on several valves, suggests that visual analysis of striae groups and cycles is an unreliable method for ontogenetic age determination of *A. colbecki* shells.

The number of striae in any single group or cycle ranges from fewer than half the number expected to more than double. Fewer than 40% of striae groups or cycles conformed to expectations based on fortnightly formation or data from previous authors (Lartaud et al. 2010). This result highlights

the importance of expanding analyses of subannual growth increments to include and report data from both more individuals and longer periods of shell growth.

Wavelet analysis of ISI on individual valves reinforces the inconsistencies observed in visual analysis of striae grouping. Only two valves, one each from EC and BOS, had “perfect” or near-perfect cycles of ~26 striae throughout juvenile growth. More commonly, valves displayed either cycles that repeated at higher periods than expected (~32+ striae) or at periods that change throughout juvenile growth (up

to 13 striae), and sometimes both (Figs. 4, 5). Because of high inter- and intra-individual variability, most valves do not conform to previous expectations of striae grouping or periodicity and is further evidence striae groups should not be used to age *A. colbecki*.

A potential explanation for the coincidence of striae formation with spring tides at Dumont D'Urville (Lartaud et al. 2010) and the apparent irregularity of striae formation at EC and BOS is the tidal regime in the Ross Sea. In contrast to the mixed diurnal/semidiurnal tides that occur at Dumont D'Urville (Lartaud et al. 2010), the Ross Sea has diurnal declinational tides governed by the moon's transit of the equator with a period of 13.66 days (Goring and Pyne 2003). Goring and Pyne (2003) suggested that tidally influenced biological rhythms may conform to ~13.66 day periodicity rather than the more common ~14.77 day periodicity expected in a lunar fortnight (Tran et al. 2011). Possible links between striae formation and tidal patterns at EC, BOS, and other Ross Sea sites merits further exploration.

For our study, we assumed that striae form fortnightly during juvenile growth (after Lartaud et al. 2010). Indeed, the wavelet analysis is predicated upon that assumption. The results of our study did not support this except for one shell from each site, but neither can our study, as designed, refute fortnightly formation. We recommend two things if age-studies are to be done with *A. colbecki*: first, that mark-recapture studies include individuals of diverse ages and size classes and second, that striae groups should not be used to age *A. colbecki*, although it is tempting to attribute this pattern to yearly seasonal cycles.

Striae as environmental indicators

Despite recommending against striae groups and cycles to age *A. colbecki*, interstrial increments (ISIs) may archive useful environmental information. Extremely similar patterns in ISI during concurrent growth of the juveniles collected from EC in 2016 suggest a strong exogenous (environmental) control on increment size and several differences between ISI in BOS and EC may provide evidence of past sea ice duration in fossil and subfossil valves.

First, the mean ISI at the annual site, BOS, was 15–18% higher than at EC, the multi-annual sea ice site. Annual growth increments also indicate that scallops from BOS grow faster than scallops from EC (Cronin et al. 2020). Growth rates of *A. colbecki* may therefore be a method to differentiate between sea ice duration around Antarctica, like growth rates of *Clinocardium ciliatum* in the Arctic (Sejr et al. 2009).

Additionally, both the number of abraded valves and the worn fraction on abraded valves were higher at BOS than EC. Though abrasion has the effect of erasing useful striae data, we speculate that it also provides environmental

evidence: silt in the EC sediment may reduce valve abrasion compared to BOS. In contrast, the worn fraction of striae may be evidence of sea ice duration that is preserved on fossil and subfossil valves if more valve abrasion is connected to overall higher metabolic activity and valve movement at the annual sea ice site. This is corroborated by faster growth (larger ISI) at BOS but must be confirmed by behavioral studies and evidence from other *A. colbecki* populations.

Finally, the median number of striae in narrow *versus* wide groups were similar at both EC and BOS. While individual groups varied widely, median striae per narrow or wide group ranged from ~11 to 14. The similar number of striae in wide and narrow groups suggest that *A. colbecki* growth may slow, but not stop entirely, during juvenile growth under both annual and multi-annual sea ice. In contrast, temperate scallops decrease the number of striae formed as their growth slows or stops (e.g., Helm and Malouf, 1983; Owen et al. 2002; Chauvaud et al. 2005), resulting in unequal numbers of striae accreted during winter growth compared to summer growth (Owen et al. 2002). Continuous growth in juvenile *A. colbecki* is corroborated by lack of obvious growth disruptions on the juvenile growth portion of the valves used in this study (pers. obs.) and by previous analysis of juvenile valves (Lartaud et al. 2010).

