



Long-term observations of pteropod phenology along the Western Antarctic Peninsula

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ABSTRACT

Shifts in phenology – annually occurring life history events – have been observed among many marine organisms due to global warming. We examined if phenological changes in the pteropod (pelagic snail) *Limacina helicina antarctica* have occurred along the Western Antarctic Peninsula, one of the most intensely warming regions on Earth, which would have important implications for regional food web dynamics. Pteropod shell diameters were analyzed from samples collected in the Palmer Antarctica Long-Term Ecological Research (PAL LTER) program year-round sediment trap from 2004 to 2018. There was considerable interannual variability in the time of appearance of a new pteropod cohort, which ranged from day of year 22–255, but no long-term, directional change. Mean *L. h. antarctica* growth rate for the time series was 0.009 mm day⁻¹ and there was no significant long-term change in growth rate. This study represents the first in the Southern Ocean to illustrate that pteropods actively grow throughout the winter season. Sea ice was the dominant driver of pteropod phenology, with earlier sea ice retreat the year prior, lower winter sea surface temperature (SST) the year prior, and higher primary productivity in the same year leading to earlier pteropod time of appearance. Similarly, more open water with higher autumn SST, both the year prior, and elevated chlorophyll *a* the same year, promoted faster pteropod growth. These results indicate that while pteropods are responsive to considerable environmental variability, their phenology has remained relatively stable. The identified responses of pteropod phenology to environmental shifts are key for determining future effects of climate change on biogeochemical cycling and plankton trophic interactions in the region.

1. Introduction

Shifts in phenology (i.e., annually occurring life history events) have been observed among many marine organisms due to global warming (Edwards and Richardson, 2004), resulting in regional trophic mismatches and significant impacts on local food webs (Edwards and Richardson, 2004; Ji et al., 2010; Poloczanska et al., 2013). Zooplankton have some of the fastest habitat expansion rates as well as the fastest rates of spring advancement of all marine organisms according to a meta-analysis of marine phenology studies from 1960 to 2009 (Poloczanska et al., 2013). However, most time series that focus on marine

zooplankton phenology have only occurred in the Northern Hemisphere (reviewed in Ji et al., 2010), limiting our ability to broadly interpret the effects of warming on zooplankton life history. In this study, we examine phenological changes of the pteropod (pelagic snail) *Limacina helicina antarctica* in the Western Antarctic Peninsula (WAP), a highly dynamic and productive region of the Southern Ocean that has experienced some of the highest rates of warming observed on Earth (Vaughan et al., 2003; Meredith and King, 2005). In the past two decades this warming has plateaued, and a notable increase in sea ice and its interannual variability has occurred in the coastal WAP (Henley et al., 2019). While prior studies in the WAP have examined the effects of both long-term

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warming and sub-decadal-scale climate variability on components of the pelagic food web (Montes-Hugo et al., 2009; Ducklow et al., 2012a; Schofield et al., 2013; Saba et al., 2014; Steinberg et al., 2015), including pteropods (Thibodeau et al., 2019), no studies have determined potential phenological shifts of zooplankton due to environmental change.

The pteropod *L. h. antarctica* is an abundant zooplankton species in the Southern Ocean, efficient grazer of phytoplankton, prey for higher trophic level organisms, and an important contributor to the biological pump through fecal pellet production, excretion, and sloppy feeding (Pakhomov et al., 1996; Hunt et al., 2008; Giraldo et al., 2011; Gleiber et al., 2012; Bernard et al., 2012; Manno et al., 2017; Steinberg and Landry, 2017; Thibodeau et al., 2019). Shelled pteropods (known as thecosomes) such as *L. h. antarctica* collect sinking particles for feeding by producing a mucous web. This mucus contributes to carbon flux through sinking and by forming aggregations with other marine detritus that create a microhabitat for microbial activity (Lalli and Gilmer, 1989; Steinberg and Landry, 2017). In addition, shelled pteropods contribute to the solubility pump (Manno et al., 2018), through the formation and dissolution of their calcium carbonate (CaCO_3) shells composed of aragonite, which has implications for short-term ocean alkalinity cycles and associated carbon dioxide (CO_2) buffering capacity (Lalli and Gilmer, 1989; Honjo, 2004; Honjo et al., 2008; Manno et al., 2018). However, thecosomes' susceptibility to shell dissolution from ocean acidification, caused by the uptake of anthropogenic CO_2 into the ocean, may disrupt their influence on the solubility pump in the future (Lalli and Gilmer, 1989; Sabine et al., 2004; Orr et al., 2005; Doney et al., 2009). Along the WAP, *L. h. antarctica* abundances have remained stable and the non-shelled pteropods (known as gymnosomes) have increased in abundance over the past 25-years due to a shortening sea ice season that results in longer periods of open water for feeding in spring/summer (Thibodeau et al., 2019). The previous study only analyzed adult pteropods sampled during the summer, thus significant effects of environmental controls on earlier phases in their life cycle may have been missed. Indeed *Limacina* spp. phenology is poorly documented throughout the world's oceans and a necessary area of increased research, particularly in the Southern Ocean (Hunt et al., 2008; Hoshijima et al., 2017).

In order to predict the potential effects of climate change on polar species like *Limacina* spp., it is important to characterize their general population dynamics and life history patterns, including phenology. Primary methods for measuring phenological variability include population size, development, and timing of dormancy (Ji et al., 2010). Only a handful of studies globally have determined growth rates of *Limacina* spp. and their time of appearance as related to life history. Results from two prior studies using net tows in austral spring/summer determined *L. h. antarctica* grow on average 0.01 mm day^{-1} and live between 1 and 3 years (Dadon and De Cirdre, 1992; Bednaršek et al., 2012). Studies of pteropod growth rates in the Arctic and North Pacific oceans using net tows concluded *Limacina* spp. generally live 1–2.5 years, with growth rates ranging from 0.01 to 0.6 mm day^{-1} , depending on the season (Kobayashi, 1974; Fabry, 1989; Gannefors et al., 2005; Hunt et al., 2008; Wang et al., 2017).

Moored sediment traps that sample year-round, typically used to quantify seasonal and interannual trends in particulate organic and inorganic carbon (POC/PIC) export, can also be a useful tool for analyzing zooplankton population dynamics and phenology. For example, Collier et al. (2000) found increased vertical fluxes of *L. h. antarctica* shells collected in sediment traps in the Ross Sea, Antarctica from 1996 to 1998 during the late austral fall. They posited that *L. h. antarctica* may feed in surface waters during austral summer but then migrate closer to the trap depth as the ice edge begins to advance in autumn (Collier et al., 2000). Howard et al. (2011) observed a contrasting trend in the seasonal flux of *L. h. antarctica* in the Sub-Antarctic Zone near Tasmania, as recorded in a sediment trap, with the greatest flux during mid-summer and minimal flux from May to October. This flux pattern was corroborated with pteropod water column densities

analyzed from a Continuous Plankton Recorder (CPR) (Howard et al., 2011). *L. h. antarctica* shell weight became significantly lighter from 1997 to 2007 based on samples collected in an Antarctic sediment trap; however, the study suggests this response is due to multiple factors beyond aragonite undersaturation, since there was a greater reduction in calcification than expected (Roberts et al., 2014). While these studies provide important information about pteropod population dynamics or phenology, none combine the two to elucidate the long-term effects of environmental factors on pteropod life history.

In this study, we use shell diameters from *L. h. antarctica* collected by a sediment trap deployed over the WAP continental shelf from 2004 to 2018 to determine if a shift in phenology has occurred due to warming or other environmental controls. Characterizing pteropod phenology provides needed metrics for modeling population dynamics, which is important for understanding the effects of climate variability on WAP food web processes and on organic and inorganic carbon export.

2. Methods

2.1. Sediment trap deployment and retrieval

L. h. antarctica samples were collected from the Palmer Antarctica Long Term Ecological Research (PAL LTER) sediment trap (year-round coverage) (<https://pal.lternet.edu/data>, Palmer Station Antarctica LTER et al., 2017). The conical trap (PARFLUX Mark 78H 21-sample trap, McLane Research Labs) is bottom-moored and located over the northern WAP continental shelf ($64^\circ 30' \text{ S}$, $66^\circ 00' \text{ W}$) (Fig. 1) (Ducklow et al., 2008). This deployment site has a bottom depth of 350 m and the trap is suspended at 170 m. The location of the sediment trap is seasonally covered with sea ice 111 ± 8 days (mean $\pm$ standard error) per year (data from 1979 to 2017, $n = 38$), with a mean advance in June (day of year 157 ± 31) and a mean retreat in early October (day of year 276 ± 34 ; Ducklow et al., 2012b; Gleiber et al., 2012, S. Stammerjohn pers. comm.).

We analyzed *L. h. antarctica* collected in sediment trap samples from the most recent trap recoveries, January 2004 to January 2018. This time series is continuous except for the 2009–2010 season when the trap was not recovered. Trap deployments and recoveries were performed aboard the ARSV *Laurence M. Gould* in January of each year on the PAL LTER annual cruises. The trap contains 21 plastic sample bottles that collect sequential samples throughout the year at 7–60 day intervals, which correspond to anticipated seasonal particle flux (Ducklow et al., 2008). During peak particle flux in austral summer (November to April), the sample bottles rotate weekly while in the austral winter (May to October), intervals are monthly (bimonthly in July–August). There are gaps of 1–5 days between mooring recovery and deployment depending on the year. The 21 sample collection bottles on the trap were prepared before deployment with a Milli-Q deionized water (DI) rinse and filled with $7.5 \text{ g NaCl l}^{-1}$ solution and 2% borate-buffered formalin in filtered seawater (34 psu), with a final salinity concentration of 41 psu (Ducklow et al., 2008; Gleiber et al., 2012).

