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Contrasting life cycles of Southern Ocean pteropods alter their vulnerability to climate change

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Pteropods are a key part of biogeochemical cycling and epipelagic food webs in the Southern Ocean. However, shelled pteropods are vulnerable to climate change, due to their aragonite shells being particularly sensitive to ocean acidification. Currently our understanding of pteropod responses to environmental change is hindered by uncertainties surrounding their life cycles and population dynamics. In this study, we describe polar shelled pteropod diversity in the north-eastern Scotia Sea, inferring life history and population structures of the dominant pteropod species, *Limacina rangii* (formerly *Limacina helicina antarctica*) and *Limacina retroversa*. An annual timeseries of *Limacina* shell morphometrics was derived from individuals collected in a moored sediment trap at 400 m depth. We found that *L. rangii* and *L. retroversa* have contrasting life history strategies. *L. rangii* has a continuous spawning and recruitment period from November to March and can overwinter as juveniles and adults. *L. retroversa* has discrete spawning events from November to May, producing non–overlapping cohorts of juveniles and adults. Their development to the adult stage takes between two and five months, upon which they overwinter as adults. Our findings suggest different vulnerabilities of *L. rangii* and *L. retroversa* to a changing ocean. For example, since all life stages of *L. rangii* co-exist, vulnerability of one cohort is not detrimental to the stability of the overall population whereas, if one *L. retroversa* cohort fails to recruit, the entire population is threatened. Changes in pteropod populations could have cascading ramifications to Antarctic ecosystems and carbon cycling.

KEYWORDS

pteropod life history, sediment trap, Scotia Sea, *Limacina helicina antarctica*, marine ecology, Antarctic, population dynamics, zooplankton

1 Introduction

Thecosome (shelled) pteropods are holoplanktonic gastropods with a cosmopolitan distribution throughout the world's oceans. In the Southern Ocean, pteropods can occur in high densities (Bednaršek et al., 2017; Burridge et al., 2017), especially in regions characterized by high phytoplankton concentrations (Hunt et al., 2008; Ward et al., 2008) where they play a key role in the marine ecosystem. Pteropods are efficient omnivorous grazers (Hopkins and Torres, 1989; Bernard and Froneman, 2009), are prey for higher trophic levels (Hunt et al., 2008) and form an important contribution to organic and inorganic carbon cycling (Bednaršek et al., 2012c; Manno et al., 2018).

Despite extensive research into pteropods there remains considerable uncertainty in estimates of their growth rate, longevity, spawning season(s), and seasonal population structures within and between species (i.e. Kobayashi, 1974; Fabry, 1990; Gannefors et al., 2005; Hunt et al., 2008; Bednaršek et al., 2012a; Thibodeau et al., 2020). Such uncertainties arise from differences in sampling protocols (McGowan John and Fraundorf Vernie, 1966; Cermeño et al., 2014) and geographical ranges and scales (Wiens, 1989) between studies. For example, sampling net mesh sizes may select or exclude certain cohorts, biasing the size distribution of sampled populations (Hunt et al., 2008). Furthermore, each pteropod species inhabits specific geographical ecoregions, such that life cycles tend to be species-specific in response to local environmental conditions. Certain life stages, such as the high growth veliger phase (the immature pteropod stages that have yet to develop wings), which demand high energy budgets, often coincide with local phytoplankton blooms (Maas et al., 2011). Acclimation and adaptation of pteropods to localized conditions therefore leads to inter- and intra-species differences in environmental tolerances (Bednaršek et al., 2017). Variation in life history may also occur within taxonomic sub-units, for example, *Limacina helicina* comprises of several morphotypes (not classed as separate species) in the Arctic Ocean (*acuta*, *helicina*, and *pacifica*). Similarly, several *L. retroversa* formae are found in the Arctic (*balea and retroversa*) and the Southern Ocean (*australis*) (Hunt et al., 2010; Jennings et al., 2010).

Shell morphometric analyses are an effective tool to assess age structure and spawning events of pteropods (Wang et al., 2017) based on the assumption that the rate of shell extension is linear throughout Limacinidae life cycles (Hsiao, 1939; Lalli and Wells, 1978; Lalli and Gilmer, 1989). Thibodeau et al. (2020) and Weldrick et al. (2021) estimated *L. rangii* phenology using shell morphometrics of specimens collected from sediment traps deployed along the Western Antarctic Peninsula and the Indian sector of the Southern Ocean, respectively. While sediment traps primarily record the vertical flux of passive particulate matter from the upper ocean (Turner, 2015), Makabe et al. (2016) showed that the abundance of live pteropods entering the sediment trap (active "swimmers", likely in search of prey) correlates well with their relative abundance in corresponding net samples. Identifying swimmers within sediment trap samples can therefore be considered representative of the seasonal population structure. Moored sediment traps allow year-round sampling at a fixed geographical location at user-defined temporal intervals. Sediment trap sampling is particularly valuable in remote and difficult to access areas, such as in the Southern Ocean. Furthermore, sediment traps do not select for specific size cohorts, making sediment traps an effective tool to estimate pteropod life history and population dynamics (Makabe et al., 2016).

In this study, we estimate the abundance and seasonal variability of thecosome pteropod species collected within a sediment trap moored for one year downstream of South Georgia in the northeast region of the Scotia Sea. We investigate life history and population structures (i.e., spawning, growth rates, cohort and life stage dynamics and longevity) by assessing the shell morphometrics of the two dominant pteropod species *L. rangii* and *L. retroversa australis* (hereafter *L. retroversa*) through December 2014 to November 2015. Characterizing local life history and population structures of pteropods is critical to forecast potential cascading impacts on biogeochemical cycling and epipelagic food webs in the face of anthropogenic climate change. The Scotia Sea is undergoing some of the fastest rates of climatic change in the Southern Ocean (Henson et al., 2017). Due to their aragonite shells being particularly sensitive to ocean acidification (Manno et al., 2017), and the rapidity of change in this region, there is an urgency to better understanding and monitoring the ecology of this sentinel species.

2 Materials and methods

2.1 Sample collection

A McLane PARFLUX sediment trap (0.5 m^2 capture area, McLane Labs, Falmouth, MA, USA) was deployed at 400 m water depth (sea floor depth of 3787 m) on a bottom-tethered mooring line for 350 days (12 December 2014-28 November 2015) at the sustained observation location P3 in the north eastern Scotia Sea (52°48.7" S, 40°06.7" W) (Figure 1). The site P3 is bounded by the Polar Front to the north and the Southern Antarctic Circumpolar Current Front to the south and east and is situated in an area of high biological productivity, with extensive and prolonged phytoplankton blooms (Borrione and Schlitzer, 2013). In December 2014 the chlorophyll-*a* max was 2.7 $\mu g\ l^{-1}$ at ~30 m (Liszka et al., 2019).

The sediment trap was equipped with 21 x 500 ml collection cups filled with 4% formaldehyde buffered with excess sodium tetraborate (borax). These preservatives poison swimmers swiftly, minimising physical damage to the sample caused by opportunistic scavengers, arresting biological degradation and stopping pteropod shell dissolution (Goto et al., 2016). Cups rotated on a 14-17 (spring and summer) and 30-31 (autumn and winter) day schedule with 15 cups being utilised within the sampling period (Supplementary Material 1).