If striae grouping is too inconsistent to reliably identify yearly striae cycles, but ISIs are governed by environmental factors, what environmental factors control the growth increments? In temperate scallops, ISIs are correlated with temperature (Chauvaud et al. 2005) and possible seawater pressure (Thébault et al. 2006). Growth rates more generally are correlated with both temperature and nutrients (Macdonald and Thompson 1988; Pilditch 1999; Laing 2000; Kirby and Miller 2005). We suggest further in situ growth experiments monitoring seawater conditions and analysis of *A. colbecki* shell chemistry to understand the dominant factors controlling ISI in *A. colbecki*.

Conclusions

Striae groups are too variable to be used as reliable age markers in *A. colbecki*. Inter- and intra-individual variation in the number of striae per group and cycle was unacceptably high in visual analysis of striae groups. Moreover, time series analysis of interstrial growth increments revealed that most valves do not maintain periodicity consistent with ~26 striae in yearly striae cycles throughout juvenile growth. For this and other species, it is vital to report data from multiple valves over longer time periods when characterizing sub-annual growth increments.

Similarity in interstrial increments (ISI) throughout the concurrent growth of five juveniles suggest strong environmental control over ISI, and therefore these increments

may contain useful environmental information. For instance, larger mean growth increments and may indicate growth under annual, rather than multi-annual sea ice.

We recommend that striae groups and cycles not be used to determine age in *A. colbecki*, but that stria increments should be explored as archives of environmental information such as differences in sea ice persistence.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00300-021-02830-7>.

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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, and SSB edited the manuscript.

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Data availability Data will be available at the US Antarctic Program Data Center (USAP-DC) upon publication.

Code availability R code will be available at the US Antarctic Program Data Center (USAP-DC) upon publication.

Declarations

Conflict of interest The authors have no competing interests to disclose.

References

- Aguirre Velarde A, Flye-Sainte-Marie J, Mendo J, Jean F (2015) Sclerochronological records and daily microgrowth of the Peruvian scallop (*Argopecten purpuratus*, Lamarck, 1819) related to environmental conditions in Paracas Bay, Pisco, Peru. *J Sea Res* 99:1–8. <https://doi.org/10.1016/j.seares.2015.01.002>
- Antoine L (1978) La croissance journalière chez *Pecten maximus* (L.) (Pectinidae, Bivalvia). *Haloit* 9:627–636
- Barrera E, Tevesz MJS, Carter JG (1990) Variations in oxygen and carbon isotopic compositions and microstructure of the shell of *Adamussium colbecki* (Bivalvia). *Palaos* 5:149–159. <https://doi.org/10.2307/3514811>
- Barry JP, Dayton PK (1988) Current patterns in McMurdo Sound, Antarctica and their relationship to local biotic communities. *Polar Biol* 8:367–376. <https://doi.org/10.1007/BF00442028>