2.2. Sediment trap sampling and analysis of pteropods

While sediment traps are typically used to measure the export rate of sinking particulate organic matter, they are also suitable for studying zooplankton suspected to have actively swum into the trap—“swimmers” and died in the formalin (Gilmer and Harbison, 1986; Steinberg et al., 1998; Buesseler et al., 2007). Shelled pteropods, including *L. h. antarctica*, are particularly susceptible to being caught in sediment traps because they are negatively buoyant and rapidly retreat into their shells for protection when disturbed, which causes them to sink quickly (Gilmer and Harbison, 1986; Honjo et al., 2008). Zooplankton swimmers were picked from sediment trap samples using established protocols (Buesseler et al., 2007), and *L. h. antarctica* were carefully sorted from other pteropod and zooplankton species present. *L. h. antarctica*

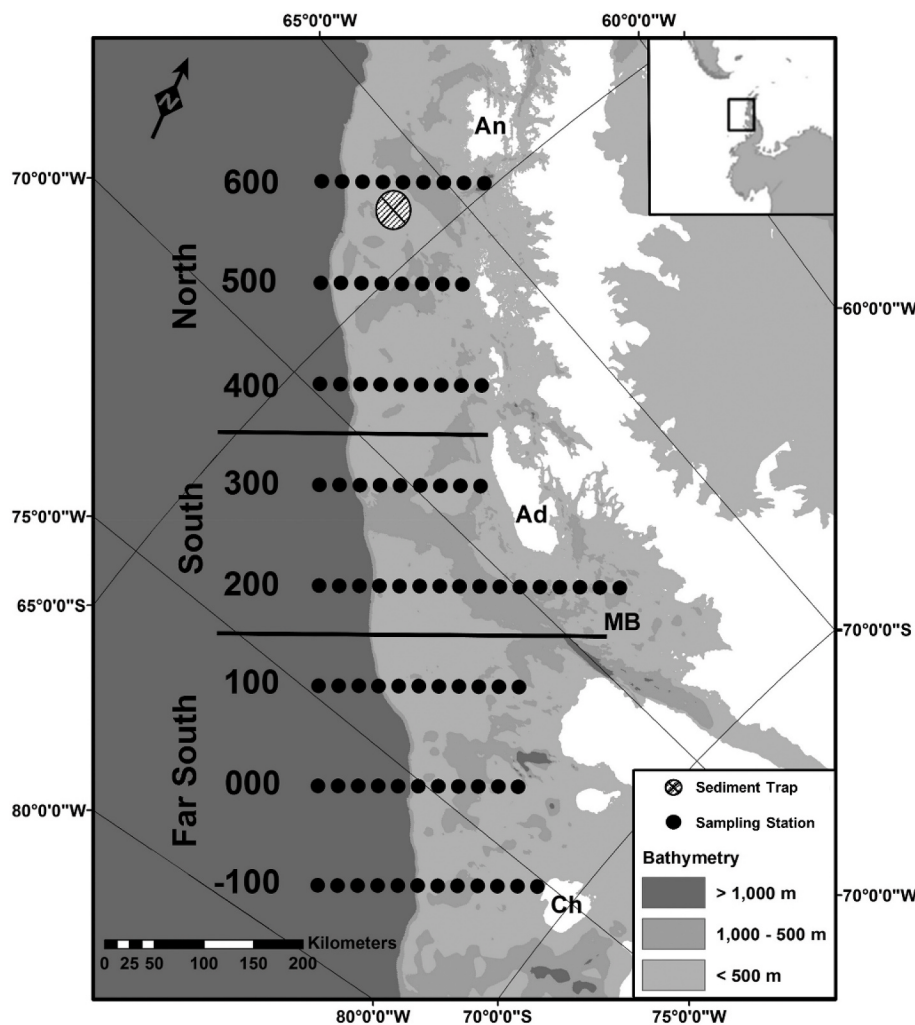


Fig. 1. Map of PAL LTER study region and sediment trap location. Study region (highlighted in box) relative to the Antarctic continent. The sediment trap is located over the continental shelf region of the sampling grid. Shades of gray illustrate bathymetry, with light gray indicating the continental shelf and dark gray the continental slope and abyssal plain. Shelf break is represented by light/dark gray interface near 1000 m, extending down to 3000 m (Ducklow et al., 2012a). The continental shelf is roughly 200 km wide and 430 m deep on average. PAL LTER grid lines are numbered from 600 to -100 and distanced 100 km apart (Waters and Smith, 1992). The sediment trap is located in the North sub-region of the sampling grid (lines 400 to 600). Individual sampling stations for a given grid line are 20 km apart. An, Anvers Island, the location of Palmer Station; MB, Marguerite Bay; Ad, Adelaide Island; Ch, Charcot Island.

shells were analyzed using an Olympus SZX12 dissecting scope with an Olympus DP71 digital camera under bright-field illumination. Digital images were analyzed with Image-Pro Plus© to measure shell diameter. As described by Wang et al. (2017), specimens were measured from the opening of the shell aperture directly across the diameter of the shell (Fig. 2) with a measurement error of 0.007 ± 0.001 mm. Only shells with body tissue still present (indicating they were alive upon swimming into the trap) were measured (Steinberg et al., 1998; Buesseler et al., 2007). In order to maintain an adequate and consistent sample size, up to 120 shells were randomly selected to analyze from each cup when present, with broken shells subsequently excluded from diameter analyses. All shell diameter data collected are available through the Palmer LTER long-term dataset (<https://pal.lternet.edu/data>, Palmer Station Antarctica LTER and Thibodeau, 2020).

Size-frequency histograms were then constructed based on the shell diameters measured in each cup. The histograms were used to identify time of first appearance of a new *L. h. antarctica* cohort and track seasonal growth throughout the time series, our two primary metrics for measuring phenology (Ji et al., 2010). Different terms are used in the literature to describe the rate of growth for calcifying plankton including pteropods such as growth rate, calcification rate, and calcium carbonate precipitation rate. We define growth rate as the rate of increase in shell diameter. Median shell size for each cup of each year was determined to identify potential long-term trends in *L. h. antarctica* growth. Any cups that contained <10 unbroken *L. h. antarctica* shells were excluded from the analysis. The years 2006, 2008, and 2010 were removed from the growth analysis due to low sample size (2006), inability to fit a

statistically significant growth curve to these data (2008), and failure to recover the sediment trap (2010). Growth of juvenile (<1 mm) and adult (>1 mm) size classes were initially modeled separately (Table 1); however, due to insufficient sample size it was difficult to compare across the entirety of the time series using this approach. Growth was modeled for each year of the time series by fitting linear regression to natural log-transformed median shell diameters against day of year. The estimated slope of each linear regression is the modeled growth coefficient, which is unitless due to the log-transformation. Thus, growth rates in mm day^{-1} were also determined as described in Bednaršek et al. (2012) by taking the maximum and minimum median shell diameters for each year, and dividing by the sampling period. Time of appearance was determined as the median date during the first sampling interval when >10 unbroken *L. h. antarctica* shells were present in a cup for a given year.

2.3. Net sampling and analysis of pteropods

L. h. antarctica specimens were opportunistically collected for size analysis during the PAL LTER 2018 January offshore cruise and for 4 months at Palmer Station, Anvers Island (November 2017 to February 2018). *L. h. antarctica* and all other macrozooplankton collection on the PAL LTER cruise were performed with a 2 m square frame Metro net (700 μm mesh), towed obliquely to a depth of 120 m (Ross et al., 2008; Steinberg et al., 2015; Thibodeau et al., 2019). Net depth was determined in real time with a depth sensor attached to the bottom of a conducting wire and verified with a temperature-depth recorder. At