Sensors attached to the mooring line measured temperature (°C, SAMI) and pH (total scale, SAMI) were measured at 200 m depth and oxygen (μM, optode within the Aquadopp current meter) at

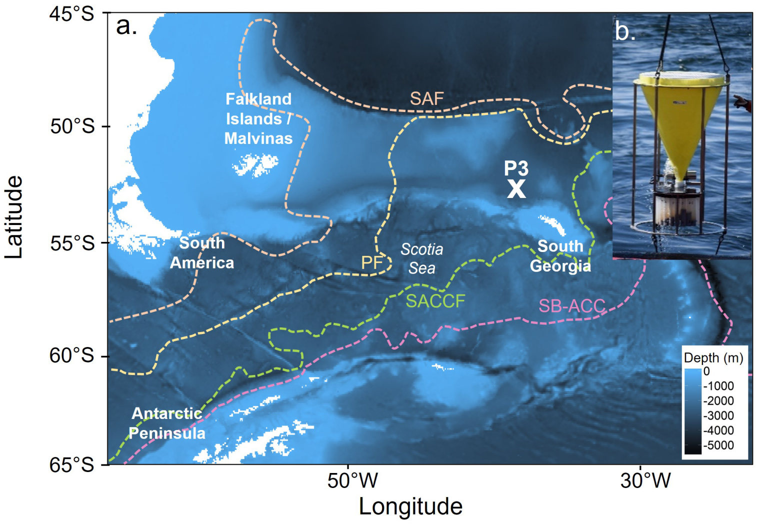


FIGURE 1
(A). The location of the sediment trap mooring (P3: 52°48.7" S, 40°06.7" W) sampling site and **(B)**. An image of the sediment trap as it was recovered in November 2015. The blue shading indicates the seafloor depth, while the white represents the land. Dashed lines indicate the position of the Sub-Antarctic Front (SAF), Polar Front (PF), Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary of the Antarctic Circumpolar Current (SB-ACC). Positions of the SAF, PF and SB-ACC were taken from Orsi et al. (1995), while the position of the SACCF was from Thorpe et al. (2002).

400 m depth. Chlorophyll-*a* data (mg m^{-3}) from Aqua MODIS with a 4 km resolution, (NASA Ocean Biology) from a 12 x 12 km box centered on P3. A current meter 1 m underneath the sediment trap recorded mean current speeds of 0.05 (range: 0-0.22) cm/s (SeaGuard TD262a). Current speed measurements were taken adjacent to the sediment trap every 15 minutes and averaged over a 1 minute intervals. Hydrodynamic bias was negligible since current speeds over the sampling period were below the level where trapping efficiency is considered to decrease (Supplementary Material 2), and where considerable lateral advection might occur (10-12 cm/s) (Baker et al., 1988; Whitehouse et al., 2012).

2.2 Pteropod identification

The sediment trap samples were analysed in their entirety to avoid splitting biases and to maximize morphometric information (Gerhardt et al., 2000; Chiarini et al., 2013). Specimens were identified, counted and photographed dorsoventrally for shell morphometric characteristics under a dissection microscope (Olympus SZX16 fitted with a Canon EOS 60D DSLR camera).

Identification of unbroken specimens was to species and formae level as described by Van der Spoel and Dadon (1999) and Hunt et al. (2008). Pteropods generally had shells fully intact, however, some shell fragments were found. Shell fragments were only counted as an individual if a protoconch was present. Damaged shells were excluded from morphometric analyses. Unbroken pteropod shells were classed into three categories (Figures 2E–H) to reflect their condition, being 1. Well preserved, retracted soft body with a transparent shell, 2. Signs of degradation of the relaxed soft body with the shell being uniformly frosted or 3. The soft body missing but the shell intact and completely transparent. All pteropods fitting category 1 were assumed to have been alive upon entering the trap (swimmers) and representative of the living cohort present within the area at that time. Those in category 2 were most likely dead when entering the trap (passive sinkers) since uniform shell dissolution is an indicator of post-mortem decay (Oakes et al., 2019). Pteropods in category 3 are most likely to have been predated, i.e. the shells entered the trap empty after the soft body was removed and there was no internal dissolution by decaying tissue. Gymnosomes are specialized predators on thecosome pteropods, grasping the shell and inserting their modified mouth parts inside the aperture to extract the soft body within (Lalli and Gilmer, 1989). Damaged apertures on many of the category 3 shells is consistent with gymnosomes discarding the shell after predation.

2.3 Assessment of shell morphometrics

Shell diameter, shell width (otherwise called the line of aperture or aperture length), spire height and the number of whorls of *L. rangii, L. retroversa* and *Limacina* spp were measured using ImageJ software (Schindelin et al., 2012) (Figure 2). A Principal Component Analysis (PCA; run in R using prcomp{base}) determined that any of the shell morphometrics are adequate for representing pteropod shell size throughout the sampling period. Hereafter, shell width for *L. rangii* and *Limacina* veligers and spire height for *L. retroversa* will be used since these are common measures in the literature. Full details of the shell morphometric assessment are given in Supplementary Material 3.

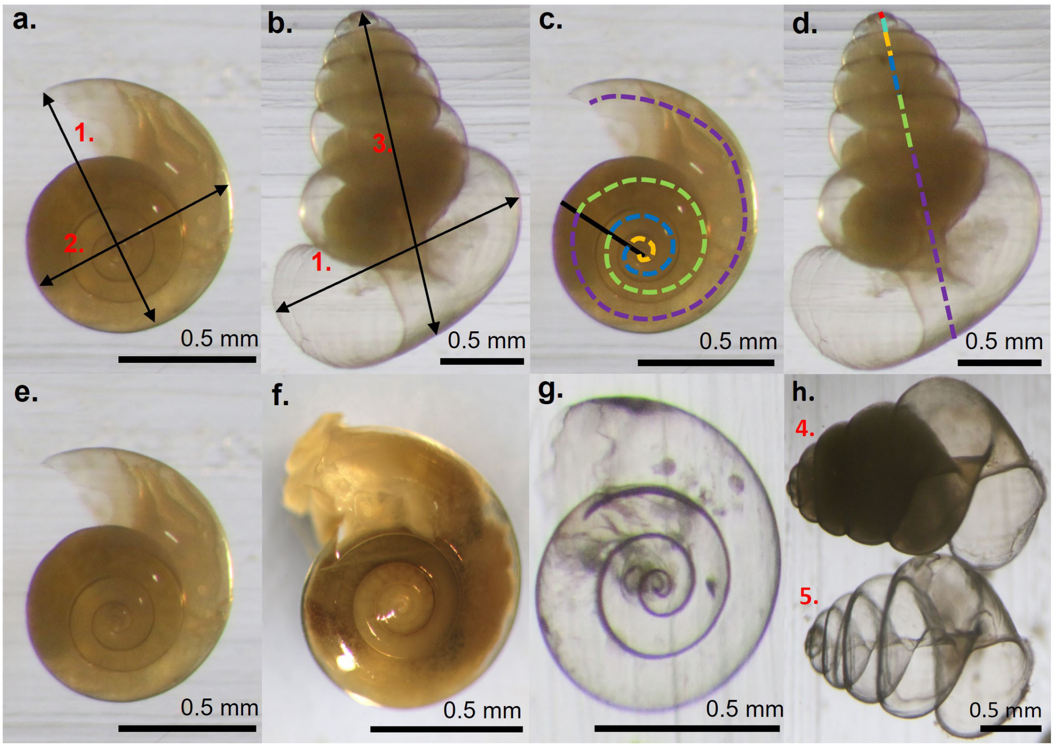


FIGURE 2
Shell morphometrics used to define pteropod cohorts of **(A)** *L. rangii* and **(B)**, *L. retroversa* where 1. is the shell width (otherwise known as the line of aperture), 2. the shell diameter and 3. the spire height (for *L. retroversa*). Insets **(C, D)**. indicate how the number of whorls was measured on *L. rangii* and *L. retroversa*, respectively, where each colour corresponds to one whorl. **(E–H)** indicate pteropod shell conditions being category 1/swimmers **(E)**: *L. rangii*, **(H)**4: *L. retroversa*), category 2/passive sinkers **(F)**: *L. rangii*) or category 3/predated **(G)**: *L. rangii*, **(H)**5: *L. retroversa*).