- Berkman PA (1990) The population biology of the Antarctic scallop, *Adamussium colbecki* at New Harbor, Ross Sea. In: Kerry KR, Hempel G (eds) *Antarctic ecosystems: ecological change and conservation*. Springer, Berlin, pp 281–288
- Berkman PA (1994) Epizoic zonation on growing scallop shells in McMurdo Sound. *J Exp Mar Biol Ecol* 179:49–67. [https://doi.org/10.1016/0022-0981\(94\)90016-7](https://doi.org/10.1016/0022-0981(94)90016-7)
- Berkman PA, Cattaneo-Vietti R, Chiantore M, Howard-Williams C (2004) Polar emergence and the influence of increased sea-ice extent on the Cenozoic biogeography of pectinid molluscs in Antarctic coastal areas. *Deep Sea Res II* 51:1839–1855. <https://doi.org/10.1016/j.dsr2.2004.07.017>
- Bernhard JM (1987) Foraminiferal biotopes in Explorers Cove, McMurdo Sound, Antarctica. *J Foraminiferal Res* 17:286–297. <https://doi.org/10.2113/gsjfr.17.4.286>
- Bowser SS, Bernhard JM (1993) Structure, bioadhesive distribution and elastic properties of the agglutinated test of *Astrammia rara* (Protozoa: Foraminiferida). *J Eukaryot Microbiol* 40:121–131. <https://doi.org/10.1111/j.1550-7408.1993.tb04891.x>
- Broom MJ, Mason J (1978) Growth and spawning in the pectinid *Chlamys opercularis* in relation to temperature and phytoplankton concentration. *Mar Biol* 47:277–285. <https://doi.org/10.1007/BF00541005>
- Cattaneo-Vietti R, Chiantore M, Albertelli G (1997) The population structure and ecology of the Antarctic scallop *Adamussium colbecki* (Smith, 1902) at Terra Nova Bay (Ross Sea, Antarctica). *Sci Mar* 61:15–24
- Cerrano C, Bertolino M, Valisano L, Bavestrello G, Calcinai B (2009) Epibiotic demosponges on the Antarctic scallop *Adamussium colbecki* (Smith, 1902) and the cidaroid urchins *Ctenodidaris perrieri* Koehler, 1912 in the nearshore habitats of the Victoria Land, Ross Sea, Antarctica. *Polar Biol* 32:1067–1076. <https://doi.org/10.1007/s00300-009-0606-5>
- Chauvaud L, Lorrain A, Dunbar RB, Paulet Y-M, Thouzeau G, Jean F, Guarini J-M, Mucciarone D (2005) Shell of the Great Scallop *Pecten maximus* as a high-frequency archive of paleoenvironmental changes. *Geochim Geophys Geosyst* 6:Q08001. <https://doi.org/10.1029/2004GC000890>
- Chauvaud L, Thouzeau G, Paulet Y-M (1998) Effects of environmental factors on the daily growth rate of *Pecten maximus* juveniles in the Bay of Brest (France). *J Exp Mar Biol Ecol* 227:83–111. [https://doi.org/10.1016/S0022-0981\(97\)00263-3](https://doi.org/10.1016/S0022-0981(97)00263-3)
- Chiantore M, Cattaneo-Vietti R, Povero P, Albertelli G (2000) The population structure and ecology of the Antarctic scallop *Adamussium colbecki* in Terra Nova Bay. In: Faranda FM, Letterio G, Ianora A (eds) *Ross sea ecology, ross sea ecology: Italianartide expeditions (1987–1995)*. Springer, Berlin, pp 563–573
- Cronin KE, Walker SE, Mann R, Chute AS, Long MC (2020) Growth and longevity of the Antarctic scallop *Adamussium colbecki* under annual and multiannual sea ice. *Antarct Sci* 32:466–475. <https://doi.org/10.1017/S0954102020000322>
- Cummings V, Thrush S, Norkko A, Andrew N, Hewitt J, Funnell G, Schwarz AM (2006) Accounting for local scale variability in benthos: implications for future assessments of latitudinal trends in the coastal Ross Sea. *Antarct Sci* 18:633–644. <https://doi.org/10.1017/S0954102006000666>
- Goring DG, Pyne A (2003) Observations of sea-level variability in Ross Sea, Antarctica. *N Z J Mar Fresh* 37:241–249. <https://doi.org/10.1080/00288330.2003.9517162>
- Gruffydd LLD (1981) Observations on the rate of production of external ridges on the shell of *Pecten maximus* in the laboratory. *J Mar Biol* 61:401–411. <https://doi.org/10.1017/S0025315400047032>
- Hancock LG, Walker SE, Pérez-Huerta A, Bowser SS (2015) Population dynamics and parasite load of a foraminifer on its Antarctic scallop host with their carbonate biomass contributions. *PLoS ONE* 10:e0132534. <https://doi.org/10.1371/journal.pone.0132534>