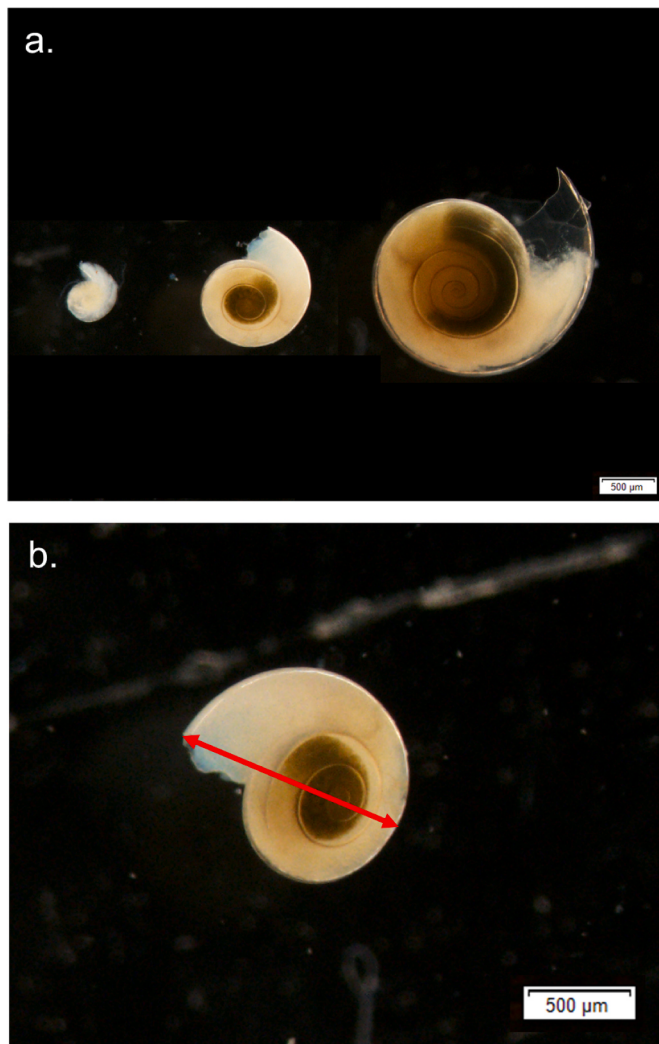


Fig. 2. *Limacina helicina antarctica* shell growth and measurement. (a) Examples of *L. h. antarctica* shells collected from the sediment trap in 2017 when pteropods first appear in June (left) then continue to develop in September (middle) and November (right). (b) Method for measuring shell diameter. Measured shell diameters in (a) (from left to right) are as follows: 0.57 mm, 1.16 mm, 2.28 mm. The yellow and brown colors in the pteropod shells are the body tissue.

Palmer Station, zooplankton were collected with a 1 m × 1 m square frame Metro net (700 µm mesh) and a 1 m diameter ring net (200 or 500 µm mesh), towed obliquely to a depth of ~50 m. Zooplankton sampling at Palmer Station was conducted two days per week from November 2017 to March 2018. Zooplankton samples were sorted live in the laboratory at Palmer Station, and up to 50 *L. h. antarctica* shell diameters were measured per net tow. Shell diameters from *L. h. antarctica* collected in the sediment trap were compared to those collected by net during the annual PAL LTER summer research cruise and at Palmer Station. All net tow data used for this study are available through the Palmer LTER long-term dataset (<https://pal.lternet.edu/data>, Palmer Station Antarctica LTER and Steinberg, 2020).

2.4. Comparison with environmental parameters and climate indices

Environmental factors potentially affecting pteropod phenology included phytoplankton biomass (chlorophyll *a*; chl *a*), primary production (PP), carbonate chemistry variables, sea surface temperature (SST), sea ice cover, and climate indices as described in Steinberg et al. (2015) and Thibodeau et al. (2019). Ship-based measurements were

collected at each station throughout the entire PAL LTER grid but for the purpose of this study were only analyzed in the 'North' sub-region that was within 200 km south and west of Anvers Island and includes the sediment trap location (Fig. 1). The trap is not equipped with additional environmental sensors during deployment; therefore, all environmental data are only available from cruise, station, and satellite observations. Chl *a*, PP, dissolved inorganic carbon (DIC) and total alkalinity (TA) were measured within the mixed layer at each station in the North PAL LTER sampling region during austral summer, as described in Vernet et al. (2008), Ducklow et al. (2012a) and Hauri et al. (2015), respectively. Discrete measurements of chl *a* were integrated to 100 m, and PP to the deepest PP measurement (i.e., bottom of the euphotic zone). Chl *a* data were available from 2003 to 2017 and PP data from 2003 to 2015. Carbonate chemistry variables including calculated pH measured on the total scale and saturation state for aragonite (Ω_{ar}) were determined from averaged values of DIC, TA, temperature, salinity, phosphate, silicate, and pressure collected from the euphotic zone in summer using the CO2SYS MATLAB version 4.0.9 (van Heuven et al., 2011) and as described in Hauri et al. (2015). No TA data were collected in 2003–2004. Year-round SST was determined by the NOAA optimal interpolation (OI) sea surface temperature analysis (version OI.v2) using *in situ* and satellite SSTs as well as SSTs simulated by sea ice cover (Reynolds et al., 2002). These data are located at <http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.ReynSmithOIv2/>. Monthly data were used to determine annual and seasonal means as follows: spring (Sept.–Oct.–Nov.), summer (Dec.–Jan.–Feb.), fall (Mar.–Apr.–May) and winter (Jun.–Jul.–Aug.). SST concomitant with the time of trap recovery in January was also estimated via OI.

Year-round sea ice parameters included extent, area, duration, date of advance, date of retreat, number of ice days, and open water area in the North PAL LTER study region as described in Thibodeau et al. (2019). Retreat for each sea ice year (March 15 of current year to March 14 of following year to correspond to the beginning and end of the mean summer sea ice extent minimum) is defined as the last day when sea ice concentration decreased past 15% and remained below that threshold for at least five consecutive days (Stammerjohn et al., 2008b). These data were derived from satellite imagery (Scanning Multichannel Microwave Radiometer and Special Sensor Microwave/Imager; SMMR-SSM/I) as described in Stammerjohn et al., 2008a. SMMR-SSM/I sea ice concentration data were from the Earth Observing System Distributed Active Archive Center at the National Snow and Ice Data Center, University of Colorado (<http://nsidc.org>). All the above data in the analyses are available at: <https://pal.lternet.edu/data>.

The relationship between pteropod phenology and climate indices known to influence the pelagic Antarctic Peninsula region was analyzed (Ross et al., 2008; Stammerjohn et al., 2008b; Loeb and Santora, 2013; Saba et al., 2014; Steinberg et al., 2015; Thibodeau et al., 2019). These indices include the El Niño/Southern Oscillation (ENSO) indicator based on sea surface temperature (referred to as the Multivariate ENSO Index (MEI) (<http://www.esrl.noaa.gov/psd/people/klaus.wolter/ter/MEI/>) and the Southern Annular Mode (SAM) (<http://www.antarctica.ac.uk/met/gjma/sam.html>) index based on sea level pressure. These climate indices are seasonally adjusted (e.g., Hurrell, 1995).

In order to test relationships between pteropod phenology and environmental forcing concurrent with the time of the summer (Jan./Feb.) cruise sampling, we lagged the explanatory variables with zero- and one-year lags. The sediment trap sampling season spans two calendar years (e.g., Jan. 2016 through Jan. 2017). The calendar year for the end of the sediment trap sampling (retrieval) season was used to designate each sampling year. Measurements for summer chl *a*, PP, and carbonate chemistry occur during the cruise sampling period in summer (e.g., Jan. 2017 and Feb. 2017) so the calendar year for the summer sampling season was used to define the lag for these parameters. Satellite SST and climate indices span two calendar years and are averaged throughout the year (e.g., Dec. 2016 to Feb. 2017). For example, a

Table 1

Linear model results of natural log-transformed median *Limacina helicina antarctica* shell diameter data for the sediment trap time series (2004–2018). Presented are statistical scores obtained from the model for each year with 1) adult and juvenile size classes combined, 2) juvenile size class only, and 3) adult size class only. Test statistics include sample size (*n*, number of median diameters (samples) per year), the coefficient (slope) for the regression equation, the adjusted R^2 , *p*-value, and growth rates in mm day^{-1} . Significant models ($p < 0.05$) are in bold. Certain age classes for 2006–2008 did not yield enough data ($n < 3$) to run a linear model and thus were excluded. Juveniles are defined as < 1 mm while adults are defined as > 1 mm (Wells, 1976). Note: Juvenile models 2012 and Adult models 2004 and 2017 were not natural log-transformed to produce the best model fit indicated by *. Modeled growth coefficient for adults and juveniles combined includes all years to show interannual variability but the coefficients in 2006 and 2008 (indicated by +) were not included in subsequent analyses (i.e., general linear models) due to low sample size (2006) and inability to fit a statistically significant growth curve to these data (2008). Mean growth coefficients and growth rates ($\pm$ standard error) are for entire time series.

