

Growth and ecophysiology of two Antarctic benthic predators; *Isotealia antarctica* and *Urticinopsis antarctica*.

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ARTICLE INFO

Keywords:

Antarctic benthos
Buoyant weight
Cnidaria
Ectotherms
Ecophysiology
Faecal egestion
Generalist feeders
Respirometry
Vagile predators
Soft-bodied predators

ABSTRACT

There is a dearth of basic life history and physiological data from Southern Ocean species, particularly from benthic vagile predators. This is an important data gap because species inhabiting the Southern Ocean live in a more temperature stable but seasonally varying environment than temperate and tropical counterparts. For many species living below 0 °C for a significant proportion of the year, bodily functions are slowed to disproportionately lower rates than would be predicted by temperature alone. Certain life history and physiological processes are often aligned with the short summer season of productivity. However, predators may behave differently because they are decoupled from the phytoplankton bloom and some have been shown to exhibit less seasonal physiological change. To further our understanding of Antarctic predator growth and seasonal ecophysiology, field growth rates were measured for two soft-bodied Antarctic anemone benthic predators, *Isotealia antarctica* and *Urticinopsis antarctica*, using *in situ* sampling of anemones on uniquely marked tiles. *Ex situ* measurements of oxygen consumption and seven-day faecal output were obtained from recently collected specimens in aquaria and compared between summer and winter. Winter physiological data for Antarctic species are rare, and we tested the hypothesis that generalist feeders or predators continue to feed during the winter. Growth rates differed between species and between years. *I. antarctica* and *U. antarctica* both exhibited overall positive field growth rates across a 15 month period between 2020 and 2021; with *U. antarctica* increasing 199.80% (\pm SE 25.8) in mass compared to a 16.85% (\pm SE 8.9) increase in *I. antarctica*. There was no significant difference in *I. antarctica*'s growth between 15 and 25 months field deployment. After 25 months, *I. antarctica* showed an average 7.96% (\pm SE 8.05) increase in buoyant weight. *Ex situ* oxygen consumption and faecal egestion did not differ seasonally, which, demonstrates that anemones fed at similar rates during the winter and summer. In contrast to some members of the Antarctica benthos, *I. antarctica* and *U. antarctica* actively feed all year round, whereas several other species have been reported to enter a state of torpor in winter.

1. Introduction

Understanding growth patterns and the ecophysiology of animals inhabiting the most extreme polar environments is high on the conservation agenda (Kennicutt et al., 2015; McCormack et al., 2021). Antarctic marine animals survive in sub-zero temperatures for a substantial proportion of the year and experience some of the most intense and rapid climate forcing, as seen on the Antarctic Peninsula (Carrasco et al., 2021; Meredith and King, 2005). Growth and physiological information provide an insight into species responses to environmental factors dictated by seasonality, such as primary and secondary productivity and

temperature (Clarke, 1988). Improving our understanding of soft-bodied vagile predator growth and ecophysiology is crucial to both building accurate food webs and to contribute towards making informed predictions about their resilience to a changing climate (Morley et al., 2019). In the shallow, coastal waters of Antarctica, there is an abundance of soft bodied ectothermic benthic invertebrates (Clarke and Johnston, 2003), making this area a suitable study site to understand the drivers of vagile predator growth and ecophysiology.

A review of studies of physiological data, including growth, for an array of Antarctic marine ectotherms concluded that ectotherm growth is slow, relative to temperate and tropical counterparts across multiple taxonomic groups (Peck, 2018). However, there were exceptions, such

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<https://doi.org/10.1016/j.jembe.2024.152045>

Received 19 December 2023; Received in revised form 22 May 2024; Accepted 16 July 2024

Available online 24 July 2024

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Glossary

- Benthic-** The ecological region at the lowest level of a body of water.
- Durophagous-** the eating behaviour of animals that consume hard-shelled or exoskeleton bearing organisms.
- Ectotherms-** Animals depending on an external source of heat to maintain body temperatures.

as some ascidians, bryozoans and sponges. Existing studies conducted in Antarctica have measured growth rates in suspension feeders such as bryozoans (Barnes, 1995), bivalve molluscs (Higgs et al., 2009), spirorbid worms (Ashton et al., 2017), brachiopods (Peck et al., 1997), in deposit feeding bivalves (Peck et al., 2000), in grazing echinoids (Brey et al., 1995), and in omnivorous octocorals (Peck and Brockington, 2013). A key component of growth, protein synthesis, has been investigated in Antarctic limpets and sea cucumbers and been found to be greatly reduced compared to warmer water species (Fraser et al., 2004, 2007, 2022). These pioneering studies exhibit the variability of polar organisms' response and demonstrate a variety of feeding and growth strategies in polar environments. Within the Bryozoa, one species, *Cellarinella watersi* exhibited distinct seasonality in growth in comparison to *Alloeflustra tenuis*, which grew continually throughout the year (Barnes, 1995). Although the Antarctic limpet, *Nacella concinna*, feeds all year round, it grows more slowly in winter (measured by protein synthesis rates), and has reduced faecal egestion and oxygen consumption rates (Fraser et al., 2007). In contrast, the physiology of *Heterocucumis steineri*, a suspension feeding holothurian, is tightly coupled with the phytoplankton bloom. It enters a period of winter dormancy for ~ four months, when it ceases to feed (Fraser et al., 2004). *H. steineri* exhibits a larger seasonal decrease in oxygen consumption but similar growth rates (measured by protein synthesis rates) to *N. concinna* (Fraser et al., 2007; Fraser et al., 2004). In contrast, although growth was not measured in the nemertean *Parborlasia corrugatus*, the metabolism of this exclusively carnivorous species, exhibited no marked seasonal differences (Obermüller et al., 2010). To date, no Antarctic studies have specifically collected growth rate data from vagile benthic predators such as anemones. Our first hypothesis is that anemone growth is uncoupled from the phytoplankton bloom.

Until now, growth rate data from Antarctic benthic predators, have been reported for taxa with hard skeletons. Data on growth rates of Antarctic benthic predators, excluding fish where otolith rings can be used to age individuals (Everson, 1970; Eastman, 2013), are rare, and restricted to evaluations of changes in population size structure in, for example, relatively fast growing predatory amphipods (e.g. Thurston, 1970). Most research on benthic predators in lower latitudes has been on durophagous species with hard skeletons (e.g. Vermeij, 1987; Harper and Peck, 2016). However, the most common durophagous predators, reptant decapods, are absent from the polar regions, likely because of restrictions to power generation by muscles (Aronson et al., 2007). This shift away from the dominance of predators with hard skeletons, to soft-bodied species at high latitudes, creates problems in assessing life histories and energetics because measuring growth in soft bodied species, that do not have large populations, and grow slowly, is very difficult.

Previous studies on the seasonal ecophysiology in Antarctic benthic fauna, from predators to scavengers to herbivores, have shown varying results, with metabolic seasonality being relatively small and not always consistent among species (Souster et al., 2018; Obermüller et al., 2010; Campbell et al., 2008). It is, therefore of interest to assess the seasonality of feeding and metabolism in Antarctic common vagile generalist predators. Faecal egestion is a common technique used to understand whether an organism is feeding or not (Schnack-Schiel and Isla, 2005; Obermüller et al., 2010; Griffiths et al., 2017; Morley et al., 2016a), and

has also been used to estimate feeding and energy intake in Antarctic limpets (Clarke, 1990). Faecal production has not previously been used to assess the seasonality of feeding in a polar vagile generalist predator.