2.4 Cohort and group identification

L. rangii with a shell width of <0.3 mm were classed as veligers, 0.3 - 4 mm as juveniles and >4 mm as adults. Similarly, *L. retroversa* individuals with a spire height of <0.3 mm, 0.3 - 1 mm and >1 mm were classified as veligers, juveniles and adults, respectively (Lalli and Wells, 1978; Lalli and Gilmer, 1989). Veligers have only a single shell whorl and cannot be distinguished to species level and are therefore classed as *Limacina* spp.

Mixture models of shell morphometrics were fitted using normal, lognormal, gamma and Weibull distributions to one, two and three components extracted based on peaks observed on the size-frequency histograms using the R package 'mixdist' (MacDonald and Juan, 2012). The best-fitting distribution type and number of components were selected based on a combination of chi-square goodness of fit and visual inspection of histograms.

2.5 Shell growth, spawning behaviour and longevity

Groups of similarly sized specimens with the sample population were identified by the mixture analysis and tracked throughout the year, from the time of recruitment to when they no longer appear within the population (due to die-off or migration out of the sample area). It was assumed these subgroups represented cohorts. Tracking cohorts across sediment trap samples enables estimation of the mean increase in shell width per day (the growth rate) for each cohort. The difference in mean shell width between the two dates of observation was divided by the intervening time. This cohort definition assumes sampling was representative of a static population and that growth was continuous and linear between each sample interval.

We assumed modal peaks in the mixdist analysis below <0.3 mm signify a hatching event of *Limacina* individuals. Continuous spawning can be detected by the persistent presence of this smaller size class. Previous studies on *Limacina* species have indicated that hatching occurs between 1- 10 days after spawning (Paranjape, 1968; Kobayashi, 1974; Lalli and Wells, 1978; Gannefors et al., 2005; Howes et al., 2014; Akiha et al., 2017) with rapid growth and development of parapodia (wings) within 30 days (Van der Spoel and Dadon, 1999). Therefore, spawning events can be assumed to have occurred within 10 days of the capture of veligers in the samples.

Longevity was estimated from the date of a cohort's recruitment until its disappearance from size-frequency histograms assuming a static population that did not migrate in or out of the sampling region. Since some life stages were not observed with the sediment trap (e.g. adult *L. rangii*) our study has limitations. To anticipate longevity of this species we extrapolated the growth rates determined in younger life stages of the cohort to estimate the amount of time it would take to reach the maximum adult sizes recorded within the literature.

3 Results

3.1 Pteropod abundance and seasonal trends

Six species of thecosome pteropod were identified within the sediment trap: *Limacina rangii*, formerly *L. helicina antarctica* (LH), *Limacina retroversa* f. *australis* (LR), *Clio pyramidata* f. *sulcata*, and *Clio pyramidata* f. *excise*. Over the entire sampling period, four *Clio piatkowski* and three *Peraclis* cf. *valdiviae* were also collected (Supplementary Material 4).

3.1.1 *Limacina rangii*

The total abundance of *L. rangii* per month peaked in austral summer, January (6696 ind.), February (5258 ind.) and March (5466 ind.) and did not exceed 201 individuals (November) in the remaining months. No adult *L. rangii* were collected during the sampling period. The majority of *L. rangii* collected each month were swimmers, with the highest proportion of swimmers in February (94% of February LH abundance, 4921 ind.) and the lowest in April (56% of April LH abundance, 98 ind.) (Figures 3A; 4A). Passively sinking *L. rangii* were most abundant in January (718 ind.), and proportionally most abundant in April (37% of April LH abundance, 64 ind.) (Figures 3B; Supplementary Material 5). The highest abundance of predated *L. rangii* was collected in January (1%, 64 ind.) while the highest proportion of predated individuals was collected in September (8% of September LH abundance, 4 ind.) and April (7% April LH abundance, 12 ind.) (Figure 3C).

3.1.2 *Limacina retroversa*

L. rangii were more abundant than *L. retroversa* between September and April (Total monthly abundance range for LH: 50-6,696 ind. and LR: 32-44 ind.), however, *L. retroversa* were more abundant than *L. rangii* between May and August (Total monthly abundance range for LR: 80-188 ind. and LH: 63-90 ind.). Both adult and juvenile *L. retroversa* were identified, with adults making up the majority of specimens collected from June to October (52-90% of monthly LR abundance, 16-166 ind.), and juveniles from November to May (56-100% of monthly LR abundance, 26-196 ind.). Most *L. retroversa* collected each month were swimmers, with the highest proportion in June (92% of June LR abundance, 153 ind.) and the lowest in December (54% of December LR abundance, 14 ind.) (Figures 3D, 4B; Supplementary Material 5). The greatest proportion of passively sinking *L. retroversa* was collected in

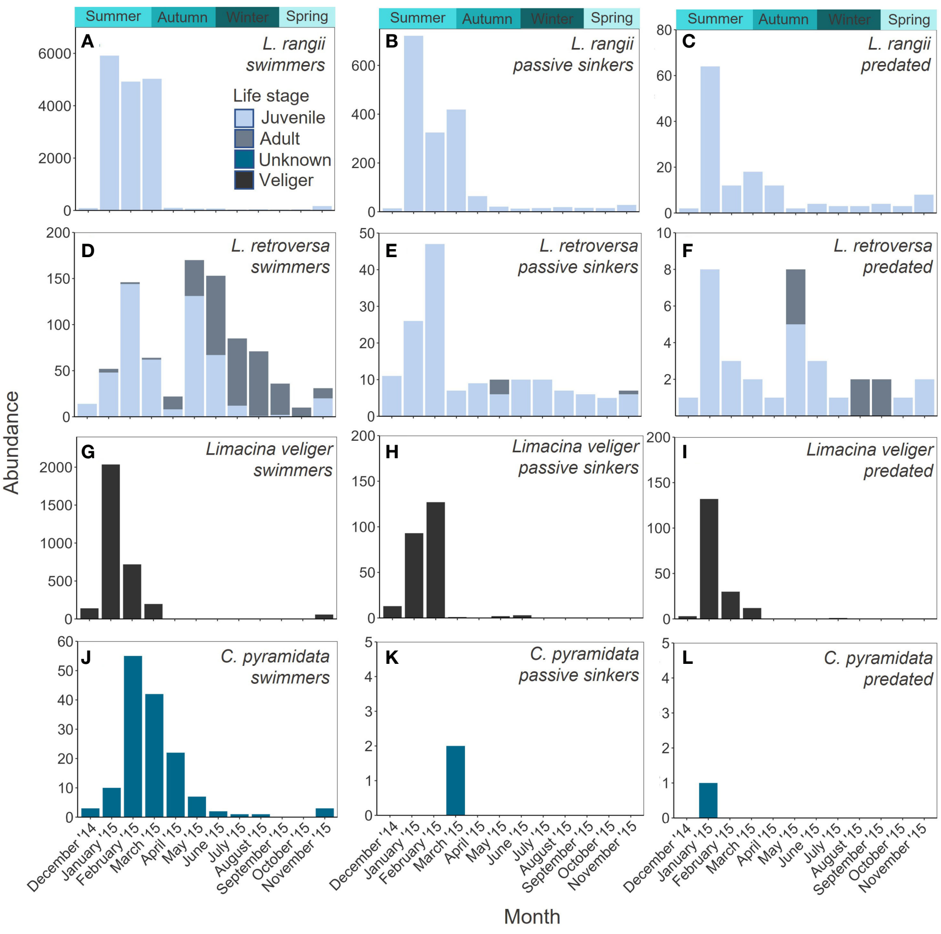


FIGURE 3
Monthly abundance of *L. rangii* **(A–C)**, *L. retroversa* **(D–F)**, *Limacina* spp **(G–I)** and *C. pyramidata* **(J–L)** collected in a sediment trap at site P3 (Scotia Sea, Southern Ocean) at 400 m depth between December 2014 and November 2015.