- Helm NE, Malouf RE (1983) Role of production of the external ridges in the bay scallop *Argopecten irradians*. *Am Zool* 23:835
- Johnson ALA, Hickson JA, Heaton THE, Chenery S, Balson PS, Harper EM, Taylor JD, Crame JA (2000) The Queen Scallop *Aequipecten opercularis*: a new source of information on late Cenozoic marine environments in Europe. In: Harper EM, Taylor JD, Crame JA (eds) The evolutionary biology of the bivalvia. Geological Society of London, London, pp 425–439
- Joll LM (1988) Daily growth rings in juvenile saucer scallops, *Amusium balloti* (Bernardi). *J Shellfish Res* 7:73–76
- Kirby MX, Miller HM (2005) Response of a benthic suspension feeder (*Crassostrea virginica* Gmelin) to three centuries of anthropogenic eutrophication in Chesapeake Bay. *Estuar Coast Shelf Sci* 62:679–689. <https://doi.org/10.1016/j.ecss.2004.10.004>
- Laing I (2000) Effect of temperature and ration on growth and condition of king scallop (*Pecten maximus*) spat. *Aquaculture* 183:325–334. [https://doi.org/10.1016/S0044-8486\(99\)00262-8](https://doi.org/10.1016/S0044-8486(99)00262-8)
- Lartaud F, Chauvaud L, Richard J, Toulot A, Bollinger C, Testut L, Paulet Y-M (2010) Experimental growth pattern calibration of Antarctic scallop shells (*Adamussium colbecki*, Smith 1902) to provide a biogenic archive of high-resolution records of environmental and climatic changes. *J Exp Mar Biol Ecol* 393:158–167. <https://doi.org/10.1016/j.jembe.2010.07.016>
- Macdonald BA, Thompson RJ (1988) Intraspecific variation in growth and reproduction in latitudinally differentiated populations of the Giant Scallop *Placopecten magellanicus* (Gmelin). *Biol Bull* 175:361–371. <https://doi.org/10.2307/1541727>
- Norkko A, Thrush SF, Cummings VJ, Gibbs MM, Andrew NL, Norkko J, Schwarz A-M (2007) Trophic structure of coastal Antarctic food webs associated with changes in sea ice and food supply. *Ecology* 88:2810–2820. <https://doi.org/10.1890/06-1396.1>
- Owen R, Richardson C, Kennedy H (2002) The influence of shell growth rate on striae deposition in the scallop *Pecten maximus*. *J Mar Biol Ass* 82:621–623. <https://doi.org/10.1017/S0025315402005969>
- Pilditch CA (1999) Effect of temperature fluctuations and food supply on the growth and metabolism of juvenile sea scallops (*Placopecten magellanicus*). *Mar Biol* 134:235–248. <https://doi.org/10.1007/s002270050542>
- Quaglio F, Whittle R, Gaździcki A, Simões M (2010) A new fossil *Adamussium* (Bivalvia: Pectinidae) from Antarctica. *Pol Polar Res* 31:291–302. <https://doi.org/10.2478/v10183-010-0006-0>
- R Core Team (2017) R: a language and environment for statistical computing. R foundation for statistical computing. <https://www.r-project.org/>. Accessed 2 Jan 2021
- Radford D, Walker SE, Bowser SS (2014) Alpha and beta diversity of foraminifera that encrust the Antarctic scallop *Adamussium colbecki*: ecological connectivity among shells and between sites. *J Foraminiferal Res* 44:255–280. <https://doi.org/10.2113/gsjfr.44.3.255>
- Roesch A, Schmidbauer H (2018) WaveletComp: computational wavelet analysis. Version R package version 1.1. <https://cran.r-project.org/web/packages/WaveletComp/index.html>. Accessed 2 Jan 2021
- Schiaparelli S, Linse K (2006) A reassessment of the distribution of the common Antarctic scallop *Adamussium colbecki* (Smith, 1902). *Deep Sea Res II* 53:912–920. <https://doi.org/10.1016/j.dsr2.2006.02.004>
- Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, Preibisch S, Rueden C, Saalfeld S, Schmid B, Tinevez J-Y, White DJ, Hartenstein V, Eliceiri K, Tomancak P, Cardona A (2012) Fiji: an open-source platform for biological-image analysis. *Nat Methods* 9:676–682. <https://doi.org/10.1016/10.1038/nmeth.2019>
- Sejr M, Blicher M, Rysgaard S (2009) Sea ice cover affects inter-annual and geographic variation in growth of the Arctic cockle *Clino-cardium ciliatum* (Bivalvia) in Greenland. *Mar Ecol Prog Ser* 389:149–158. <https://doi.org/10.3354/meps08200>
- Stockton WL (1984) The biology and ecology of the epifaunal scallop *Adamussium colbecki* on the west side of McMurdo Sound, Antarctica. *Mar Biol* 78:171–178. <https://doi.org/10.1007/s00227-005-0198-8>
- Thébault J, Chauvaud L, Clavier J, Fichez R, Morize E (2006) Evidence of a 2-day periodicity of striae formation in the tropical scallop *Comptopallium radula* using calcein marking. *Mar Biol* 149:257–267. <https://doi.org/10.1016/j.palaeo.2011.12.014>
- Thrush SF, Hewitt JE, Cummings VJ et al (2010) β -Diversity and species accumulation in Antarctic coastal benthos: influence of habitat, distance and productivity on ecological connectivity. *PLoS ONE* 5:e11899. <https://doi.org/10.1371/journal.pone.0011899>
- Torrence C, Compo GP (1988) A practical guide to wavelet analysis. *Bull Am Meteorol Soc* 79:61–78. <https://doi.org/10.1175/1520-0477>
- Tran D, Nadau A, Durrieu G, Ciret P, Parisot J-P, Massabuau J-C (2011) Field chronobiology of a molluscan bivalve: how the moon and sun cycles interact to drive oyster activity rhythms. *Chronobiol Int* 28:307–317. <https://doi.org/10.3109/07420528.2011.565897>

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