A variety of anemone species inhabit the shallow depths (≤ 50 m) of Antarctic coastal waters, including species such as *Edwardsiidae* sp., *Isoetalia antarctica*, *Stomphia selaginella* and *Urticinopsis antarctica*. *Isoetalia antarctica* and *U. antarctica* are particularly abundant in the sub-tidal around Rothera Research Station in Marguerite Bay (Fig. 1, Supplemental file S1a), where they live in sympatry (N.F. pers. obs.). Anemones boast numerous long tentacles which facilitate the capture of benthic and epibenthic prey. While little is known about the diet of *I. antarctica*, *U. antarctica* is known to be a generalist predator that consumes an array of mobile invertebrates from bivalves, urchins (*Sterechinus neumayeri*), sea cucumbers (*Heterocucumis steneni*), sea stars (e.g. *Perknaster fuscus antarctica*, *Odontaster validus*, *Diplasterias brucei*) and some fish such as *Trematomus* sp (Ivanova and Grebelnyi, 2017). Anemones are ecologically important generalist predators and ecosystem engineers. For example, benthic predators can transform prey carbon into faeces which is then available to grazers, deposit feeders and the microbial loop (Wotton and Malmqvist, 2001).

This study aimed to measure growth, metabolism, and field faecal production rates for two species of Antarctic vagile benthic predators, the anemones *I. antarctica* and *U. antarctica*. We hypothesise that anemone growth is uncoupled from the phytoplankton bloom and that anemones will not exhibit seasonal responses in their metabolism or faecal production. From these data, we aim to evaluate seasonality in the ecophysiology of these ubiquitous benthic predators, that are likely to be important energy and carbon transformers on the seabed in the Southern Ocean.

2. Methods

Research was conducted at Rothera Research Station (67°34.'07 S, 68°07.'30 W), located to the west of the Antarctic Peninsula on Adelaide Island (Fig. 1). The station is equipped with analytical laboratories, a flow through aquarium, and has the facilities to accommodate year-round SCUBA diving. An *in situ* experiment was installed in 2020 and terminated in 2022 to compare growth across years in two anemone species with interannual variation in oceanography and therefore primary production (Venables et al., 2023).

2.1. Anemone identification confirmation

In January 2020, 28 anemones (12 *Isoetalia antarctica* and 16 *Urticinopsis antarctica*) were collected by SCUBA divers from South Cove and Cheshire Island (Fig. 1). Identifications were confirmed via DNA barcoding because both species show phenotypic overlap.

Anemones were initially identified visually; orange colour and multiple thin tentacles were assigned as *U. antarctica* while a more pinkish-red colour and thicker, fewer tentacles were associated with *I. antarctica*. A ~ 10 mm snip of a single tentacle was collected from each anemone in the trial group ($n = 28$), which was preserved in ethanol for barcoding (574 bp fragment of the 18 s gene).

DNA was extracted from tentacles using the DNeasy extraction kit (Qiagen) according to manufacturer's instructions. A 574 bp fragment of the 18S rDNA gene was amplified using NSF4 (CTGGTTGATYCTGCCAGT) and NSR581 (ATTACCGCGGCTGCTGGC) primers using MyTaq PCR ready mix (Meridian Bioscience) and a PCR annealing temperature of 60 °C. PCR products were sequenced using the NSR581 primer by Source Bioscience, with verification using NSF4, if required (Supplemental file S2). Initial species identities were confirmed by blastn sequence similarity searching against the NCBI nucleotide database. Assignment of different individual animals to each species was then performed using ClustalX.

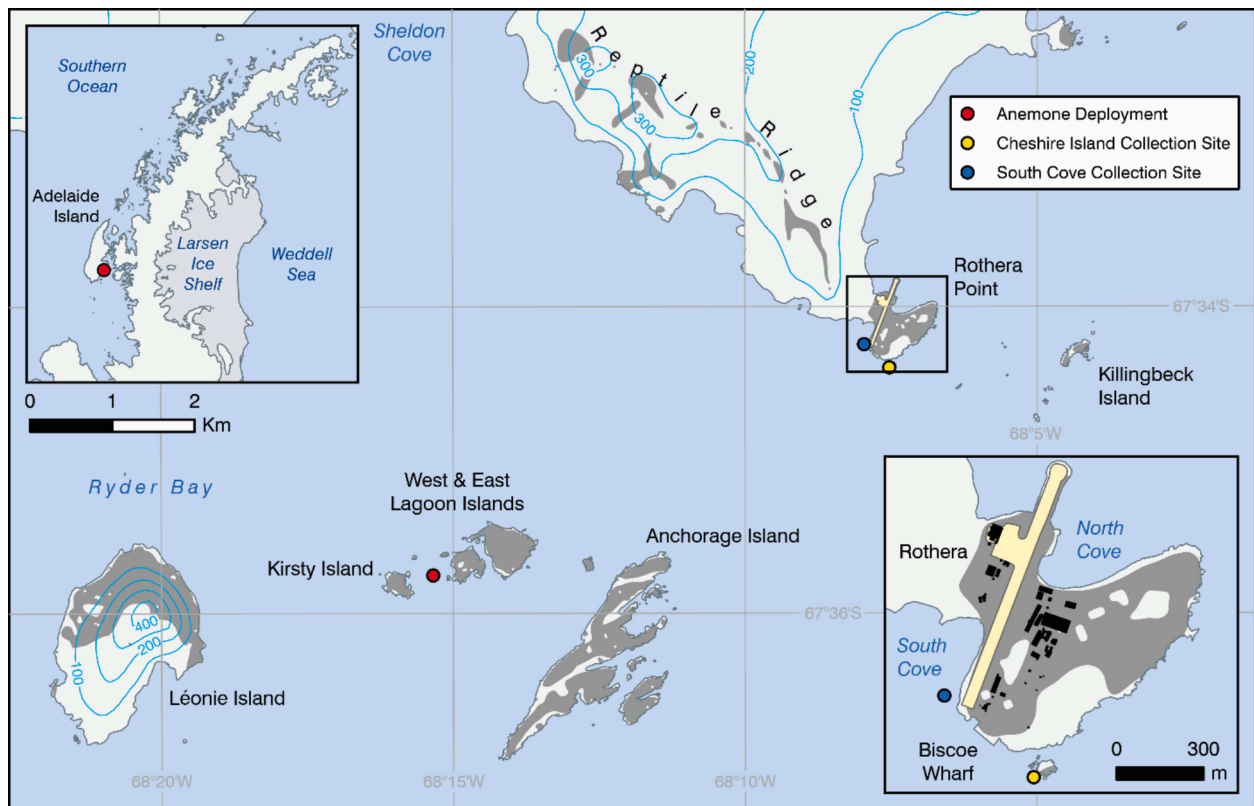


Fig. 1. Map showing collection sites near the British Antarctic Survey station on Rothera Point, Adelaide Island, and the experimental site 'Backbay', located to the West of Lagoon Island, where anemones were deployed to facilitate the measurement of *in situ* changes in mass. Produced by the Mapping and Geographic Information Centre, © British Antarctic Survey, UK Research and Innovation, 2023. Data from the SCAR Antarctic Digital Database, 2023.

2.2. Growth metrics

Following tentacle collection, the same trial group (section 2.1) was used to calculate regressions between anemone buoyant weight, ash free dry mass (AFDM) and pedal disc area (Supplemental file S3). Some soft-bodied organisms, including anemones, can change their water content substantially over short periods of time, by orders of magnitude in some species such as *Dactylanthus antarcticus* (Peck and Brockington, 2013). As a result, anemone morphology and volume can fluctuate within as little as 24 h, as detected in the study species here (N.F. pers. obs.), meaning that metrics such as wet weight and volume would be unable to accurately capture changes in tissue mass. The density of animal tissue is generally greater than seawater, though large fat deposits are positively buoyant (Phleger, 1998). Thus, for most animals, buoyant weight provides a reasonable estimate of animal tissue mass (Franzisket, 1964; Jokiel and Maragos, 1978). A conversion of buoyant weight to ash-free dry mass allows the estimation of metabolising tissue mass and was adopted in the study as the most appropriate metric to quantify mass changes in anemone tissue (Supplemental file S3). Furthermore, Antarctic growth rates are slow (Peck, 2018), and measurements need to be precise to detect small changes in size, between seasons and across years.