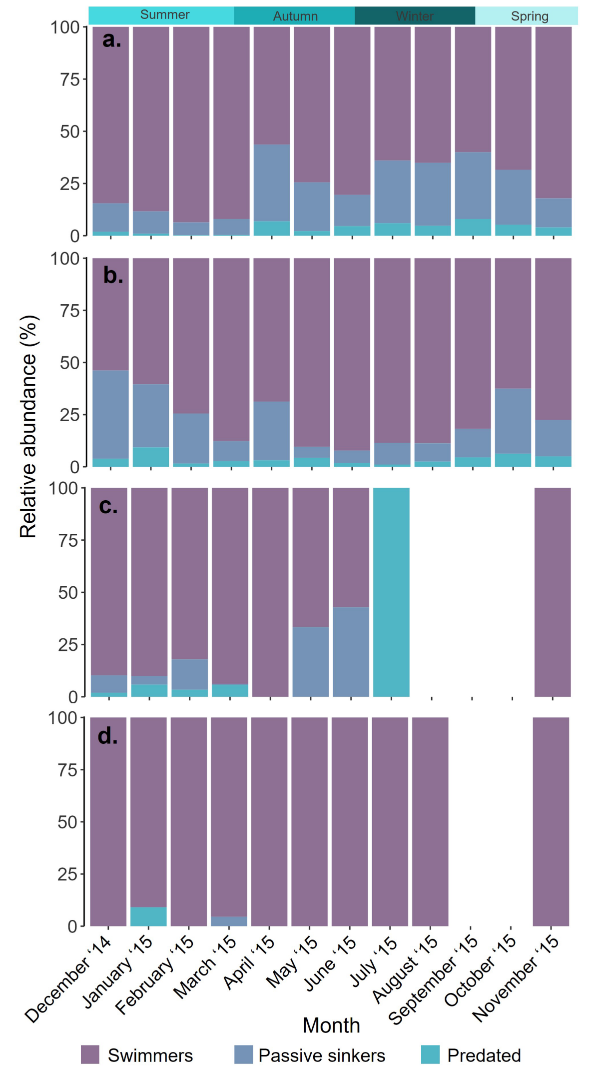


FIGURE 4
Proportional abundance (%) of the number of swimming, passively sinking and predated **(A)**. *Limacina rangii*, **(B)**. *Limacina retroversa*, **(C)**. *Limacina* veliger and **(D)**. *Clio pyramidata* each month between December 2014 and November 2015 in a sediment trap deployed at 400 m depth at site P3 (Scotia Sea, Southern Ocean).

December (42% of December LR abundance, 11 ind.) and the lowest proportion in May (5% of May LR abundance, 10 ind.) (Figure 3E). The highest abundance of predated *L. retroversa* was collected in January (9% of January LR abundance, 8 ind.) and lowest in July (1% of July LR abundance, 1 ind.) (Figure 3F).

3.1.3 *Limacina* veligers

Limacina veligers were only collected between November and July, with total abundance peaking in January (2260 ind.), February (877 ind.) and March (210 ind.) (Figure 3C). The majority of *Limacina* veligers collected were swimmers between November and June (57- 100% of veliger monthly abundance) (Figures 3G, 4C; Supplementary Material 5). Passively sinking *Limacina* veligers were most abundant in February (14% of veliger February abundance, 127 ind.) and proportionally most abundant in June (43% of veliger June abundance, 3 ind.) (Figure 3H). No passively sinking *Limacina* veligers were collected in April or July-November. The highest abundance of predated *Limacina* veligers was collected in January (132 ind.) accounting for 6% of total abundance in January (Figure 3I).

3.1.4 *Clio pyramidata*

The total abundance of *C. pyramidata* peaked in February (55 ind.), March (46 ind.) and April (22 ind.). Almost all *C. pyramidata* collected were swimmers (Figures 3J, 4D; Supplementary Material 5), with two passively sinking individuals being collected in March and one predated individual being collected in January (Figures 3K, L).

3.2 *Limacina rangii* population structure and growth rates

The recruitment of *L. rangii* veligers into the juvenile life stage and the similarly-sized subgroups LH1 - 5 can be deduced from the mean shell sizes identified by the Mixture analysis (Figures 5.1, 6A; Supplementary Materials 6-7). However, the entire life cycle of *L. rangii* was not captured by the Mixture analysis since no *L. rangii* adults were collected. We do not consider LH1 - LH5 to represent discrete cohorts given their wide and overlapping distributions (Figures 5.1, 6A). LH1 represents young, newly recruited juveniles with a mean shell width range of 0.34-0.37 mm and were collected between December and March 2014. LH2 is comprised of larger, older juveniles than LH1 (mean shell width range 0.47-1.01 mm) and was collected between December and April. LH3 (mean shell width 0.5 mm) and LH4 (mean shell width 0.38 mm) were collected in May and June, respectively. Finally, LH5 was collected between June and November (monthly mean shell width 0.52-1.79 mm) and represents overwintering juveniles.

The prolonged presence of LH1 and LH4, which contain small juveniles (mean shell width 0.34 and 0.38 mm), as well as the presence of veligers between December and March, indicates protracted spawning by *L. rangii*. Growth rates can only be estimated for LH3 and LH4, as they were present after the last spawning event in March. Since it is unclear when LH1, LH2 or LH5 were spawned, growth rates could not be calculated for these subgroups. If LH3 individuals were spawned in February or March, the shell growth rate of LH3 would be 0.005-0.008 mm d^{-1} to reach a shell width 0.50 mm by May (Figure 6B). The growth rate of LH4 would be 0.003-0.004 mm d^{-1} to reach a shell width of 0.38 mm by June. These growth rate calculations assume that *L. rangii* veligers emerged from the egg-sac 10 days after spawning with a shell size of 0.07 mm.