1. Adults & Juveniles combined						2. Juveniles only					3. Adults only				
Year	<i>n</i>	Coefficient	R^2	<i>p</i>	mm day^{-1}	<i>n</i>	Coefficient	R^2	<i>p</i>	mm day^{-1}	<i>n</i>	Coefficient	R^2	<i>p</i>	mm day^{-1}
2004	7	0.009	0.97	< 0.001	0.01	4	0.004	0.93	< 0.02	0.004	7	0.008*	0.69	< 0.02	0.007
2005	6	0.007	0.90	< 0.002	0.007	5	0.003	0.92	< 0.005	0.003	4	0.003	0.28	< 0.28	0.006
2006	6	0.01	0.65	< 0.03+	0.03	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2007	6	0.005	0.83	< 0.007	0.005	5	0.002	0.39	< 0.15	0.002	NA	NA	NA	NA	0.00
2008	4	0.003	0.46	= 0.19+	0.001	4	0.002	0.66	< 0.11	0.002	NA	NA	NA	NA	−0.004
2009	6	0.006	0.90	< 0.001	0.006	4	0.003	0.99	< 0.001	0.003	4	0.003	0.47	< 0.19	0.004
2011	8	0.01	0.82	< 0.001	0.01	4	0.004	0.98	< 0.005	0.004	4	0.02	0.92	< 0.02	0.04
2012	7	0.005	0.91	< 0.001	0.004	4	0.002*	0.91	< 0.03	0.002	7	−0.001	0.03	< 0.32	−0.008
2013	7	0.004	0.81	< 0.003	0.005	4	0.001	0.96	< 0.01	0.001	3	0.008	0.87	< 0.16	0.01
2014	9	0.007	0.87	< 0.001	0.007	5	0.003	0.88	< 0.01	0.003	5	0.007	0.66	< 0.057	0.01
2015	6	0.008	0.82	< 0.008	0.01	3	0.001	0.89	< 0.15	0.001	5	0.007	0.91	< 0.007	0.01
2016	7	0.006	0.89	< 0.001	0.008	4	0.0006	−0.47	< 0.85	0.0006	6	0.003	0.71	< 0.02	0.007
2017	7	0.007	0.94	< 0.001	0.009	3	0.003	0.97	< 0.07	0.003	3	0.02*	0.99	< 0.04	0.02
2018	7	0.006	0.74	< 0.007	0.01	4	0.0005	−0.26	< 0.6	0.0005	6	0.005	0.63	< 0.03	0.01
Mean		0.007 $\pm$ 0.0005			0.009 $\pm$ 0.001		0.002 $\pm$ 0.0003			0.001 $\pm$ 0.0001		0.006 $\pm$ 0.001			0.009 $\pm$ 0.003

significant relationship between *L. h. antarctica* time of appearance in 2017 (trap deployed Jan. 2016, retrieved Jan. 2017) and a 1-year lag in summer satellite SST would indicate that variation in *L. h. antarctica* appearance was affected by SST in summer 2016 (mean of Dec. 2015, Jan. 2016, and Feb 2016). A 1-year lag in sea ice extent would indicate that sea ice extent in the spring of 2015 affected *L. h. antarctica* appearance in 2017 (i.e., Jan. 2016 through Jan. 2017).

2.5. Anomaly calculations

Annual summer-time anomalies (A_y) for environmental parameters from 2004 to 2018 were calculated consistently across sampling methods. For parameters that were measured on PAL LTER cruises in the same sampling year (chl *a*, PP, and carbonate chemistry), mean grid station values were $\log_{10}$ -transformed before calculating the annual mean for year *y* ($\bar{A}_y$):

$$1) \bar{A}_y = \frac{1}{n} \sum_{i=1}^n \log_{10}(a_i)$$

where *n* is the number of grid stations sampled and a_i is the mean value for each grid station. For satellite derived parameters (SST and sea ice), a single annual value was $\log_{10}$ -transformed to calculate $\bar{A}_y$. Annual anomalies (A_y) were then calculated using the following formula:

$$2) A_y = \bar{A}_y - \bar{A}$$

where $\bar{A}$ is the mean of the yearly $\log_{10}$ -transformed means ($\bar{A}_y$) (Mackas et al., 2001; O'Brien et al., 2011; Steinberg et al., 2015; Wiebe et al., 2016). These equations are modified from Steinberg et al. (2015) and Thibodeau et al. (2019) to indicate clearly that data were $\log_{10}$ -transformed prior to calculating annual means. Chl *a*, PP, carbonate chemistry variables, and sea ice anomalies were calculated specifically for the PAL LTER North sub-region only. Anomalies of year-round SST for the North sub-region were determined with NOAA OI sea surface temperature analysis (version OI.v2) using *in situ* and satellite SSTs as well as SSTs simulated by sea ice cover (Reynolds et al., 2002). Climate indices are already in anomaly form and do not have sub-regional anomalies.

2.6. Comparison of environmental parameters and climate indices

General Linear Models (GLMs), with data in annual anomaly form for the North sub-region, were developed to identify the effects of covariates on the growth and time of appearance of *L. h. antarctica*. The covariates included annual chl *a*, PP, carbonate chemistry variables, seasonal SST, the seven ice variables, and two climate indices. In order to meet all assumptions of multiple linear regression including homogeneity of variance, normally distributed data, fixed predictors, and no multicollinearity among predictors, time of appearance data were natural log-transformed. The (unitless) growth coefficient from each linear model for the pooled shell diameters (adults and juveniles) (Table 1) was used for the growth GLM and no additional transformation was needed for these data. Assumptions were verified by plotting residuals versus fitted values and covariates (Zuur and Ieno, 2016). Covariates from the GLMs were assessed for outlying and influential observations and normality of residuals. Positive autocorrelation was tested with the Durbin-Watson test (Neter et al., 1996). Chosen covariates in the models were based on *a priori* hypotheses about how those covariates affect pteropod phenology as described in Thibodeau et al. (2019). The final best fitting models for growth and time of appearance were identified based on the highest adjusted R^2 value (Quinn and Keough, 2002). Significance for all statistical analyses was determined at $\alpha = 0.05$. All analyses were performed in R statistical framework version 3.2.4 (R Statistical Core Team, 2016).

3. Results

3.1. Pteropod seasonal population size structure

A new *L. h. antarctica* cohort typically first appeared in the trap during late austral autumn into early winter (May–June) with a median size ($\pm$ standard error) of the first pteropods appearing of 0.62 ± 0.05 mm for the entire time series. The cohort continued to grow over the winter season, with shell size frequency following a normal distribution (Fig. 3). *L. h. antarctica* was present in the sediment trap consistently from austral autumn to late spring or early summer (Nov.–Dec.) ranging in median size from 0.72 ± 0.03 mm in austral winter to 1.6 ± 0.14 mm in early summer for the entire time series. *L. h. antarctica* shell diameter

typically reached a maximum diameter between the months of Jan.–Feb. with the largest median recorded size, 7.52 mm, collected in early-Feb. 2018 (Fig. 3). Pteropods were usually not present in the trap from Jan. to Mar. (austral summer to early autumn), but occasionally a large adult appeared in the trap in summer—such as occurred in late Jan. and Feb. 2018 (Fig. 3). Typically, only one cohort was identified throughout the period *L. h. antarctica* were present in the trap. A smaller, second size-class was sometimes observed (e.g., Jul.–Sept. 2004, Oct. 2014) (Fig. 4) but did not develop into a second generation throughout the entire season (Fig. 3). In addition, a small number of veliger *L. h. antarctica* sporadically appeared in the trap in austral summer (e.g., Dec. 2009, Dec. 2014, Dec. 2016) (Fig. 4).

L. h. antarctica collected with net tows at Palmer Station from Nov. 2017 to Feb. 2018 exhibited a normal size distribution that followed a similar growth pattern to sediment trap samples (Fig. 5). Median shell size of pteropods collected at Palmer Station increased from 3.45 mm in Nov. 2017 (late spring), to 4.43 mm in Dec. 2017 (early summer), to 5.90 mm in Jan. 2018 (summer), and to 6.43 mm in Feb. (late summer). These median shell diameters are consistent with those obtained from the sediment trap, except for Dec. 2017 when <5 individual *L. h. antarctica* were collected in the trap – the low sample size explaining the discrepancy in median diameter for this month (Fig. 5). Further comparison with additional net tows collecting above the sediment trap location during Jan. 2018 exhibited a median size of 5.77 mm, indicating pteropods at the trap location were most likely from the same

cohort as those collected near Palmer Station.

3.2. Long-term observations of pteropod phenology

There was no significant long-term trend in *L. h. antarctica* time of appearance; however, there was high interannual variability within the time series (Fig. 6). A new *L. h. antarctica* cohort typically first appeared between 125 and 170 day of year (i.e., ~Apr.–June) with the first cohort for half of the sampling years appearing in May (i.e., day 138) (Fig. 6). The years 2006, 2007, and 2012 were considerably different, with time of appearance of the first *L. h. antarctica* cohort much later at day of year 255 (Sept.) in 2006, early at day of year 50 (late Feb.) in 2007, and extremely early at day of year 22 (late Jan.) in 2012. (We note that the sample size of specimens in the 2006 sediment trap was overall much lower compared to other years in the time series, thus we interpret the late appearance in 2006 with caution.)