AFDM was obtained by drying anemones to a constant weight at 60 °C and then ignited at 460 °C for 12 h in a muffle furnace. Pedal disc area was measured as the widest diameter of the anemone pedal disc at the point of contact with the substratum using callipers. Three measurements were collected for each individual and the average was presented.

2.3. Anemone collection, deployment, and sampling

In February 2020, 45 anemones (hereafter referred to as *in situ*

experimental individuals), comprising two species, *Istoealia antarctica* ($n = 22$) and *Urticinopsis antarctica* ($n = 23$), were collected using SCUBA at depths between 10 and 30 m from sites in South Cove and Cheshire Island in Ryder Bay, Adelaide Island (Fig. 1). Individuals were removed by gently peeling the anemones basal plate away from the underlying rock by hand or using a spatula.

After initial collection, the *in situ* experimental individuals were held in the laboratory where they were maintained in a flow-through aquarium at ambient temperatures with water extracted directly from the bay to the South of Rothera station. Anemones were identified visually by comparison with previously barcoded reference material (section 1.1). Initial buoyant weight measurements were conducted for each anemone; animals were placed on a scale suspended in ambient sea water and weights were recorded (± 0.001 g) using a Sartorius LA3200D balance (Supplemental file S4). Individual anemones were subsequently placed on numbered clay tiles surrounded by a plastic mesh 'fence' to prevent them from transferring to adjacent tiles. Both anemone species exhibit large basal plates and they readily settled onto artificial substrata (Supplemental File S1c&d). This attribute was used to allow subsequent identification and repeat collection of individual anemones. Anemones were checked daily and, if necessary, re-positioned onto their tiles with all anemones adhering within 14 to 21 days. After this, anemones were maintained for 28 days in the laboratory, during which they were fed a mixture of limpets and white fish.

In March 2020, all 45 anemones on clay tiles were deployed at 26 m by SCUBA divers at a dive site off Backbay Lagoon Island, Ryder Bay (67°35.43 S, 68°15.12 W, Fig. 1). Although the site is located six kilometres away from the station, it was selected because it offered greater protection against ice scour than other potential sites, and the locality had both species naturally occurring near the field experimental site. The habitat is characterised by soft sediment and the vagile anemones were deemed unlikely to move off their tiles due to the unfavourable

substratum, as the authors had previously only observed the study species on hard substrata.

The original experimental design was to resample anemones seasonally and across years. However, poor sea-ice conditions, low visibility and sediment burial of tiles resulted in low recovery rates and meant that resampling was only carried out at 15 and 25 months intervals. During subsequent resampling, animals were gently removed from their tiles, cleaned of debris and anemone buoyant mass was then re-measured. All measurements were conducted using the same balance at each sampling interval.

2.4. Respirometry

To minimise stress on the *in situ* experimental animals, respirometry was conducted on a separate collection of anemones. Ten anemones (6 *Isotealia antarctica* and 4 *Urticinopsis antarctica*) were collected in January 2022 from Cheshire Island at 18 m depth, using SCUBA (Fig. 1). Summer respirometry measurements were conducted ten days after collection in February 2022 upon individuals that had not been fed. Winter measurements were conducted in June 2022 on the same anemones which had been maintained in the aquarium overwinter and fed half a limpet twice a month for four months.

Respiration measurements were conducted in appropriately sized respiration chambers (1000–1700 ml), chosen after preliminary trials were conducted to identify chamber sizes and trial durations needed for approximately 20% reduction in oxygen concentration in respirometers. Prior to respiration measurements, animals were placed within the chambers and left for 24 h to habituate to the experimental conditions; chambers were left open to allow continual water exchange with the flow through aquarium, with a 1 mm mesh preventing anemone escape. This gave anemones time to settle within their respirometer and reduce metabolic rates to routine levels, which has been shown to take 6–10 h previously in Antarctic bivalve molluscs (Peck and Conway, 2000).

Prior to measuring oxygen consumption, chamber water was exchanged, all air bubbles were removed, and the lids sealed. In addition, three control chambers, without anemones, were sealed to account for any changes in background oxygen levels. Oxygen concentrations were then recorded within each chamber at ‘time 0’ (3 repeat measurements per chamber at each sampling interval) using a Fibox-3 oxygen system (PreSens GmbH with SP-PSt3-NAUspots and OxyView PST3-V5.31 b software) together with temperature readings from the aquarium tank containing the respiration chambers. Before taking samples, chambers were gently inverted three times to mix the contents, prevent any build-up of oxygen gradients and ensure that three stable readings were recorded. Measurements were taken again at the end of a six-hour period, when oxygen saturation did not fall below 70% in any chamber (Souster et al., 2018). At the end of the respirometry measurements, the volume of each anemone was measured by displacement in sea water. This volume was then subtracted from the volume of the respirometer to calculate the final volume of water within the chamber from which oxygen was extracted.

The Fibox-3 system uses oxygen spots inside chambers. During each calibration, the amplitude from each spot was checked to ensure it read over 10,000 V/m, a measure of the integrity of the oxygen sensitive foil. Measurements were standardised by calibrating each chamber spot 24 h post measurement. The Mean Sea Level (QFF) atmospheric pressure was recorded prior to calibration measurements. Spots inside the chambers were calibrated with 100% saturated oxygen, which had been vigorously aerated for 30 min and then left to stand for 10 min. They were then calibrated for 0% oxygen using seawater with added sodium dithionite (2.5%) at the ambient experimental temperatures.

2.5. Faecal egestion

Faecal measurements were conducted from a separate population of anemones collected using SCUBA from Cheshire in January 2022 ($n =$

24, 12 *Isotealia antarctica* and 12 *Urticinopsis antarctica*). For winter faecal measurements, a new collection was made at 20 m depth from South Cove in September 2023 ($n = 20$, 6 *I. antarctica* and 14 *U. antarctica*). Spatially, South Cove and Cheshire Island (Fig. 1) are separated by ~300 m and are characterised by very similar environmental conditions and substratum.

Immediately after collection, anemones were placed in individual, standardised 5632 cm³ floating containers, in the Bonner Laboratory flow through aquarium. Faeces were pipetted from each container every 24 h for seven days and comprised a combination of mucus and undigested prey items, e.g. calcareous skeletons (Supplemental file S5). Samples were labelled according to individual anemone ID and the day of faecal collection. Container water was refreshed after each faecal collection to maintain oxygenated water levels.

Faecal samples ($n = 282$) were first rinsed in MiliQ water and placed in pre-weighed foil boats. Samples were dried to a constant weight at 60 °C and then ignited at 460 °C for 12 h in a muffle furnace. Ash free dry mass (AFDM), an estimate of organic content, was calculated by subtracting the ash mass after ignition from the dried mass.

2.6. Statistical analysis

2.6.1. Growth

Regressions were used to interpret size changes because repeated measurements from re-deployment and re-sampling of the same individuals over time allowed tracking of individual size changes. In addition, the relationship between buoyant weight and AFDM was used to estimate AFDM for respirometry calculations and summer faecal analysis assessments. In a few cases, the relationship between pedal disc area and buoyant weight was used to predict AFDM when it was not possible to obtain winter buoyant weight measurements (Supplemental file S3, section 2.6.3).

Growth data were compiled from independent buoyant weight measurements from both *Isotealia antarctica* and *Urticinopsis antarctica* individuals from February 2020 to May 2021 (15 months) and for *I. antarctica* from February 2020 to March 2022 (25 months). Only one individual *U. antarctica* was sampled after 25 months and this individual was not included in the growth experiment due to paucity of data. Data were converted into proportional change in mass for each individual relative to the starting weights obtained in February 2020 to control for size differences for analysis. For data visualisation, raw buoyant weight metrics were plotted.