3.3 *Limacina retroversa* population structure and growth rates

Four non-overlapping cohorts of *L. retroversa* juveniles and adults were identified, spawning in December (cohort LR1), February (cohort LR2), May (cohort LR3) and November (cohort LR4) (Figures 5.2, 6C). Each cohort can be observed to increase in size to achieve adulthood (>1 mm) over two to five months with rates of

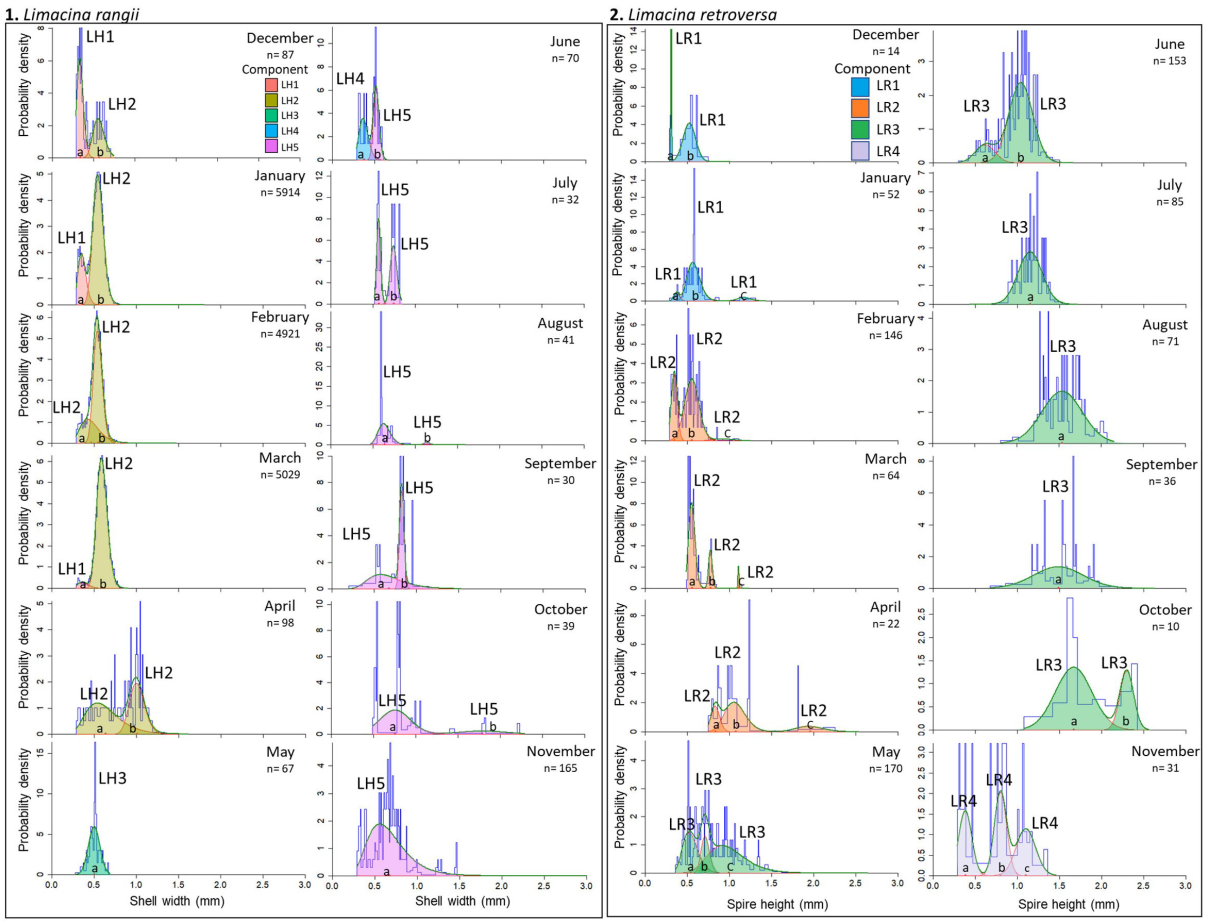


FIGURE 5
Components identified by the mixture analysis on shell width data of 1. *L. rangii* (L.H.) swimmers and 2. *L. retroversa* (L.R.) swimmers for each month of a year-long sampling period. Mixture analysis was performed by the R package *Mixdist*. Tracking components through the course of the year provides an estimate of growth rate. Blue lines represent the original length-frequency distribution representing the shell heights/widths, red lines are the individual fitted distributions (a-c) and green lines are the sum of fitted distributions.

shell spire height increase averaging LR1: 0.014 mm d^{-1}, LR2: 0.018 mm d^{-1}, LR3: 0.010 mm d^{-1} and LR4: 0.24 mm d^{-1} (Figure 6D). Adult individuals were not collected in samples containing veligers of the subsequent cohort, suggesting *L. retroversa* have a longevity of one to seven months.

The veligers recruited into cohort LR1 in December (mean spire height 0.31 mm) likely hatched in November, making the growth rate 0.006 mm d^{-1}. Veligers recruited into LR2 in February (mean spire height 0.35 mm) hatched in January and grew 0.007 mm d^{-1}. Because juvenile LR3 were first recorded in May (mean spire height of 0.54 mm), the growth rate of LR3 veligers was 0.005 mm d^{-1} or 0.006 mm d^{-1} assuming they hatched in February or March, respectively. LR4 individuals hatched in November, with veligers growing at 0.016 mm d^{-1} and becoming juveniles in the same month (mean shell size 0.39 mm).

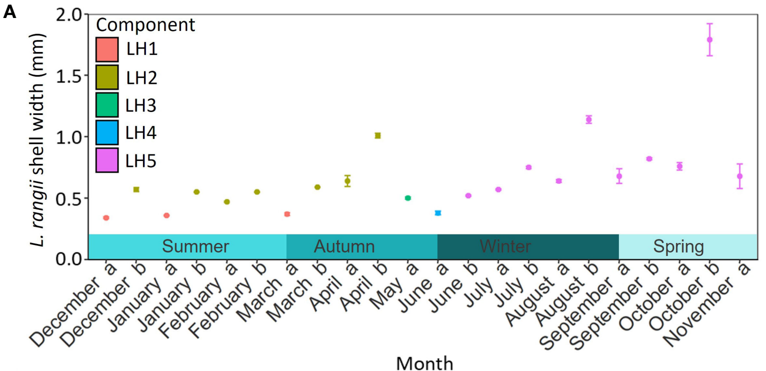
3.3.1 Environmental data

Mean temperature ranged from 0.73°C (± 0.03 S.E.) in October to 1.15°C (± 0.01 S.E.) in May with the greatest intra-month variability occurring in November (1.03°C) (± 0.03 S.E.) (Figure 7). pH reached a maximum of 8.13 (± 0.00 S.E.) in November and a minimum of 7.95 in December (± 0.01 S.E.) with the greatest variation in December (7.95 ± 0.01 S.E.). The highest oxygen concentration occurred in November and 200.1 µM (± 0.02 S.E.) while the lowest mean values occurred in December and January (191.3 µM (± 0.02 S.E.) and 192.6 µM (± 0.01 S.E.), respectively). The greatest mean chlorophyll-*a* concentrations were in December 2014 (2.07 mg m^{-3} ± 0.02 S.E.), November 2015 (2.03 mg m^{-3} ± 0.03 S.E.) and February 2015 (2.32 mg m^{-3} ± 0.05 S.E.). Cloud cover was too dense from May to July to allow satellite chlorophyll-*a* measurements. An initial bloom started to form in October (1.32 mg m^{-3} ± 0.02 S.E.), which expanded and intensified around P3 through November and December (Supplementary Material 8). The minimum chlorophyll-*a* concentration was recorded in August (0.01 mg m^{-3} ± 0.00 S.E.).