L. h. antarctica shell diameter growth was exponential for each year of the time series (2004–2018) (Fig. 7). All annual growth models were significant ($p < 0.05$) with R^2 ranging from 0.65 to 0.90 except 2008 ($p > 0.05$) and 2010 (because the trap was not recovered) (Table 1). The average ($\pm$ standard error) modeled growth coefficient for the time series (2004–2018) for adults and juveniles combined was 0.007 ± 0.0005 , and growth rate was 0.009 ± 0.006 mm day⁻¹ (Table 1). Modeled growth coefficients varied inter-annually by a factor of two, with the slowest significant growth of the time series occurring in 2013

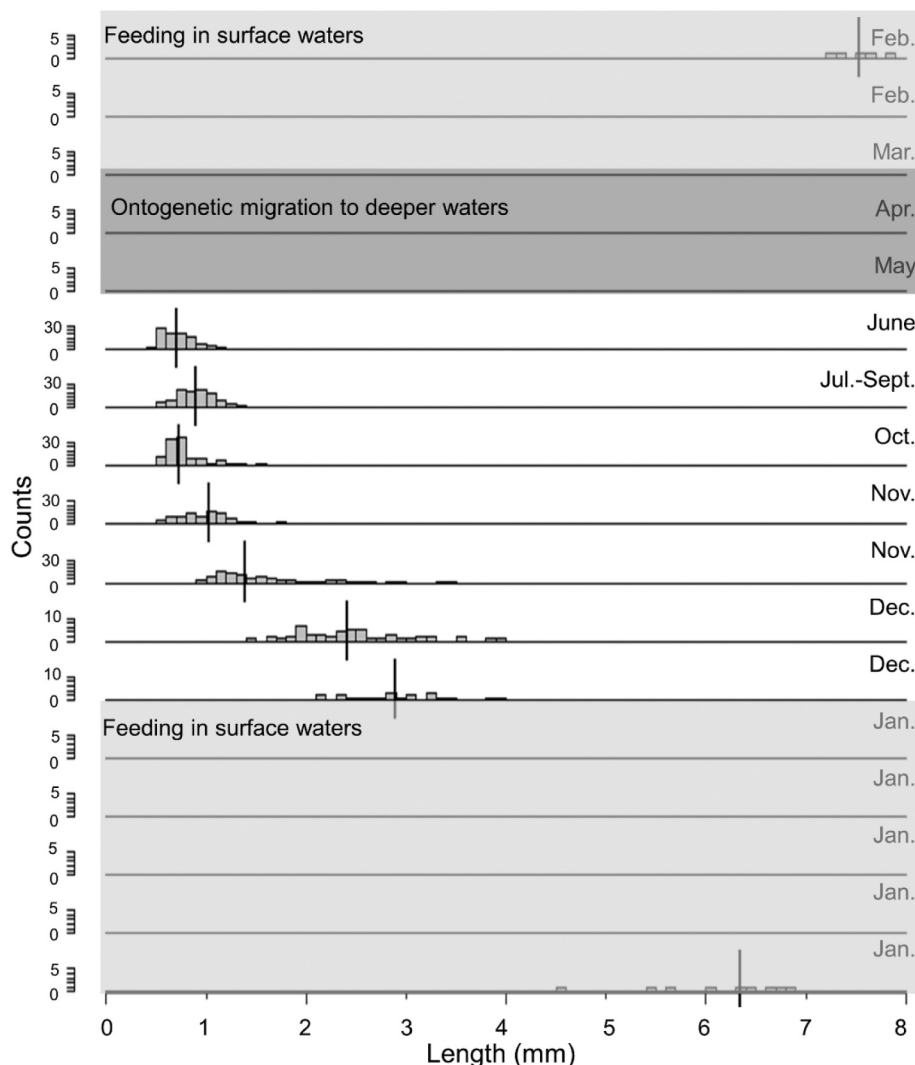


Fig. 3. Size-frequency histogram of *Limacina helicina antarctica* shell diameter for the 2017–2018 sediment trap sampling season (February 1, 2017–January 31, 2018). Similar histograms were constructed for each year of the time series (2004–2018). Each sampling period/trap cup for the year is shown. Black vertical lines indicate median shell diameter for each sample cup. Light gray shaded region shows period when *L. h. antarctica* is hypothesized to be feeding in the surface waters. Dark gray shaded region indicates when *L. h. antarctica* larvae begin ontogenetic (seasonal) migration into deeper waters (see Discussion for additional explanation of these periods). Note different y-axis scales (left) and that *L. h. antarctica* were not present during some sample periods.

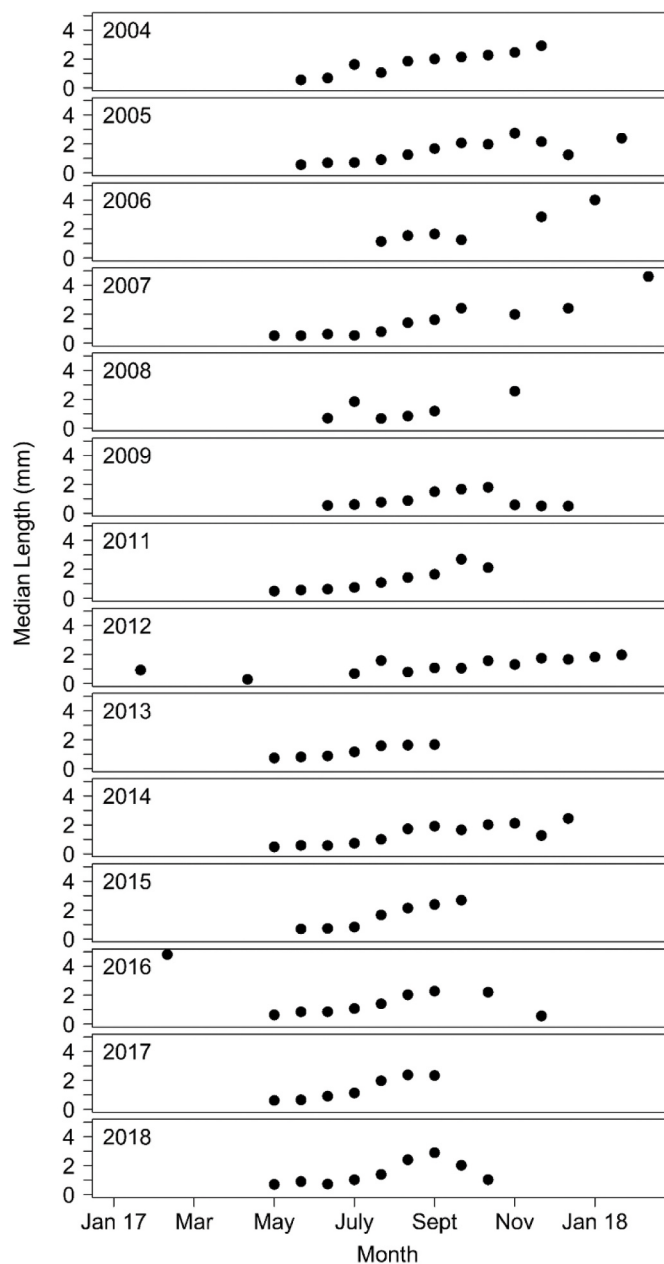


Fig. 4. Median shell diameter for each sediment trap sample cup in which *Limacina helicina antarctica* was present. To best compare seasonal and inter-annual size variation, the y-axis scale is set at a maximum of 5 mm, which excludes $n = 7$ data points (collectively from 2011, 2017, 2018; see Fig. 7 for complete dataset). No data are available in 2010 because the trap was not successfully recovered.

(0.004) and the fastest occurring in 2011 (0.01) (Fig. 8). There was no significant long-term directional trend in *L. h. antarctica* growth coefficient over the time series ($p > 0.05$) (Fig. 8). Growth of juveniles and adults for the time series (2004–2018) are each also summarized in Table 1. The average modeled growth coefficient for juveniles was 0.002 ± 0.0003 and for adults was 0.006 ± 0.001 ; however, only half of the juvenile and adult growth models were significant, so these life stages were pooled for use in GLMs.

Finally, a growth rate determined for median shell diameter data collected from Nov. 2017 to Feb. 2018 at Palmer Station, was 0.04 mm day^{-1} . Growth rate determined from *L. h. antarctica* shell diameters collected in the sediment trap from Mar. 2017 to Nov. 2017 combined with shell diameters collected from Nov. 2017 to Feb. 2018 at Palmer

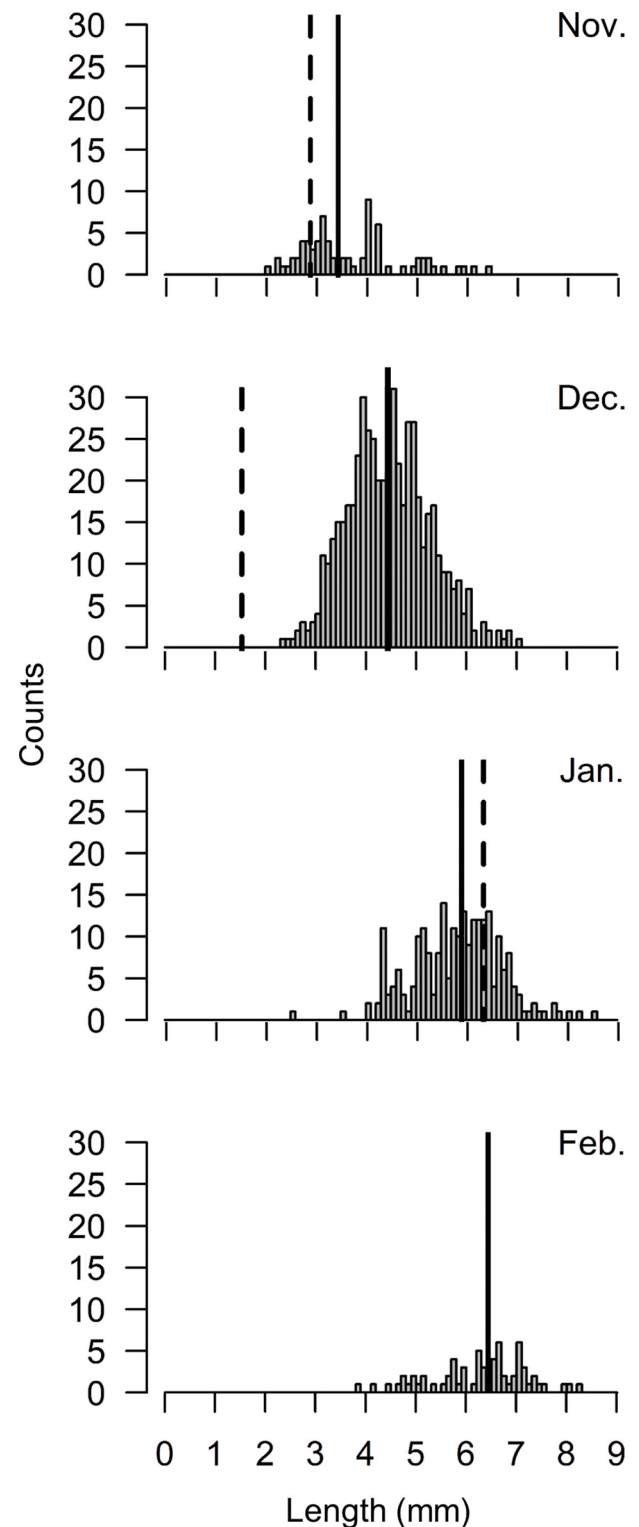


Fig. 5. Size-frequency histogram for *Limacina helicina antarctica* collected from net tows at Palmer Station, Antarctica from November 2017 to February 2018. Median pteropod shell diameter for each sampling month at Palmer Station from net tows (black vertical bars) versus in sediment trap cups corresponding to the same sampling period by calendar month (dashed vertical bars) is shown.