Initial buoyant weights of resampled anemones satisfied the assumption of homogeneity of variance and were analysed to test for species-specific differences in buoyant weight using a Welch Two Sample *t*-test (Levene’s test $F_{1,20} = 0.66$, $p = 0.42$). A Box-Cox transformation ($\lambda = -1$) was applied to proportional anemone growth data to satisfy the assumption of homogeneity for subsequent analysis (Levene’s test statistic $F_{1,20} = 0.02$, $p = 0.89$). Two separate linear models were constructed (lm) (R version 4.3.1). The first tested the effects of the transformed proportional growth data against fixed factors of species, *I. antarctica* and *U. antarctica*. The second tested the effects of year (2020–2021 and 2020–2022) upon *I. antarctica* growth. *P* values were obtained from a type I sums of squares.

2.6.2. Respirometry

Oxygen concentrations were converted into oxygen consumption values (O₂ μmol hr⁻¹ g AFDM⁻¹) for each individual anemone across summer and winter 2022. Summer and winter respirometry were conducted on the same individuals and therefore these data are treated as repeated measures.

Seasonal metabolism of two anemone species satisfied the assumption of homogeneity of variance, (Levene’s test statistic $F_{3,16} = 0.54$, $p = 0.66$). A linear mixed effects model (lme) using Maximum Likelihood (package lm4 in R version 4.3.1) tested the effects of season and species upon respiration. To account for the nature of the repeated measures

design, individual anemone ID was included as a random factor. Model substitution provided an improved AIC value without the addition of the random factor. *P* values were obtained from type II Wald χ^2 tests. Residuals were further inspected and satisfied the assumption of homogeneity of variance.

2.6.3. Faeces

Anemone AFDM was compared between independent groups of summer and winter *ex situ* anemones using a Welch Two Sample *t*-test (Levene's test $F_{1,42} = 0.18$, $p = 0.67$). Daily faecal production, per individual was standardised to the mass of the animal and compared between summer 2022 and winter 2023.

Daily faecal production data, per species, per day, satisfied the assumption of homogeneity of variance (Levene's test statistic $F_{3, 278} = 2.47$, $p = 0.06$). To test for temporal significance in seven days of faecal egestion, an initial linear model (lm) was built with species and season as fixed factors and day as a covariate. *P* values were obtained from a type II sums of squares.

A second linear model was built with seven days of pooled faecal data per individual. Data satisfied the assumption of homogeneity of variance (Levene's test statistic $F_{3,40} 2.12$, $p = 0.11$) and a linear model was constructed with pooled AFDM faecal data and with species and seasons as fixed factors. *P* values were generated from a type II sums of squares.

3. Results

3.1. Anemone barcoding results

The sequence of the PCR product was used to differentiate between the two species, which were 96.5% identical over 574 bp. The characteristic differences were a GA insertion in *Urticinopsis antarctica* and a CCGCAAGGGC in *Isotealia antarctica* along with several species-specific SNPs (Supplemental file S2). Using combined data from the initial trial group ($n = 28$) and the experimental individuals ($n = 45$), barcoding confirmed that 4% of *U. antarctica* had been visually identified as *I. antarctica* and were used to update species ID. Of the May 2021 resampled anemone group, 90.9% of individuals (10/11) were confirmed to be same species as originally deployed on the respective tiles. Of this group, one *U. antarctica* individual was misidentified as *I. antarctica* and was removed from the experiment because a different

individual appeared to have moved onto the tile.

3.2. Growth metrics

A regression was calculated between buoyant weight and AFDM ($R^2 = 0.94$, Supplemental file S3) ($n = 18$ anemone) from a subset of the initial trial group of anemones (Section 1.2). Predicted buoyant weights were also calculated from the relationship between pedal disc area and buoyant weight ($n = 28$ anemones) ($R^2 = 0.73$) (Supplemental file S3).

3.3. Growth

The relocation of deployed experimental animals resulted in the total recovery of 23 anemones, (17, *Isotealia antarctica*, 6 *Urticinopsis antarctica*), representing 50% success (Fig. 2). The remaining anemones were either impacted by icebergs (Section 1.3) or the anemones had moved off their tiles. As only one *U. antarctica* was recovered after 25 months of field deployment, no two year growth data are presented for this species due to the lack of replication. A *t*-test of the recovered individuals revealed that there was no significant difference in initial buoyant weight of *I. antarctica* and *U. antarctica* and growth could therefore be compared ($t_{1,17} 1.52$, $p = 0.15$).

The results of the linear model, using mass corrected changes in buoyant weight, showed species-specific significant differences in growth ($F_{1,20} 35.95$, $p \leq 0.001$). Both species grew during the first 15 months, with *U. antarctica* growing significantly faster than *I. antarctica* (Fig. 2). Three out of five resampled *I. antarctica* individuals grew during the first 15 months, exhibiting an average 16.85% (\pm SE 8.9) increase in body mass (Supplemental file S6). All *U. antarctica* grew during the first 15 months, resulting in 199.80% (\pm SE 25.79) average increase in body mass (Supplemental file S6).

Year did not influence growth in *I. antarctica* between 15 months and 25 months post field deployment ($F_{1,15} 0.95$, $p = 0.35$). Of the *I. antarctica* individuals that grew, a 16.85% (\pm SE 8.9) increase in body mass occurred in 15 months compared to an 7.96% (\pm SE 8.05) increase after 25 months (Supplemental file S6).

3.4. Metabolic rate

There was no significant effect of season upon anemone oxygen consumption ($\chi^2_{1,8} = 3.20$, $p = 0.07$) (Fig. 3) nor was there any

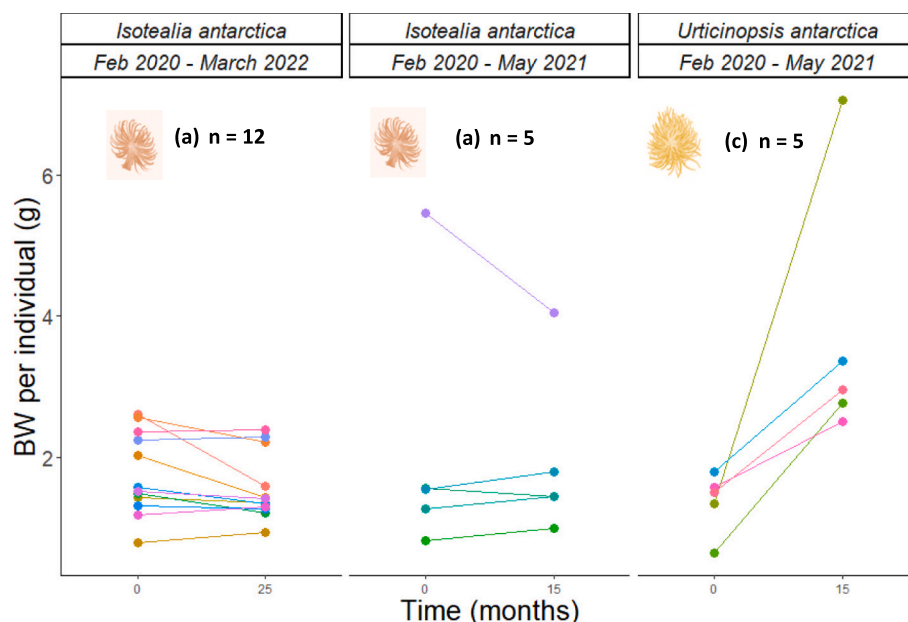


Fig. 2. Changes in buoyant weight (BW) of two Antarctic predatory anemones, between 2020 and 2021 (15 months) and between 2020 and 2022 (25 months).