4 Discussion

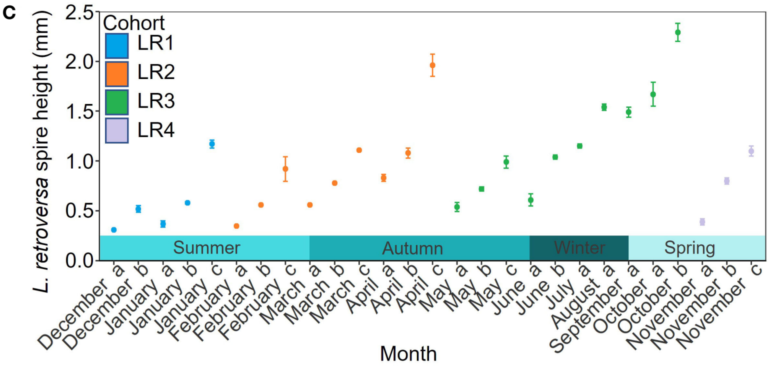
4.1 Pteropod diversity

True polar species *L. rangii* was the most abundant pteropod collected at P3, consistent with similar observations made south of



B

Group	Month Spawned	Number of days growth	Mean shell width (mm)	Shell width minus embryonic shell growth (mm)	Growth rate (mm/day)
LH3	March	52	0.50	0.43	0.008
LH3	February	80	0.50	0.43	0.005
LH4	March	83	0.38	0.31	0.004
LH4	February	111	0.38	0.31	0.003



D

Cohort	Month recruited	Number of days growth	Minimum cohort spire height (mm)	Maximum cohort spire height (mm)	Overall spire growth (mm)	Growth rate (mm/day)
LR1	December	62	0.31	1.17	0.86	0.014
LR2	February	89	0.35	1.96	1.61	0.018
LR3	May	184	0.54	2.29	1.75	0.010
LR4	November	30	0.39	1.1	0.71	0.024

FIGURE 6

The temporal sequence of mean shell width from the mixture analysis of **(A)** *Limacina rangii* (LH) with standard error of each component. **(B)** Growth rates of *L. rangii* for LH3 and LH4. Two calculations were made for each component to capture uncertainty on whether spawning was in February or March. **(C)** The temporal sequence of mean spire height of L. retroversa australis (LR) with standard error of each component computed by the mixture analysis (a-c). **(D)**. Growth rates of LR are based on tracking each of the four components over time. Individuals were collected in a sediment trap deployed at P3 (Scotia Sea, Southern Ocean) at 400 m depth between December 2014 and November 2015.

the Polar Front (Dadon, 1990; Ward et al., 2004; Hunt et al., 2008; Bernard and Froneman, 2009; Akiha et al., 2017). Subpolar species *L. retroversa* was the second most abundant species, as it is typically most abundant north of the Polar Front (Chen and Bé, 1964; Van der Spoel, 1967; Van der Spoel, 1976).

C. pyramidata forma *sulcata* is commonly captured in small numbers alongside *Limacina* species throughout the Southern Ocean (Hunt et al., 2008). No records could be found of the thecosome pteropods *Clio piatkowskii*, *Peraclis* cf. *valdiviae* and *C. pyramidata* f. *excise* in the Scotia Sea. *C. piatkowskii* have been documented in the Weddell Sea (Van der Spoel et al., 1992; Van der Spoel and Dadon, 1999), Lazarev Sea (Flores et al., 2011) and near Bouvetøya (Hunt et al., 2008) at 300-1000 m water depth. *Peraclis* cf. *valdiviae* has previously been recorded south of Tasmania, within the Sub-Antarctic Zone down to 150 m water depth (Van der Spoel and Dadon, 1999; Howard et al., 2011; Roberts et al., 2011). *C. pyramidata* f. *excise* has been recorded in the Lazarev Sea (MSIP, 2017). The high diversity and abundance of pteropods collected in this study highlights that *s*ediment traps are effective at long-term, remote sampling of pteropods in regions that are difficult to access.

4.2 Environmental conditions

The chlorophyll-*a* observations indicate that high primary productivity persisted north of South Georgia from October until February, peaking in November, as is typical for this region (Korb

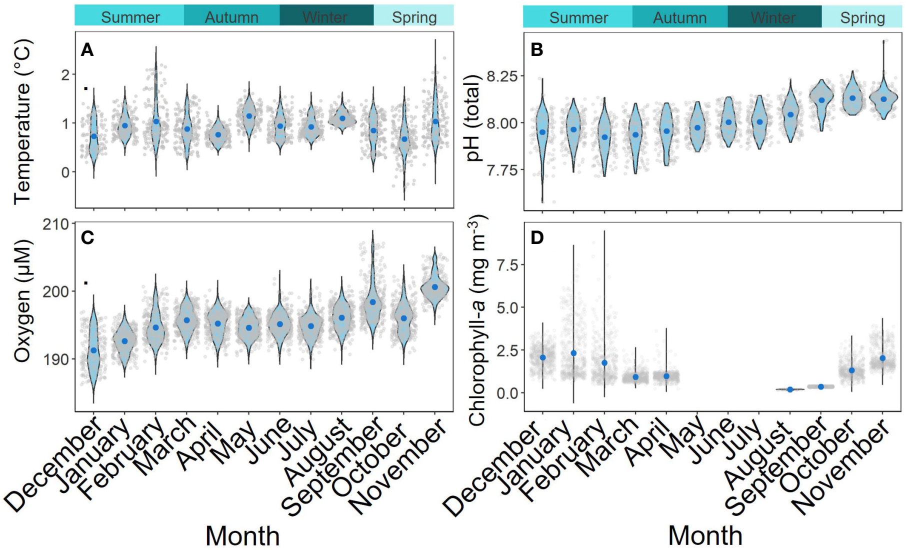


FIGURE 7
Monthly environmental conditions associated with the sediment trap deployed at P3 (Scotia Sea; Southern Ocean) between December 2014-November 2015. Temperature **(A)** and pH **(B)** were measured *in-situ* at 200 m. Oxygen **(C)** (µM) was measured *in-situ* at 400 m. Chlorophyll-*a* **(D)** measurements were taken from Aqua MODIS at 4 km resolution satellite data (NASA; Ocean Biology). Grey dots are individual data points, Blue dots are the means and the thickness of the violin plot represents data probability density.

and Whitehouse, 2004; Korb et al., 2005; Atkinson et al., 2012). The high oxygen concentrations observed from September to November likely reflects deep wind-driven mixing entraining surface water down to 200 m depth. The lowest mean oxygen concentrations between December and January likely reflect a reduction in surface mixing, and increased respiration and remineralisation following the bloom.

4.3 The life cycle of *Limacina rangii* in the Scotia Sea

Five similarly-sized subgroups of juvenile *L. rangii* were identified (LH1 - 5) as being recruited into the population between November 2014 and December 2015. *L. rangii* is inferred to have continuously spawned between November and March and with concurrent recruitment of juveniles into LH1 - 2. The spawning and early growth period of LH1 - 2 was coincident with the warmest temperatures and peak of the of the South Georgia bloom, providing sufficient food for these energetically expensive life stages (Seibel et al., 2012; Bednaršek et al., 2016; Manno et al., 2017).