Station was 0.02 mm day^{-1} .

3.3. Environmental controls of pteropod phenology

The best fitting GLM indicated that earlier sea ice retreat the year

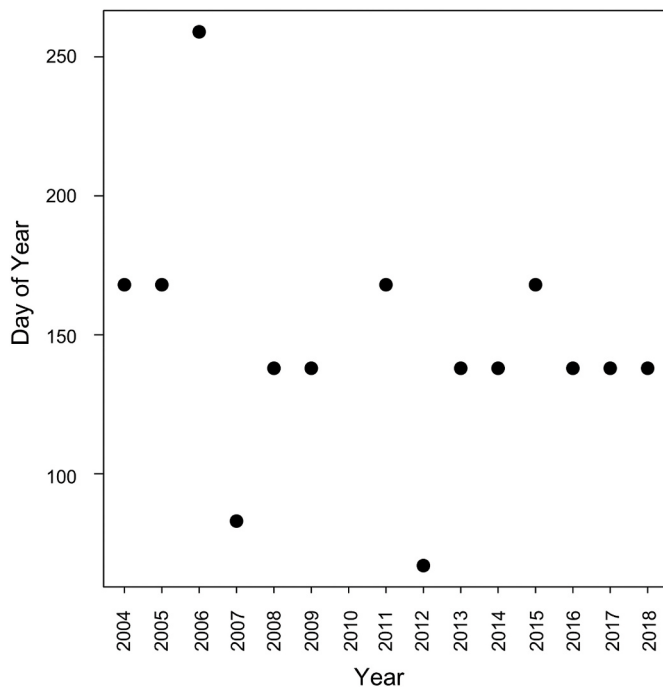


Fig. 6. First day of appearance for a new *Limacina helicina antarctica* cohort to occur in the sediment trap each year for the entire time series (2004–2018). There was no significant linear relationship between year and day of appearance. No data are available in 2010 because the trap was not successfully recovered.

prior, lower winter SST the year prior, and higher PP during the same sampling year best explained earlier *L. h. antarctica* time of appearance (Table 2). Sea ice retreat and winter SST were the only statistically significant predictors in the model, but PP accounted for some of the explained variance. Larger area of open water the year prior, higher autumn SST the year prior, and higher chl *a* during the same sampling year best explained higher annual modeled *L. h. antarctica* growth coefficients. Open water and autumn SST were the only statistically significant parameters in the model but chl *a* accounted for some of the explained variance. The best fitting GLMs did not identify any carbonate chemistry parameters or climate indices as significant in explaining *L. h. antarctica* phenology.

Individual regression relationships between environmental

predictors and *L. h. antarctica* phenology metrics identified by the GLM are shown in Fig. 9 (note that no individual regressions with single environmental parameters were statistically significant but do illustrate directional relationships determined by the GLMs). Earlier sea ice retreat the year prior was associated with earlier *L. h. antarctica* time of appearance and more open water the year before corresponded to faster *L. h. antarctica* growth (Fig. 9a and b). Higher autumn SST the year prior was associated with faster growth but higher winter SST the year prior was associated with a later time of appearance (Fig. 9c and d). Higher chl *a* corresponded with faster growth in the same year and higher PP was associated with earlier time of appearance (not shown). Individual regressions were also conducted with the same environmental parameters for growth of juvenile and adults. More open water the year before corresponded to faster juvenile growth, and earlier sea ice retreat the year prior was associated with faster adult growth. These results agree with the GLMs using pooled adult and juvenile shell diameters (Table 2; Fig. 9).

4. Discussion

4.1. Long-term observations of pteropod phenology

While the considerable interannual variability in growth and time of appearance of each new *L. h. antarctica* cohort reveals fluctuating life history patterns, a significant unidirectional change in *L. h. antarctica* phenology has not occurred in the WAP over the past 14 years (2004–2018). Typically, *L. h. antarctica* were absent in sediment trap samples from late Dec. to Mar. with a new *L. h. antarctica* cohort first appearing in the trap between Apr. and June. Diel, depth-discrete net tows sampling the full water column (0–500 m) along the WAP shelf during summer from 2009 to 2017 show that although *L. h. antarctica* performs diel vertical migration in austral summer, their population was concentrated within the surface 150 m during both night and day (Conroy et al., 2020). Thus, an absence of *L. h. antarctica* in our sediment trap infers the majority of pteropods remained entirely above the depth of the sediment trap (170 m) likely to take advantage of the high productivity in surface waters during summer. Collier et al. (2000) also observed an absence of *L. h. antarctica* during austral summer (Jan.–Feb.) in sediment traps from the Ross Sea most likely because pteropods were feeding in the surface waters. Habitat partitioning may also explain the absence of *L. h. antarctica* from the sediment trap in austral summer. Horizontal habitat partitioning was observed for the Antarctic Krill, *Euphausia superba*, in which adult males and females occur over Antarctic continental shelves, whereas larvae are concentrated offshore

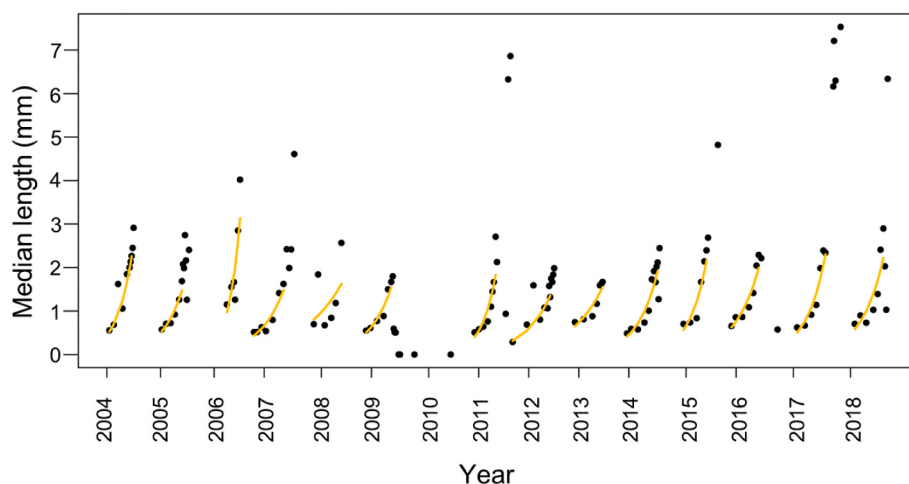


Fig. 7. Time series of median *Limacina helicina antarctica* shell diameter determined from each sediment trap cup from 2004 to 2018. Orange line indicates predicted model growth (see Table 1 for model summaries). No data are available in 2010 because the trap was not successfully recovered. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

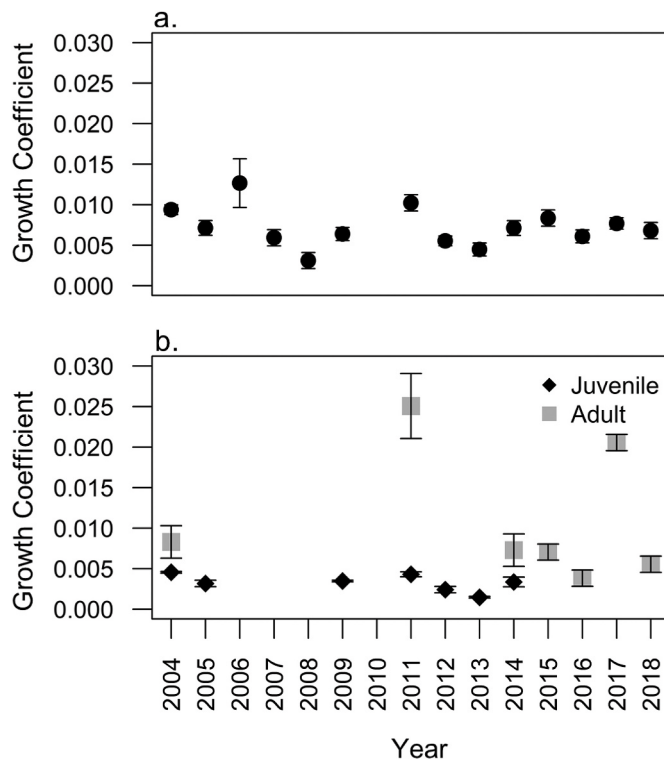


Fig. 8. Modeled growth coefficient ($\pm$ standard error) of *Limacina helicina antarctica* determined for each year of the sediment trap time series (2004–2018) with all diameters combined (a) and with juvenile and adult growth rates separated (b). Juveniles are defined as < 1 mm while adults are defined as > 1 mm (Wells, 1976). Modeled growth coefficient (a) includes all years to show interannual variability but the coefficients in 2006 and 2008 were not included in the analysis due to low sample size (2006) and inability to fit a statistically significant growth curve to these data (2008). Data from 2010 are not available because the trap was not successfully recovered. Years 2006–2008 did not yield enough data ($n < 3$) to run a linear model for juveniles or adults and thus were excluded from (b) (see Table 1). Note some error bars are small and covered by symbols in (a). There was no significant linear relationship between year and growth coefficient.