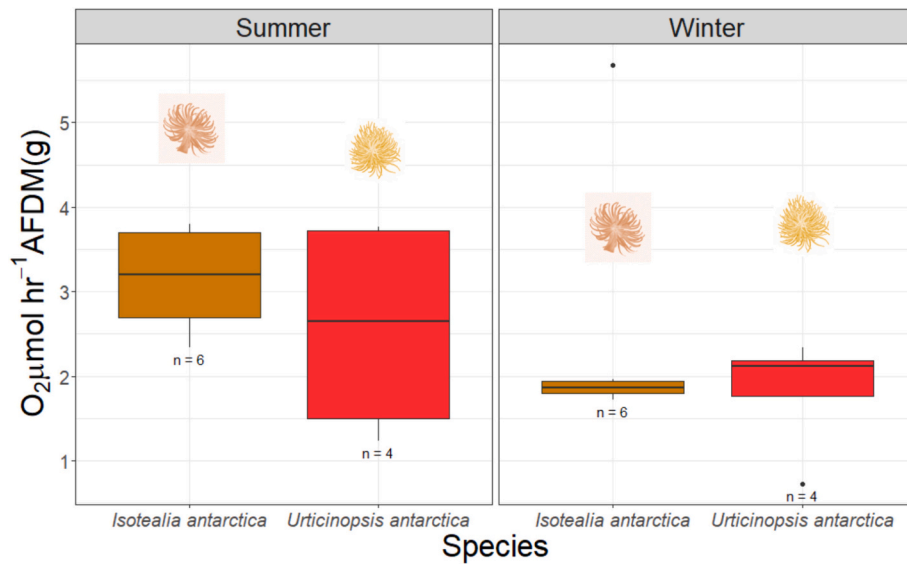


Fig. 3. Summer and winter oxygen consumption h^{-1} of animal AFDM (g) for two species of Antarctic predatory anemones ($n = 10$), measurements constitute repeated measures.

significant difference in oxygen consumption between *Isotealia antarctica* and *Urticinopsis antarctica* ($\chi^2_{1,8} = 1.36, p = 0.25$), or any significant interaction between species and season ($\chi^2_{1,8} = 0.01, p = 0.93$). Anemone ID, the random factor implicit in the repeated measure design, was not significant and therefore the non-independence of repeated measures did not influence the results.

3.5. Faeces

There was no significant difference in anemone AFDM from two independent groups sampled in summer 2022 and winter 2023 sampled for faeces ($t_{1,37} = 0.20, p = 0.84$).

Faecal matter was first analysed to assess the rate of faecal production over time. The results of the linear model showed that faecal

production did not significantly change over the seven day assessment period ($F_{6,272} = 1.38, p = 0.22$) and there was no significant difference between species ($F_{1,272} = 2.86, p = 0.09$) (Supplemental file S7). However, when analysing daily faecal data, the effect of season was significant ($F_{1,272} = 4.96, p = 0.03$). This is due to high pulses of faecal material from a few individuals that resulted in higher faecal production during the winter. Based on the results of the model, day was removed as a covariate and data were pooled for individuals across seven days.

The results of an updated linear model, using pooled faecal data, showed there was no significant difference between anemone mass corrected faecal production between species ($F_{1,40} = 1.24, p = 0.27$) and across the season ($F_{1,40} = 2.97, p = 0.09$). Unsurprisingly, there was also no significant species and season interaction ($F_{1,40} = 1.11, p = 0.30$) (Fig. 4).

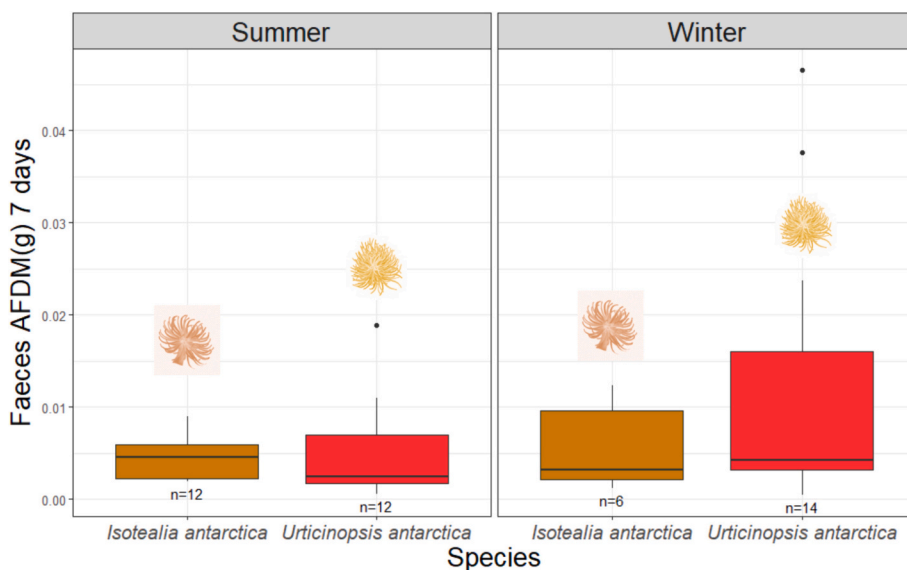


Fig. 4. Faecal production for two Antarctic predatory anemones, *Isotealia antarctica* and *Urticinopsis antarctica* expressed as AFDM (g) of faeces per g of anemone AFDM across 7 days.

4. Discussion

4.1. Physiological measurements

Field growth rates are reported for two Antarctic benthic predatory anemones across a two-year period. The species exhibited different trends in growth across time. Notably, *Urticinopsis antarctica* grew faster than *Isotealia antarctica* across a 15-month growth period. Anemone faecal egestion post collection did not decline across a seven-day period and so daily faecal egestion per individual, in the field population, could be estimated from this. There were no seasonal differences in faecal egestion for both anemone species. Furthermore, anemones kept in the aquarium and fed over winter had a similar metabolic rate to wild collected anemones in the summer, in line with data showing they continue to feed all year round when food is available.

Repeat *in situ* measurements of size from soft bodied animals is a data gap that was identified nearly 50 years ago by Dayton et al. (1974), and such data are still very rare or absent globally. Our results show that two benthic predatory anemone species grew at very different rates in the field. *Isotealia antarctica* and *U. antarctica* both exhibited positive field growth rates across a 15 month period between 2020 and 2021; with *U. antarctica* increasing 199.80% (\pm SE 25.8) in mass compared to a 16.85% (\pm SE 8.9) increase in *I. antarctica*, a >11 - fold difference. However, there was high variability between individuals within the same species, which most likely reflects the stochastic encounter rate between a vagile predator and mobile prey items. There was no significant growth in *I. antarctica* between February 2020 and March 2022, after 25 months field deployment. In this species, there was little change in size across the two years. This is likely due to the fact that only some individuals grew (Supplemental file S6). There was a small increase in the first year but no significant change across two years. This might reflect little change in either year or a small decrease in mass in the second year, with fairly small numbers recovered, hampering our ability to detect small changes in size.

In support of our hypothesis that vagile predator growth is uncoupled from the phytoplankton bloom, measured proxies for productivity were plotted from Ryder Bay and compared against the two growth periods of this study. Data from the Rothera Antarctic Time Series (RaTS) (Venables et al., 2023), revealed that anemone growth in the present study was uncoupled from the phytoplankton bloom productivity. The chlorophyll plot, (Supplemental file S8), reveals that higher productivity, in terms of bloom intensity and duration (121 days above 2.5 mg m³), occurred between May 2021 and March 2022, and hence in the second half of this study when growth was nil or negative in *I. antarctica* (Fig. 2). The greatest increase in body mass for *I. antarctica* was recorded between February 2020 and May 2021, coinciding with two comparatively shorter phytoplankton blooms between 2020 and 2021 and 2019–2020 (37 days and 64 days respectively above 2.5 mg m³) compared to the bloom in 2021–2022.