The absolute abundance of *L. rangii* juveniles collected in the sediment trap dropped by 97% at the end of the productive period (April). This dramatic decline in abundance is a phenomenon observed by numerous studies (Gilmer and Harbison, 1986; Seibel and Dierssen, 2003; Maas et al., 2011) and has been attributed to: 1. a fatal environmental perturbation, 2. a die-off event, 3. a change in current speed or direction transporting the population away or 4. active migration (Gilmer and Harbison, 1986; Collier et al., 2000; Accornero et al., 2003; Seibel and Dierssen, 2003; Maas et al., 2011). Current activity did not change, suggesting that the population was not physically transported away, ruling out scenario 3. Swimmers remained the dominant classification of specimens collected in the trap, suggesting that this was not a mass mortality event affecting the entire population. However, the relative abundance of type 2 (passive, dead) specimens of *L. rangii* did increase somewhat in April, as did the number of predated shells. There are no notable anomalies within the environmental parameters beyond the natural, seasonal decline in chlorophyll-*a* at the end of the bloom. It would seem that the decline in the population is related closely to the cessation of the phytoplankton bloom. As food resources became scarce the incidence of natural and predated deaths increased. It may be possible that the population migrated laterally, possibly following food availability elsewhere, however we have no evidence to support or dispute this. Another possibility is that once juveniles had matured enough to perform their diurnal migrations, the end of the bloom meant that there was no longer any incentive to migrate into the shallow waters. That is, once the phytoplankton bloom had ceased and the remaining organic matter sank through the water column, there was no reason for *L. rangii* to migrate vertically above the depth of the sediment trap. *L. helicina* are known to enter a diapause at depth during the winter in the Arctic when food is scarce (Gannefors et al., 2005). Our findings here suggest that *L. rangii* may well do the same outside of the bloom season in the Scotia Sea (Figures 3, 7; Supplementary Material 2, respectively). The specimens of *L. rangii* collected during the winter months (LH5) were all juveniles. This overwintering population appears to have adopted two different growth patterns, with some entering diapause (a state of suspended growth) and others continuing to grow. Such contrasting growth patterns likely reflect the patchiness of food sources during the winter, meaning not all juveniles had the available resources to invest into growth (Meyer et al., 2017). As Akiha et al. (2017), we collected no adult *L. rangii* in the sediment trap. The absence of adults may reflect the tendency of more mature specimens to dwell below the depth of the sediment trap by day, reducing the potential incidence of adult *L. rangii* entering the trap passively (dead). The absence of adult *L. rangii* entering the trap as swimmers may reflect a survival instinct and ability to swim out of danger (Adhikari et al., 2016; Gilmer and Harbinson, 1986).

The current study found that *L. rangii* has a protracted spawning period, ending at the end of the productive period in March. After March individuals continued growing and some overwintered as juveniles. Hunt et al. (2008) and Van der Spoel (1967) postulated that *L. rangii* could spawn twice in a year, with the first occurring during the summer, and the second in the autumn, where these late comers enter a diapause and overwinter without growth. The autumnal spawning theory was based on observations of *L. helicina helicina* in the Arctic (Kobayashi, 1974; Gannefors et al., 2005) and limited winter net samples in the Southern Ocean (Hunt et al., 2008). Bednaršek et al. (2012b) inferred from net samples in the Scotia Sea that the spawning of *L. rangii* was a discrete event, occurring predominantly during the summer. While the timing of the discrete spawning event identified by Bednaršek et al. (2012b) corresponds to the peak of spawning at P3 in the current study, the continuous recruitment of small *L. rangii* juveniles evidence in the sediment trap at P3 indicates that spawning occurred over a much longer period (summer to early autumn). It is likely that the difference in spawning period estimates arises from differences in the scale of the respective studies. Bednaršek et al. (2012b) considered spawning across the entire Scotia Seaand did not have the time series of data afforded by the sediment trap.

The rate of growth for veligers to reach the small juvenile size-bins (LH3 and LH4) was calculated as between 0.005 and 0.008 mm d^{-1} (LH3) or 0.003 and 0.004 mm d^{-1} (LH4) in the current study, depending on whether spawning occurred in February or March. Bednaršek et al. (2012b) also calculated the growth rate of *L. rangii* using a cohort analysis from plankton net samples in the Scotia Sea between October and March (1996-2005). *L. rangii* in the current study are mainly comparable to their group “G2”, which had a growth rate of 0.007 mm d^{-1} (after conversion of shell diameter to shell width (Supplementary Material 3). The growth rates estimated for LH3 (0.005- 0.008 mm d^{-1}) largely in agreement Bednaršek et al. (2012b), however, LH4 growth rates are about half (0.003 - 0.004 mm d^{-1}) those estimated by Bednaršek et al. (2012b). The lower growth rates for LH4 may reflect the scarcity of food towards the end of the bloom for this subgroup that spawned later (Figure 7; Supplementary Material 8). Since we have established that growth rates are not continuous or linear, rather dependent on life stage and environmental conditions we were unable to calculate the amount of time to reach maturity or longevity for *L. rangii.*

4.4 The life cycle of *Limacina retroversa* in the Scotia Sea

Four generations of *L. retroversa* were collected that included all life stages and no overlapping of cohorts. These distinct cohorts were identified as juveniles and adults between December and January (LR1), February and April (LR2), May and October (LR3) and in November (LR4). Individuals that reach adulthood in late summer/autumn appear to stay in the upper 400 m of the water column and overwinter as adults until the spring, when they spawn. The veligers then hatch and undergo a rapid period of growth to reach adulthood in the summer and then spawn themselves. Veligers that hatch in late summer reach adulthood in the autumn and overwinter before spawning in the spring.

L. retroversa adults in autumn (LR2) and winter (LR3) were larger (mean spire height: 2.19 - 2.42 mm) in comparison to the spring (LR4) and summer (LR1) cohorts (mean spire height: 1.15 - 1.19 mm). This growth strategy was also observed in *L. retroversa* of the Argentine Sea, where the mean spire height of wintertime cohorts measured 1.99 - 3.20 mm while the summer mean spire heights measured 1.25 - 1.80 mm (Dadon and de Cidre, 1992). In many gastropods, fecundity is directly related to gonad volume, which increases with shell size (Ghiselin, 1969; Dillon, 2000). Therefore, investing in shell growth and delaying spawning until conditions are favourable for early life stages increases reproductive output and veliger survival rate (Lalli and Wells, 1978; Lalli and Gilmer, 1989).

The greatest rate of shell growth in *L. retroversa* (LR4: 0.024 mm d^{-1}) occurred during the spring when juveniles, fueled by the parallel phytoplankton bloom, reached maturity. This same cohort spawned during the summer, when food supply remained sufficient to support another generation of veligers (LR1). Dadon and de Cidre (1992) also observed that growth rates were highest during springtime in the Argentine Sea, although, growth rates were lower than in the Scotia Sea, at 0.008 - 0.012 mm d^{-1} (Dadon and de Cidre, 1992). However, the autumn to winter *L. retroversa* growth rates in the Scotia Sea were similar (LR3: 0.010 mm d^{-1}) to those in the Argentine Sea (0.009 - 0.015 mm d^{-1}). Higher growth rates in the Scotia Sea are likely due to the abundant food supplied by the phytoplankton bloom north of South Georgia being more prolonged and stable between spring and autumn in comparison to the small, discrete blooms of the Argentine Sea (Dadon, 1990; Dadon and de Cidre, 1992; Lutz et al., 2009) (Figure 7; Supplementary Material 8). The longer productive season in the Scotia Sea means spawning and veliger growth of *L. retroversa* occur between November and March, supporting a four-generation per year life cycle. In comparison, *L. retroversa* in the Argentine Sea have discrete spawning events in February and September, in parallel to discrete phytoplankton bloom events, supporting a two-generation a year life cycle (Dadon, 1990; Dadon and de Cidre, 1992). During the winter, *L. retroversa* in both the Scotia Sea and Argentine Sea continue to grow, but at much lower rates than in the rest of the year due to reduced and poorer quality food supplies and/or reliance on lipid reserves (Dadon and de Cidre, 1992; Lischka and Riebesell, 2012; Lischka and Riebesell, 2016)

At the end of each growth period, adult individuals ‘disappeared’ from the sediment trap. This ‘disappearance’ was also observed in samples from the Argentine Sea, which Dadon and de Cidre (1992) concluded was due to a die-off based upon observations of *L. retroversa retroversa* in the Arctic. However, in the Scotia Sea there is no evidence for adult L. retroversa dying-off as no passive sinking or predated adults were found in any month except May. Therefore, it is most probable that adult *L. retroversa*, like many other *Limacina* species worldwide (Van der Spoel and Heyman, 2013; Almogi-Labin et al., 1988), undergo an ontogenic migration to deeper water after spawning. Based on the cohort identification, it took between one (LR4) and seven (LR3) months for *L. retroversa australis* to transition from the small juvenile stage to adult stage. However, since there was no clear die-off of adults, it is unclear what their longevity was. Dadon and de Cidre (1992) concluded that *L. retroversa* in the Argentine Sea lived for a year, while in the northern hemisphere, *L. retroversa retroversa* has a longevity of between 0.5 years (Thabet et al., 2015) and 1 year (Lebour, 1932; Hsiao, 1939), which is similar to longevity estimates in the current study.