Table 2

General Linear Model (GLM) results assessing the effect of environmental parameters on *Limacina helicina antarctica* time of appearance and growth coefficient. Presented are explanatory variables and statistical scores obtained from the best model, identified by the highest adjusted R^2 value, among multiple linear regression analyses. Test statistics include adjusted R^2 , sample size (number of years) for the overall model, the coefficient (slope) for the regression equation, the standard error (SE) associated with the model coefficient, and p-value.

Parameter	years	Coefficient	SE	p
Time of appearance (R^2 adjusted = 0.59, $p = 0.01$)	14			
Sea ice Retreat (1-year lag)		8.715	2.321	0.005
Winter SST (1-year lag)		2.019	0.701	0.020
Primary Productivity (no lag)		-0.449	0.205	0.059
Modeled growth coefficient (R^2 adjusted = 0.55, $p = 0.02$)	12			
Open Water (1-year lag)		0.019	0.005	0.006
Autumn SST (1-year lag)		0.018	0.006	0.015
Chlorophyll <i>a</i> (no lag)		0.004	0.003	0.194

(Perry et al., 2019). Adult pteropods are most abundant offshore in slope waters during summer (Thibodeau et al., 2019) which could help explain their absence in the trap, but additional seasonal data for distribution and abundance of juveniles are needed to determine if juvenile pteropods, which are caught in the sediment trap the rest of the year, are more abundant over the (northern) shelf during autumn/winter.

Ontogenetic (seasonal) vertical migration also explains the patterns of *L. h. antarctica* occurrence we observed within our sediment trap. The first appearance of a new *L. h. antarctica* cohort emerged in the sediment trap in austral autumn (Apr. to June) every year, indicative of ontogenetic migration observed in many Southern Ocean zooplankton—including *E. superba* (Fraser, 1936; Ross et al., 1996). *L. h. antarctica* produce free-floating egg sacs that are released in summer and veligers begin to develop at least 30 days later (Paranjape, 1968; Lalli and Wells, 1978; Lalli and Gilmer, 1989; Gannefors et al., 2005). Hopkins (1971) observed high epipelagic densities of *L. h. antarctica* collected in 76 μ m mesh nets (22.0 ind. m^{-3}) but individuals were absent from 202 to 330 μ m mesh nets in Apr.–May from the Pacific sector of the Southern Ocean. The prevalence of specimens smaller than 200 μ m in Apr.–May matches the time of spawning and descent revealed in this sediment trap analysis. Studies along the Antarctic Peninsula also show that the depth distribution of *L. h. antarctica* deepened from austral summer to autumn (Hunt et al., 2008; Marrari et al., 2011), and in the Arctic *Limacina* spp. conduct a seasonal vertical descent during autumn (Kobayashi, 1974; Falk-Petersen et al., 2008). Our time-series sediment trap analysis confirms *L. h. antarctica* as an ontogenetic migrator, which is important for understanding its population dynamics and contribution to biogeochemical cycling in deeper waters (La et al., 2019). In addition, pteropod migration into deeper waters as larvae over winter may lead to greater exposure of aragonite undersaturation during a critical life stage (Comeau et al., 2012; Thabet et al., 2015; Maas et al., 2020), with potential cumulative effects throughout their life history (Bednarssek et al., 2019). Given that the Southern Ocean is predicted to experience prolonged undersaturation of aragonite as early as 2030 (Hauri et al., 2016) it will be important to monitor this potential effect in the near future.

4.2. Characterizing pteropod growth and life span

This study is the first in the Southern Ocean to illustrate that *L. h. antarctica* (shells) actively grow during the ice-covered winter season. There was large variability in growth throughout the time series (2004–2018) with years of slow shell growth as low as $0.004 \text{ mm day}^{-1}$ (2012). The fastest pooled growth rates (2004, 2006, 2011, 2015, and 2018) were $\sim 0.01 \text{ mm day}^{-1}$. The mean juvenile growth rate ($0.001 \pm 0.0001 \text{ mm day}^{-1}$) is smaller than the mean adult growth rate ($0.009 \pm 0.003 \text{ mm day}^{-1}$) and may be related to the different amounts of precipitated calcium carbonate by juveniles versus adults based on the mathematics of a logarithmic spiral (discussed below). The smaller mean juvenile growth rate could have implications for the effects of environmental stressors on juvenile growth and development, but insufficient sample size makes it difficult to fully interpret these rates.

When calculating thecosome growth rates, it is important to acknowledge the different metrics used to describe the rate of growth for calcifying plankton and the effect of their shell shape on growth rate. In a logarithmic spiral that is common in mollusc shells (Cortie, 1992), such as *Limacina* spp., the radius from the spiral origin increases exponentially, but its shape is unaltered with each successive curve. Therefore, measuring increases in shell size with diameter alone is a limitation of our method for determining *L. h. antarctica* growth. While measuring a completely horizontal *Limacina* shell allows for the assessment of the spiral length, it is difficult and could lead to large measurement errors. In contrast, the measurement error used in our protocol for shell diameter is relatively small ($0.007 \pm 0.001 \text{ mm}$). Mathematically modelling *Limacina* spp. shells with a suitable dataset (e.g., aperture dimensions, radius of each turn, angle of rotation, and spiral length) as determined with high-resolution technologies, such as CT scanning (e.g.,

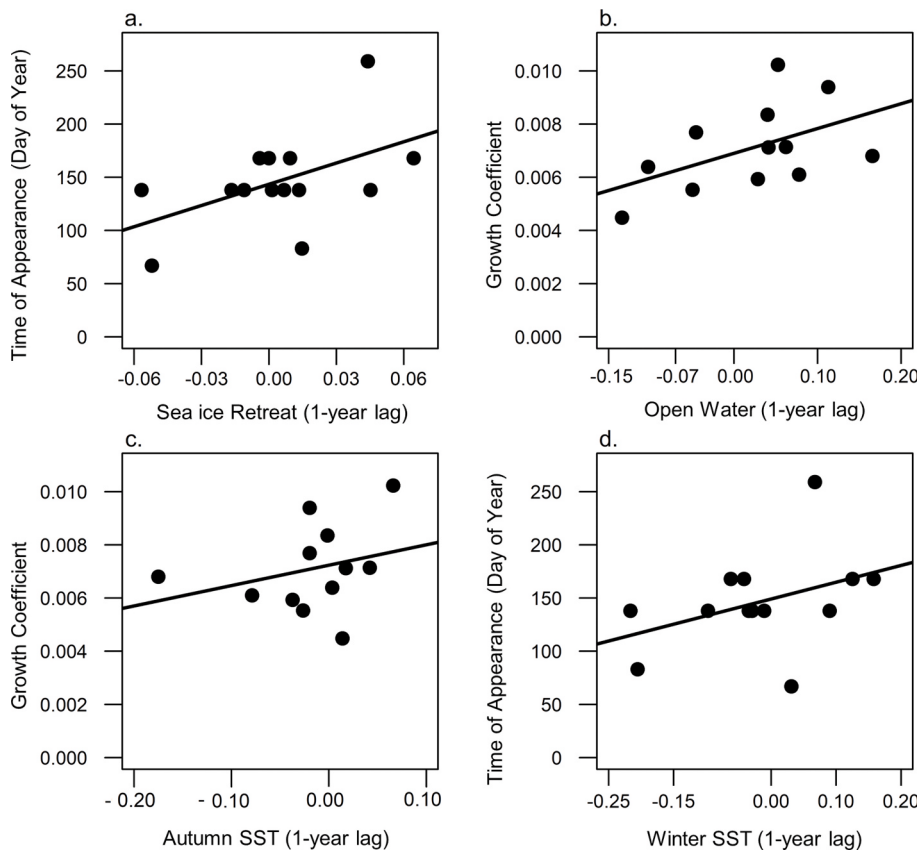


Fig. 9. Effect of environmental conditions on *Lima-cina helicina antarctica* phenology. (a) Sea ice retreat (1-year lag) vs. *L. h. antarctica* time of appearance, (b) Area of open water (1-year lag) vs. *L. h. antarctica* modeled growth coefficient, (c) Autumn Sea Surface Temperature (SST) (1-year lag) vs. *L. h. antarctica* modeled growth coefficient, (d) Winter SST (1-year lag) vs. *L. h. antarctica* time of appearance. Environmental data (x-axes) plotted are annual anomalies for each year of the time series for the North sub-region of the sampling grid. Day of sea ice retreat and winter SST are lagged 1-year behind *L. h. antarctica* time of appearance (e.g., 2017 appearance is plotted against day of 2016 sea ice retreat and SST annual anomalies). All years of the time series (2004–2018) are included in the time of appearance models (a & d) but in (d) 2009 is masked by the 2013 data point. Area of open water and autumn SST are lagged 1-year behind *L. h. antarctica* modeled growth coefficient (e.g., 2017 *L. h. antarctica* growth is plotted against 2016 open water annual anomaly). The years 2006, 2008, and 2010 were not included in the growth coefficient models (b & c) due to low sample size (2006) and inability to fit a statistically significant growth curve to these data (2008). Data from 2010 are not available because the trap was not successfully recovered. There are no significant linear relationships, but regression lines are shown to indicate direction of change (see Table 2 for significant relationships identified with GLMs).