Furthermore, the present study detected species-specific differences in temporal growth patterns between the two anemone species. Although these species are often found living in the same habitat, it is possible that the environment the anemones were deployed into was more suitable for *U. antarctica*. This may further be attributed to that fact that more vagile *U. antarctica* potentially moved off their tiles.

The re-sampling success rate of anemones on tiles amounted to 50% retrieval, and data for year one were based on ten anemones while 12 different specimens were recovered after a two year deployment. Although the buoyant weight technique accounts for error associated with variable water content contained within individuals, natural variability in feeding can still impact buoyant weight measurements. Working on wild populations eliminates the possibility to control for individuals that may have just eaten or egested a meal. Therefore, the growth data presented in this study are likely affected by natural feeding regimes, inter-individual differences in growth, and how recently individuals fed. To control for this, to some degree, anemones were

weighed immediately after re-sampling at each sampling event to capture anemone mass at the same time for each individual. The production and release of gametes will impact the buoyant weight measurements (Sebens, 1981), and hence the growth data measured here. Future work is needed to assess the reproductive cycle of *I. antarctica* and *U. antarctica* and stoichiometric changes that could affect their density.

In contrast to the growth results, there were no species-specific differences in oxygen consumption or faecal production between *I. antarctica* and *U. antarctica* (Figs. 3 and 4). This indicates that both species were likely feeding at similar rates when collected. Furthermore, there were no seasonal physiological differences detected within this small sample size of anemones. Seasonal respirometry and faecal data were close to being significantly different and could potentially yield significant results with a larger sample size. The lack of a seasonal signal, detected within this study, could indicate that the ecophysiology of the two anemone species is not coupled to phytoplankton productivity (Clarke, 1988). Lower winter temperatures and changes in productivity did not result in a decline in metabolism, or feeding rate, as exhibited by most Antarctic primary and secondary consumers studied to date (Clarke and Peat, 2022, Souster et al., 2018, Obermüller et al., 2010, Fraser et al., 2004, 2007 Supplemental file S8). In accordance with our second hypothesis, anemone predators exhibit little seasonality in their ecophysiology and continue to feed all year round. Furthermore, in our trials, Antarctic anemone faecal production did not decline across the seven days post collection period (Supplemental file S7). This indicates that the digestion period for meals in these species is well in excess of 7 days. However, when analysing faecal data production per day, higher than average faecal values were detected from certain individuals (section 3.5) demonstrating the opportunistic nature of food acquisition by vagile, anemone predators.

4.2. Trophic implications

Our data for Antarctic anemones supports the contention of Clarke (1988), that an organism's trophic position should affect its physiological response to seasonal changes in productivity and temperature. These findings concur with empirical results from Obermüller et al. (2010) where seasonality, measured by productivity and temperature, did not impact the metabolism or faecal production of the Antarctic predatory Nemertean worm, *Parborlasia corrugatus*. However, other predators in the Obermüller et al. (2010) study, including the fish *Harpagifer antarcticus*, and the nudibranch *Doris kerguelensis* did show some seasonality in their ecophysiology, though less than that reported for many primary consumers (Souster et al., 2018; Clarke and Peat, 2022) such as suspension feeding sponges which had the largest seasonal change in metabolic rates among 23 species of Antarctic marine ectotherm studied (Morley et al., 2016b).

Furthermore, Souster et al. (2018) conducted a study on benthic primary and secondary consumers. The authors reported significant seasonal differences in the metabolism of two generalist feeders, the grazing urchin *Sterechnus neumayeri* and the scavenging/predatory sea star, *Odontaster validus*, with both exhibiting lower metabolic rates in winter, than summer. Generalist predators, such as anemones, may be expected to exhibit lower rates of oxygen consumption during winter, if feeding activity is reduced, but the general hypothesis is that predators should show less seasonality of ecophysiology than species with closer dependence on phytoplankton productivity (Clarke, 1988; Clarke and Peck, 1991). When comparing across trophic groups, Souster et al. (2018) concluded that there was no difference in the seasonality of metabolic rates between primary and secondary consumers, and metabolic changes were, therefore driven by factors other than the seasonality of the phytoplankton bloom or reduced winter temperatures.

Conversely, Campbell et al. (2008) showed strong seasonality in the ecophysiology of the benthic fish, *Notothenia coriiceps*, in Antarctica and likened the reduction in metabolic rate in winter to hibernation in mammals. There is good evidence that benthic marine predators in

Antarctica show varying degrees of seasonality, but that several, if not most, are less seasonal than primary consumers, and so there does appear to be a trend towards less seasonality with position in the food web towards predation (Peck et al., 2024). The Antarctic predator/scavengers studied by Souster et al. (2018), Obermüller et al. (2010) and Campbell et al. (2008) were all mobile, which contrasts with the vagile anemones here, but similar seasonality was found here aligning with several previously reported mobile predators.

To date, studies focused on growth and metabolism in Antarctic animals have targeted suspension feeders (Barnes, 1995; Peck et al., 1997; Fraser et al., 2004; Higgs et al., 2009; Ashton et al., 2017), deposit feeders (Peck et al., 2000), grazers (Brey et al., 1995; Fraser et al., 2004), omnivores (Peck and Brockington, 2013, Souster et al., 2018), mobile predators (Obermüller et al., 2010) and scavengers (Obermüller et al., 2010). There remains a gap in knowledge of Antarctic benthic predatory anemones. This study has contributed data from two Antarctic anemone predators. Building a comprehensive trophic network will allow more accurate ecosystem modelling which will likely aid predictions of resilience to future change (Morley et al., 2019). Lower trophic levels, such as grazers, are tightly coupled with the phytoplankton bloom (Clarke 1998, Obermüller et al., 2010, Souster et al., 2018) and their ability to adjust their growth and ecophysiology in response to future changes in the duration and the intensity of the phytoplankton bloom (Henley et al., 2020; Sahade et al., 2015) will likely be reduced relative to generalist, vagile and mobile predators.

4.3. Recommendations

Anemone growth in Antarctica appears slow, and based on our results, it is unlikely that growth changes would have been detected if measurements had been made over shorter sampling intervals. Dayton et al. (2013) showed that the Antarctic sponge *Anoxycalyx joubini* did not grow for 22 years in McMurdo Sound. Following this, growth was detected across a 6 year period which was linked to a localised substantial increase in phytoplankton productivity as a result of an ice shelf calving event (Dayton et al., 2013). This demonstrates how changes in environmental conditions can have powerful effects on growth. There are clearly very large changes in growth between periods in some Antarctic species. This could be applicable to anemones but long-term, replicated *in situ* studies over multiple decades in the shallow Antarctic benthos are needed to disentangle this. Furthermore, decadal physiological measurements would separate long-term trends from effects of natural cycles such as the Southern annular mode and El Niño. Antarctic research programmes should dedicate resource towards following animal *in situ* growth and ecophysiology over extended time scales to thoroughly address the impacts of environmental change.

5. Conclusions

This study has improved our understanding of the influence of Southern Ocean seasonality on vagile, benthic predators. Notably, *Isotealia antarctica* and *Urticinopsis antarctica* exhibit very different growth rates and for *I. antarctica*, growth varied between years, which highlights the importance of collecting species specific data and collecting data over extended periods. The anemones in this study continued to feed all year round as evidenced by the lack of seasonal variability in metabolism and faecal egestion detected in our data.

Funding sources

This work was supported by core funding from the NERC, UKRI, UK to the British Antarctic Survey.