4.5 The implications of contrasting life cycle strategies in a changing Southern Ocean

Thecosome pteropods are functionally important components in the Scotia Sea ecosystem, being central to food webs, organic carbon fluxes and calcium carbonate exports (Collier et al., 2000; Hunt et al., 2008; Manno et al., 2018). However, warming and ocean acidification are environmental perturbations affecting this region that are potentially deleterious to their viability. *Limacina* populations in the northern Scotia Sea (e.g. at P3) are especially sensitive to climatic changes since *L. rangii* are at the northern limit of their polar distribution, and *L. retroversa* are at the southern limit of their boreal distribution (Hunt et al., 2008). The capacity of pteropods to maintain a viable population in the Southern Ocean depends on their capability to recruit successfully. Shallow undersaturation with respect to aragonite in the Scotia Sea is expected to occur episodically from 2030 onwards, first during the winter before becoming more prolonged and intense with time (McNeil and Matear, 2008; Hauri et al., 2016; Landschützer et al., 2018). If exposed to undersaturation events, thecosome pteropod populations in the Scotia Sea may experience higher mortality, shell dissolution and more energetic demands to maintain their shell (Manno et al., 2017; Peck et al., 2018). Pteropods that overwinter are most vulnerable to undersaturation, since undersaturation with respect to aragonite is expected to commence in the winter months before extending to other seasons (McNeil and Matear, 2008; Hauri et al., 2016; Landschützer et al., 2018). We have shown that *L. retroversa* and *L. rangii* at P3 overwinter as juveniles and adults, meaning that these life stages are most likely to be the first to be exposed to undersaturated conditions. These later life stages are potentially more capable of tolerating exposure to undersaturated waters than early developmental stages. Their higher tolerance is not just due to their established life stage, but also the likelihood that during the winter months they tend to dwell deeper in the water column, likely below the shallow saturation horizon. Overwintering pteropods appear to enter a diapause stage during the food scarcity of the winter months, where their metabolism and calcification rates drop allowing them to focus energy on egg production in the spring (Ghiselin, 1969; Dillon, 2000). This 'hibernation' strategy likely reduces their exposure to environmental perturbations in the surface waters, however as the intensity and duration of these stressors increase in the future of these factors will likely begin to impact Limacina. Laboratory incubations suggest that veligers of *L. rangii* are susceptible to shell malformation, dissolution, and high mortality when exposed to increased temperature and aragonite undersaturation (Comeau et al., 2010; Thabet et al., 2015; Gardner et al., 2018). When, as predicted, the duration of winter undersaturation events begin to overlap with the onset of the South Georgia bloom and spawning time of Limacina, vulnerable veligers restricted to surface waters will become exposed.

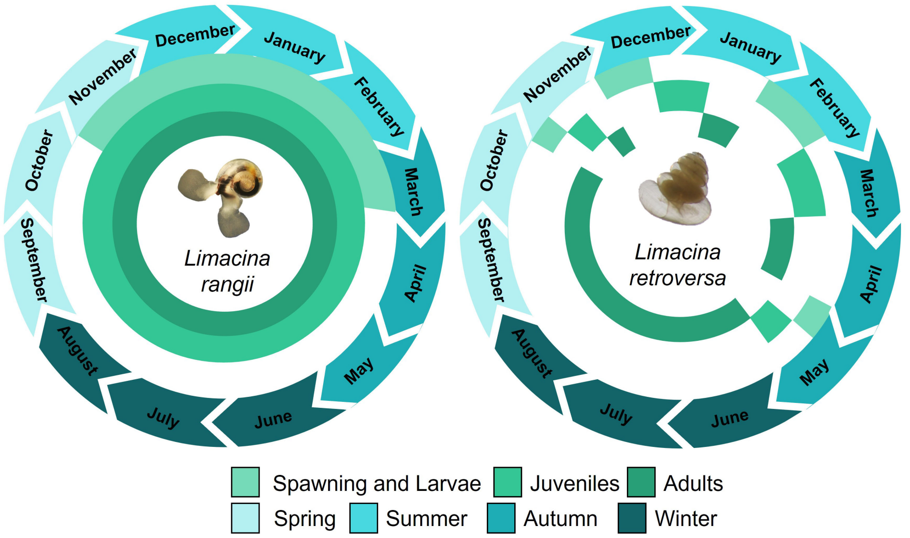


FIGURE 8
A conceptual schematic illustrating the seasonal and monthly presence of veliger, juvenile and adult *Limacina rangii* and *Limacina retroversa*, as well as their spawning period. The schematic is based on shell morphometrics of individuals collected in a sediment trap deployed at P3 (Scotia Sea, Southern Ocean) at 400 m depth between December 2014 and November 2015.

This study shows the population of *L. rangii* at P3 comprises several overlapping cohorts with a life cycle of over a year. Therefore, since all life stages of *L. rangii* co-exist, vulnerability of one cohort is not detrimental to the stability of the overall population. Conversely, there is no overlap in juvenile and adult stages in the life cycle of *L. retroversa* meaning that, if one cohort is removed, the entire population may be vulnerable. If deleterious conditions impacted a cohort of *L. retroversa* prior to sexual maturity, a population bottleneck or local extinction may result. Therefore, based on the assumption of a static population which is not advected into or out of the sampling area, *L. retroversa* populations are more likely to be impacted than *L. rangii* on exposure to episodes of undersaturation. Regardless of cohort structure, repeated or prolonged exposure to unfavourable conditions is likely to impact all cohorts across both species if rates of spawning and survival to sexual maturity decline. Such a progressive population decline was observed in the Ross Sea, where long-term food shortages due to reduced primary productivity eventually led to the short-term localized extinction of *L. rangii* (Seibel and Dierssen, 2003; Maas et al., 2011).

In conclusion, we indicate contrasting life history strategies of the dominant Southern Ocean pteropod species, *L. rangii* and *L. retroversa* (Figure 8), suggesting that *L. retroversa* populations in the Scotia Sea may be particularly vulnerable to exposure to deleterious conditions. Declines in pteropod populations in the Southern Ocean will have cascading implications on regional biogeochemical cycling and epipelagic food webs.

Data availability statement

The datasets analyzed for this study can be found in the Supplementary Material and in the UK Polar Data Centre.

Author contributions

JG, CM, VP and GT carried out the fieldwork and sample collection with support from other scientists on board cruise JR304 and JR15002. JG carried out the sample and statistical analysis with support from CM and GT. JG wrote the manuscript with support from CM, GT, VP and DB. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1118570/full#supplementary-material

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