Oakes and Sessa, 2020), is needed in future research.

Since the radius of a logarithmic spiral increases exponentially, comparing the change in shell diameter of different pteropod sizes at different times of the year is difficult when relating it to other studies. Thus, while published research of thecosome pteropod growth determined rates based on shell diameter (Bednaršek et al., 2012; Wang et al., 2017), we hesitate to directly compare our growth rates with other studies and instead, only compare measured shell diameters from the same time of year. Combining the 2017/2018 pooled sediment trap growth rate and Palmer net tow data growth rate set yields a rate of increase in shell diameter of 0.02 mm day^{-1} , and median shell diameter was 4.43 mm in Dec., 5.90 mm in Jan., and 6.43 mm in Feb. These median diameters align with those determined by Bednaršek et al. (2012) in the Scotia Sea of the Southern Ocean during the same months (range 4–10 mm). In a North Pacific temperate fjord, Wang et al. (2017) determined mean ($\pm$ SE) *Lima-cina helicina* shell diameters of $0.63 \text{ mm} \pm 0.04$ in fall, $0.75 \text{ mm} \pm 0.04$ in winter, and $1.02 \text{ mm} \pm 0.18$ in spring. These diameters align with our median shell diameters in the same austral seasons (0.62, 0.72, and 1.6 mm, respectively) indicating continued growth over winter. One question that remains is how pteropods maintain growth during the ice-covered winter season. Given that thecosomes are known flux-feeders (Jackson et al., 1993; Conley et al., 2018), they may be able to consume sinking detritus, ice algae, and protists during this period of low productivity, as observed by other pelagic zooplankton (Roman, 1984; Steinberg, 1995; Kohlbach et al., 2016, 2018). Winter-growth may also be possible through the use of internal lipid reserves (Boissonnot et al., 2019). Data for overwintering pteropod distributions and feeding are needed to fully determine the mechanisms controlling their ecology and life history in the Southern Ocean.

Over the whole time series, the mean *L. h. antarctica* growth coefficient was 0.007. Using an exponential growth function with a coefficient of 0.007, and an average median shell diameter of the first cohort of

0.62 mm, and a sampling period from May to February of the following year (270 days), results in a shell diameter of 4.08 mm in February. This diameter is less than the median shell diameter of *L. h. antarctica* collected from net tows near the sediment trap (5.77 mm) and at Palmer Station (5.90 mm) during austral summer (Jan.). Based on this growth rate, *L. h. antarctica* would need to live 320 days ($\sim$ 11 months) to achieve this diameter (5.77 mm). There is evidence from previous studies that *L. h. antarctica* collected along the Antarctic Peninsula in early summer are overwintering adults that then die off after spawning in late summer (Massey 1920 in Lalli and Gilmer, 1989; Hunt et al., 2008). Since the growth rates calculated in this study typically underestimate the maximum size of *L. h. antarctica* in summer, we agree with the conclusions of Bednaršek et al. (2012) that *L. h. antarctica* may live more than one year, but these larger, now greater than 1-year old adults may be advected offshore (as discussed above) since we did not catch them in the sediment trap at the end of their life cycle. Austral winter growth rates measured in our study are important for interpreting *L. h. antarctica* development during a critical season, and stage of their life history, that is extremely under sampled. These growth rates can be used in ecological models to address the fate and future risks of pteropods in a time of increasing environmental change.

4.3. Pteropod phenology in relation to environmental parameters

L. h. antarctica phenology was controlled primarily by sea ice, although sea surface temperature and primary production were also important factors. Earlier sea ice retreat with lower winter SST, both in the year prior, and lower PP in the same year best explained earlier *L. h. antarctica* time of appearance. Similarly, more open water with higher autumn SST, both in the year prior, and elevated chl *a* the same year were associated with faster *L. h. antarctica* growth. These model results indicate earlier sea ice retreat in austral spring could explain earlier seasonal migration into deeper waters in autumn with sustained

development through the winter with lower SST. In addition, more open water, combined with warmer SST in autumn, induces faster *L. h. antarctica* growth. This earlier migration and faster growth accelerate *L. h. antarctica*'s developmental cycle over winter, resulting in *L. h. antarctica* returning to surface waters earlier in summer. High PP/chl *a* (food) in summer further stimulates *L. h. antarctica* metabolic rates that could lead to faster growth of veliger pteropods as well as spawning, causing a new *L. h. antarctica* cohort to appear earlier in the sediment trap in autumn.

While there is limited environmental information related to pteropod entry into sediment traps, Collier et al. (2000) observed high sedimentation of *L. h. antarctica* shells in their traps at ~575 m depth in late autumn following a pulse of sinking diatoms in the Ross Sea, which corroborates the positive relationship between chl *a* and pteropod phenology observed in our study. A recent study along the WAP with the same *L. h. antarctica* specimens collected in the PAL LTER sediment trap found negative Southern Annular Mode with high chl *a* concentration best explained high pteropod fluxes (Keul et al. in prep). Roberts et al. (2014) considered the effects of carbonate chemistry, PP, and SST on *L. h. antarctica* shell weight and flux in the Polar Frontal Zone, finding that none of these environmental factors were significant predictors. In our study, SST was a significant predictor of *L. h. antarctica* phenology but there was no statistical relationship with carbonate chemistry variables in the models. While thecosomes are considered sentinel indicators of ocean acidification, whose populations may be negatively affected in the near future (Manno et al., 2017), the WAP region is currently oversaturated with respect to aragonite (Hauri et al., 2015). Therefore, the lack of a statistically significant relationship with carbonate chemistry variables is to be expected. Water column sampling of pteropods with nets along the WAP also indicates their long-term abundance is not significantly affected by trends in carbonate chemistry (Thibodeau et al., 2019). Most likely a longer time series with higher resolution data on seasonal time-scales is required to detect significant relationships (Henson et al., 2010; Hauri et al., 2015), as suggested in Thibodeau et al. (2019).

Water column sampling of pteropods with nets along the WAP also indicates sub-decadal climate oscillations are important controls on pteropod abundance, with higher abundance following warmer conditions and subsequently low sea ice (Ross et al., 2008; Loeb and Santora, 2013; Steinberg et al., 2015; Thibodeau et al., 2019). While no long-term changes in *L. h. antarctica* phenology were observed within this sediment trap dataset, high interannual variability in *L. h. antarctica* time of appearance and growth shows these pteropods are influenced by environmental changes, particularly those related to sea ice, temperature, and food. A study in the Amundsen Sea by La et al. (2019) also found zooplankton, including pteropod, seasonal migration was strongly influenced by shifts in sea ice and net primary productivity. That environmental controls such as sea ice and SST affect pteropod phenology one year later also suggests their spawning is potentially influenced by these environmental factors as well.

5. Conclusions and significance

L. h. antarctica phenology provides key information on the effects of environmental controls on pteropod time of appearance and growth. Gelatinous zooplankton phenology is understudied with respect to other zooplankton (i.e., copepods and krill) (Ji et al., 2010), and few study regions in the Southern Ocean have the necessary datasets to observe phenology shifts. This study utilized an extensive sediment trap time series (2004–2018) to illustrate *L. h. antarctica* shells actively grow during the ice-covered winter season with continued growth into the austral summer. Less sea ice and earlier retreat the year prior corresponded to earlier pteropod time of appearance and faster growth rates. Elevated sea surface temperature, in the year prior, and chlorophyll *a* the same year also led to faster pteropod growth. These results show that pteropod life history is strongly controlled by sea ice, sea surface

temperature, and food, which can be used to predict the effects of environmental change on pteropods in the future.

Despite considerable interannual variability in the time of appearance of a new pteropod cohort, no long-term, directional change in time of appearance or growth rate was observed. These results indicate that while pteropods are responsive to considerable environmental variability on both temporal and spatial scales their phenology has remained relatively stable. Long-term observations of *L. h. antarctica* abundance and distribution in the WAP with net sampling also confirm this stability in their populations (Thibodeau et al., 2019). The identified responses of pteropod phenology to environmental shifts are key for determining future effects of climate change on regional biogeochemical cycling and plankton trophic interactions within the Southern Ocean.

Author statement

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Declaration of competing interest

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

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Appendix A. Supplementary data

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