CRedit authorship contribution statement

Nadia Frontier: Writing – review & editing, Writing – original draft,

Formal analysis, Data curation, Conceptualization. **Joseph Marlow:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Adriana Giles:** Data curation. **Simon A. Morley:** Writing – review & editing, Supervision, Project administration, Formal analysis, Conceptualization. **Melody S. Clark:** Data curation. **Lloyd S. Peck:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Data availability

Double-stranded amplicon sequences for each species were submitted to NCBI BankIT (<https://www.ncbi.nlm.nih.gov/WebSub/>) with the accession numbers **OK021587** for *Urticinopsis antarctica* and **OK021588** for *Isotealia antarctica*.

Growth, respirometry and faeces data and R scripts will be available in the GitHub repository: <https://github.com/nadiafrontier/Antarctic-anemone-growth-and-ecophysiology.git>

Acknowledgements

We thank the Rothera dive team for their tremendous demonstration of conducting diving operations in a logistically complex and changeable environment. Special thanks to Ryan Mathews for his field and logistical assistance. This work was funded by NERC under the core funding to the British Antarctic Survey, Biodiversity, Evolution and Adaptation Team.

We would like to acknowledge the use of unpublished RaTS data held in the Polar data Centre, British Antarctic Survey.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2024.152045>.

References

- Aronson, R.B., Thatje, S., Clarke, A., Peck, L.S., Blake, D.B., Wilga, C.D., Seibel, B.A., 2007. Climate change and invasibility of the antarctic benthos. *Annu. Rev. Ecol. Syst.* 38, 129–154. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095525>.
- Ashton, G.V., Morley, S.A., Barnes, D.K.A., Clark, M.S., Peck, L.S., 2017. Warming by 1°C drives species and assemblage level responses in antarctica's marine shallows. *Curr. Biol.* 27, 2698–2705. <https://doi.org/10.1016/j.cub.2017.07.048>.
- Barnes, D.K.A., 1995. Seasonal and annual growth in erect species of Antarctic bryozoans. *J. Exp. Mar. Biol. Ecol.* 188, 181–198. [https://doi.org/10.1016/0022-0981\(95\)00003-A](https://doi.org/10.1016/0022-0981(95)00003-A).
- Brey, T., Pearse, J., Basch, L., McClintock, J., Slattery, M., 1995. Growth and production of *Sterechinus neumayeri* (Echinoidea: Echinodermata) in McMurdo Sound. *Antarctica. Mar. Biol.* 124, 279–292. <https://doi.org/10.1007/BF00347132>.
- Campbell, H.A., Fraser, K.P., Bishop, C.M., Peck, L.S., Egginton, S., 2008. Hibernation in an Antarctic fish: on ice for winter. *PLoS One* 3, 1743. <https://doi.org/10.1371/journal.pone.0001743>.
- Carrasco, J.F., Bozkurt, D., Cordero, R.R., 2021. A review of the observed air temperature in the Antarctic peninsula. Did the warming trend come back after the early 21st hiatus? *Polar Sci.* 28, 100653. <https://doi.org/10.1016/j.polar.2021.100653>.
- Clarke, A., 1988. Seasonality in the Antarctic marine environment. *Comp. Biochem. Physiol.* B 90, 461–473. [https://doi.org/10.1016/0305-0491\(88\)90285-4](https://doi.org/10.1016/0305-0491(88)90285-4).
- Clarke, A., 1990. Faecal egestion and ammonia excretion in the Antarctic limpet *Nacella concinna* (Strebler, 1908). *J. Exp. Mar. Biol. Ecol.* 138, 227–246. [https://doi.org/10.1016/0022-0981\(90\)90169-D](https://doi.org/10.1016/0022-0981(90)90169-D).
- Clarke, A., Johnston, N.M., 2003. Antarctic marine benthic diversity. *Oceanogr. Mar. Biol.* 41, 47–114. <https://doi.org/10.1201/9780203180570>.
- Clarke, A., Peat, H.J., 2022. Seasonal and interannual variability of feeding in Antarctic benthos. *Limnol. Oceanogr.* 67, 962–972. <https://doi.org/10.1002/lno.12048>.
- Clarke, A., Peck, L.S., 1991. The physiology of polar marine zooplankton. *Polar Res.* 10, 355–370. <https://doi.org/10.3402/polar.v10i2.6752>.

- Dayton, P.K., Robilliard, G.A., Paine, R.T., Dayton, L.B., 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol. Monogr.* 44, 105–128. <https://doi.org/10.2307/1942321>.
- Dayton, P.K., Kim, S., Jarrell, S.C., Oliver, J.S., Hammerstrom, K., Fisher, J.L., O'Connor, K., Barber, J.S., Robilliard, G., Barry, J., Thurber, A.R., Conlan, K., 2013. Recruitment, growth and mortality of an Antarctic Hexactinellid sponge, *Anoxycaalyx jobini*. *PLoS One* 8, 56939. <https://doi.org/10.1371/journal.pone.0056939>.
- Eastman, J.T., 2013. *Antarctic Fish Biology: Evolution in a Unique Environment*, second ed. Academic Press, Athens.
- Everson, I., 1970. The population dynamics and energy budget of *Notothenia neglecta* Nybelin at Signy Island, South Orkney Islands. *Brit. Antarct. Surv. Bull.* 23, 25–50. <https://nora.nerc.ac.uk/id/eprint/526300>.
- Franzisket, L., 1964. Die Stoffwechselintensität der Riffkorallen und Ihre Ökologische, Phylogenetische und Soziologische Bedeutung: Ergebnis der Xarifa-Expedition 1957/58. *Z. Vergl. Physiol.* 49, 91–113.
- Fraser, K.P.P., Peck, L.S., Clarke, A., 2004. Protein synthesis, RNA concentrations, nitrogen excretion, and metabolism vary seasonally in the Antarctic holothurian *Heterocucumis steineri* (Ludwig 1898). *Physiol. Biochem. Zool.* 77, 556–569. <https://doi.org/10.1086/420949>.
- Fraser, K.P.P., Clarke, A., Peck, L.S., 2007. Growth in the slow lane: protein metabolism in the Antarctic limpet *Nacella concinna* (Strebel 1908). *J. Exp. Biol.* 210, 2691–2699. <https://doi.org/10.1242/jeb.003715>.
- Fraser, K.P.P., Peck, L.S., Clark, M.S., Clarke, A., Hill, S.L., 2022. Life in the freezer: protein metabolism in Antarctic fish? *R. Soc. Open Sci.* 9, 211212 <https://doi.org/10.1098/rsos.211272>.
- Griffiths, J.R., Kadin, M., Nascimento, F.J.A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., Järnström, M., Kotta, J., Lindegren, M., Nordström, M.C., Norkko, A., Olsson, J., Weigel, B., Zydelski, R., Blenckner, T., Niiranen, S., Winder, M., 2017. The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. *Glob. Chang. Biol.* 23, 2179–2196. <https://doi.org/10.1111/gcb.13642>.
- Harper, E.M., Peck, L.S., 2016. Latitudinal and depth gradients in marine predation pressure. *Glob. Ecol. Biogeogr.* 25, 670–678. <https://doi.org/10.1111/geb.12444>.
- Henley, S.F., Cavan, E.L., Fawcett, S.E., Kerr, R., Monteiro, T., Sherrell, R.M., Bowie, A. R., Boyd, P.W., Barnes, D.K., Schloss, I.R., Marshall, T., 2020. Changing biogeochemistry of the Southern Ocean and its ecosystem implications. *Front. Mar. Sci.* 7, 581. <https://doi.org/10.3389/fmars.2020.00581>.
- Higgs, N.D., Reed, A.J., Hooke, R., Honey, D.J., Heilmayer, O., Thatje, S., 2009. Growth and reproduction in the Antarctic brooding bivalve *Adacnarca nitens* (Philobryidae) from the Ross Sea. *Mar. Biol.* 156, 1073–1081. <https://doi.org/10.1007/s00227-009-1154-9>.
- Ivanova, N., Grebelnyi, S.D., 2017. On the food of the Antarctic Sea anemone *Urticinopsis antarctica* Carlgren, 1927 (Actiniidae, Actiniaria, Anthozoa). *J. Mar. Biol. Assoc. UK* 97, 29–34. <https://doi.org/10.1017/S0025315415002131>.
- Jokiel, P.L., Maragos, J.E., 1978. Coral growth: buoyant weight technique. In: Stoddart, D.R., Johannes, R.E. (Eds.), *Coral Reefs: Research Methods*. UNESCO, Paris, France, pp. 529–541.
- Kennicutt, M.C., Chown, S.L., Cassano, J.J., Liggett, D., Peck, L.S., Massom, R., Rintoul, S.R., Storey, J., Vaughan, D.G., Wilson, T.J., Allison, I., 2015. A roadmap for Antarctic and Southern Ocean science for the next two decades and beyond. *Antarct. Sci.* 27, 3–18. <https://doi.org/10.1017/S0954102014000674>.
- McCormack, S.A., Melbourne-Thomas, J., Trebilco, R., Griffith, G., Hill, S.L., Hoover, C., Johnston, N.M., Marina, T.I., Murphy, E.J., Pakhomov, E.A., Pinkerton, M., Plagányi, É., Saravia, L.A., Subramaniam, R.C., Van De Putte, A.P., Constable, A.J., 2021. Southern Ocean food web modelling: Progress, prognoses, and future priorities for research and policy makers. *Front. Ecol. Evol.* 9, 624763 <https://doi.org/10.3389/fevo.2021.624763>.
- Meredith, M.P., King, J.C., 2005. Rapid climate change in the ocean west of the Antarctic peninsula during the second half of the 20th century. *Geophys. Res. Lett.* 32, 19. <https://doi.org/10.1029/2005GL024042>.
- Morley, S.A., Suckling, C.C., Clark, M.S., Cross, E.L., Peck, L.S., 2016a. Long-term effects of altered pH and temperature on the feeding energetics of the Antarctic Sea urchin, *Sterechnus neumayeri*. *Biodivers. J.* 17, 34–45. <https://doi.org/10.1080/14888386.2016.1174956>.
- Morley, S.A., Berman, J., Barnes, D.K.A., de Juan Carbonell, D., Downey, R.V., Peck, L.S., 2016b. Extreme phenotypic plasticity in metabolic physiology of Antarctic demosponges. *Front. Ecol. Evol.* 3, 157. <https://doi.org/10.3389/fevo.2015.00157>.
- Morley, S.A., Barnes, D.K.A., Dunn, M.J., 2019. Predicting which species succeed in climate-forced polar seas. *Front. Mar. Sci.* 5, 507. <https://doi.org/10.3389/fmars.2018.00507>.
- Obermüller, B., Morley, S., Barnes, D., Peck, L., 2010. Seasonal physiology and ecology of Antarctic marine benthic predators and scavengers. *Mar. Ecol. Prog. Ser.* 415, 109–126. <https://doi.org/10.3354/meps08735>.
- Peck, L.S., 2018. Antarctic marine biodiversity: Adaptations, environments and responses to change. In: Hawkins, S.J., Evans, A.J., Dale, A.C., Firth, L.B., Smith, I.P. (Eds.), *Oceanogr. Mar. Biol. CRC Press*, pp. 105–236. <https://doi.org/10.1201/9780429454455-3>.
- Peck, L.S., Brockington, S., 2013. Growth of the Antarctic octocoral *Primnoella scotiae* and predation by the anemone *Dactylanthus antarcticus*. *Deep-Sea Res. Pt. II* 92, 73–78. <https://doi.org/10.1016/j.dsr2.2013.01.024>.
- Peck, L.S., Conway, L.Z., 2000. The myth of metabolic cold adaptation: oxygen consumption in stenothermal Antarctic bivalves. *Geol. Soc. Spec. Publ.* 177, 441–450. <https://doi.org/10.1144/GSL.SP.2000.177.01.29>.
- Peck, L.S., Brockington, S., Brey, T., 1997. Growth and metabolism in the Antarctic brachiopod *Liothyrella uva*. *Philos. Trans. R. Soc. Lond. B* 352, 851–858. <https://doi.org/10.1098/rstb.1997.0065>.
- Peck, L.S., Colman, J.G., Murray, A.W.A., 2000. Growth and tissue mass cycles in the infaunal bivalve *Yoldia eightsi* at Signy Island, Antarctica. *Polar Biol.* 23, 420–428. <https://doi.org/10.1007/s003000050463>.
- Peck, L.S., Mance, H.E., Ellis, M.B., Matok, D., Grange, L.J., 2024. Population characteristics and predation rates of the dominant soft-bodied and durophagous predators on temperate intertidal shores. *R. Soc. Open Sci.* 11 (6), 240308. <https://doi.org/10.1098/rsos.240308>.
- Phleger, C.F., 1998. Buoyancy in marine fishes: direct and indirect role of lipids. *Am. Zool.* 38, 321–330. <https://doi.org/10.1093/icb/38.2.321>.
- Sahade, R., Lager, C., Torre, L., Momo, F., Monien, P., Schloss, I., Barnes, D.K., Servetto, N., Tarantelli, S., Tatián, M., Zamboni, N., 2015. Climate change and glacier retreat drive shifts in an Antarctic benthic ecosystem. *Sci. Adv.* 1, 1500050. <https://doi.org/10.1126/sciadv.1500050>.
- Schnack-Schiel, S.B., Isla, E., 2005. The role of zooplankton in the pelagic–benthic coupling of the Southern Ocean. *Sci. Mar.* 69, 39–55. <https://doi.org/10.3989/scimar.2005.69s239>.
- Sebens, K.P., 1981. Reproductive ecology of the intertidal sea anemones *Anthopleura xanthogrammica* (Brandt) and *A. elegantissima* (Brandt): body size, habitat, and sexual reproduction. *J. Exp. Mar. Biol. Ecol.* 54, 225–250. [https://doi.org/10.1016/0022-0981\(81\)90159-3](https://doi.org/10.1016/0022-0981(81)90159-3).
- Souster, T.A., Morley, S.A., Peck, L.S., 2018. Seasonality of oxygen consumption in five common Antarctic benthic marine invertebrates. *Polar Biol.* 41, 897–908. <https://doi.org/10.1007/s00300-018-2251-3>.
- Thurston, M.H., 1970. *Growth in Bovallia gigantea* Pfeffer (Crustacea: Amphipoda). *Antarctic ecology. Vol. 1. SCAR Symposium on Antarctic Biology*, 2nd, Cambridge, 1968. Academic Press, London, pp. 269–278.
- Venables, H., Meredith, M.P., Hendry, K.R., Ten Hoopen, P., Peat, H., Chapman, A., Beaumont, J., Piper, R., Miller, A.J., Mann, P., Rossetti, H., 2023. Sustained year-round oceanographic measurements from Rothera Research Station, Antarctica, 1997–2017. *Sci. Data* 10, 265. <https://doi.org/10.1038/s41597-023-02172-5>.
- Vermeij, G.J., 1987. *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton. <https://doi.org/10.1046/j.1420-9101.1988.1040369>.
- Wotton, R.S., Malmqvist, B., 2001. Feces in aquatic ecosystems: feeding animals transform organic matter into fecal pellets, which sink or are transported horizontally by currents; these fluxes relocate organic matter in aquatic ecosystems. *BioSci* 51, 537–544. [https://doi.org/10.1641/0006-3568\(2001\)051\[0537:FAEJ\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0537:FAEJ]2.0.CO;2).