Seasonal and interannual variability of feeding in Antarctic benthos

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Abstract

The seasonal and interannual variability of feeding in 15 species of benthic marine suspension feeder was studied over 8 yr at Ryder Bay, Antarctica. Feeding was strongly seasonal in bryozoans, gorgonians, polychaetes, and dendrochirote holothurians. The winter non-feeding period was longest in the holothurians and shortest in bryozoans. Bryozoans started feeding in late winter at very low chlorophyll concentrations, often when surface fast-ice was still present. In hydroids and actinians, feeding tentacles were deployed continuously throughout the year, though hydroid feeding intensity declined slightly in late winter. Water column phytoplankton biomass was strongly seasonal with marked interannual variability in the timing and intensity of the bloom, driven principally by ice dynamics. Correlation across years between the start of feeding and the development of the bloom was poor, and in seasons when a dense spring bloom of benthic filamentous microalgae developed, the start of feeding in many benthic species was delayed. This study indicates that feeding in benthic marine suspension feeders in Antarctica is influenced by factors additional to the seasonal availability of food in the water column.

Polar oceans are strongly seasonal environments. At high latitudes, photoperiod varies from zero in winter to continuous daylight in summer, constraining primary production to a few sunlit months. Furthermore once surface ice forms in winter, the underlying water column stabilizes and much of the larger phytoplankton sediments out. This extreme seasonality means that for many polar marine invertebrates, feeding, growth, and reproduction are possible only during the summer. Pelagic invertebrates in polar waters typically fuel metabolism over winter from large lipid reserves accumulated during the preceding summer (Clarke 1983). In contrast, those Antarctic benthic invertebrates studied to date metabolize somatic tissue during winter rather than a dedicated lipid store (Clarke and Lakhani 1979; Brockington et al. 2001; Obermüller et al. 2010). This striking difference is presumably because living on the sea floor is less expensive metabolically than living in the water column (Clarke and Peck 1991). Organisms living below the mixed layer have to rely on the seasonal pulse of

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phytodetritus but the persistence of a long-term sediment food bank buffers the deeper benthos against this seasonality (Smith et al. 2006).

Suspension feeders comprise an important functional link between primary producers in the water column and higher trophic levels of the food web. Suspension feeders are important in all seas, but they are a particularly significant component of the benthos of the Antarctic continental shelf (Dell 1972; Gili et al. 2006; Gutt 2007). Because of the strong seasonality at high latitudes, benthic suspension feeders in polar waters are usually regarded as being inactive in winter, and have even been described as "hibernating" (Gruzov 1977). It was therefore something of a surprise when year-round observation at Signy Island (60.72°S), in the South Orkney Islands, revealed that many Antarctic benthic suspension feeders remain active well into winter, with at least one bryozoan species feeding all year (Barnes and Clarke 1994). Polychaetes and dendrochirote holothurians did, however, cease feeding in winter (Barnes and Clarke 1995) emphasizing how the different groups of benthic suspension feeders vary in their trophic ecology.

With the advent of year-round ecological and oceanographic work at Rothera Point (67.57°S), it was decided to build on this early work by undertaking a longer-term study of feeding activity in a range of benthic suspension feeders. The aim of this second study was to determine if variation in the timing of feeding can be related to environmental factors, specifically the phenology of the phytoplankton bloom and sea-ice.

Methods

The study was undertaken at the British Antarctic Survey research station at Rothera Point, Adelaide Island, Antarctica (*see* Supplementary Appendix S1 for details).

Selection of species

The criteria for selecting species for this study were that they were common, simple to identify, easily accessible to SCUBA divers, and had a clear visual indication of feeding activity (such as extended tentacles). Species were selected that fed on a range of particle sizes, from the nanophytoplankton taken by bryozoans to the individual pelagic invertebrates or small fish taken by actinians (sea anemones). Species identities were confirmed by consulting original descriptions, identification of voucher specimens by taxonomic experts, and genetic bar-coding. Two taxa, however, could be identified only to genus level in the field: *Primnoella* and *Edwardsiella*. The species selected are listed in Table 1, with ecological and taxonomic information in the Supplementary Appendix S1. For convenience, species are referred to by genus alone in the text.

Measurement of feeding activity

All the study species could be monitored in two SCUBA dives within a small area ($< 50 \, \text{m}^2$) adjacent to the research station. The study transect was marked with a lead-line and pellet buoy, and a standardized dive protocol allowed the same individuals or colonies to be recorded each time. Light levels were low in the deeper sections of the transect, so a torch was used to aid observation. Care was taken not to disturb the animals during observation as this could cause feeding tentacles to be rapidly retracted and false negative data recorded.

The median interval between observations was 16 d, though observations were less frequent in winter when weather and ice conditions often limited opportunities for diving. There was a gap in observations from September 2000 to January 2001 when diving operations were not possible. This meant that while the study extended over eight austral summers, feeding data were collected for only seven of these.

For each species, the total number of individuals or colonies observed, and the number of these that were feeding, were recorded; the feeding score is the fraction of individuals or colonies observed that were feeding. Most species were clearly visible even when not feeding, the exception being the two dendrochirote holothurians where non-feeding individuals often contracted strongly and could be invisible among the dense surrounding fauna. They were also difficult to detect in those seasons when a dense benthic microalgal bloom developed.

An alternative approach was needed for the burrowing anemone *Edwardsiella* and the infaunal bivalve *Laternula*, as non-feeding individuals were often not visible. For these two species, the

Table 1. Species monitored during the feeding study. The columns show the mean number of individuals or colonies scored on each dive, with the range in parentheses (individuals), the total number of dives on which data were recorded for that species (observations), and the number of austral summers included in the data series for that species (seasons).

Species	Individuals	Observations	Seasons
Cnidaria			
Anthozoa			
Alcyonium antarcticum	21 (5–66)	133	7
Primnoella sp.	20 (7–52)	122	7
Isotealia antarctica	16 (2–85)	47	2
Urticinopsis antarctica	20 (4–50)	83	6
Edwardsiella sp.	13 (0–53)	125	7
Hydrozoa			
Antarctoscyphus elongatus	12 (1–36)	123	7
Ptychogena crocea	10 (1–39)	112	7
Mollusca			
Bivalvia			
Laternula elliptica	16 (3–35)	56	5
Annelida			
Polychaeta			
Perkinsiana magalhaensis	20 (4–73)	120	7
Paralaeospira levinseni	~100	122	7
Bryozoa			
Gymnolaemata			
Lageneschara lyrulata	8 (1–17)	111	7
Isoschizoporella similis	8 (3–17)	111	7
Isosecuriflustra tenuis	12 (3–46)	123	7
Reteporella frigida	5 (1–28)	55	5
Arachnopusia inchoata	4 (2–10)	21	2
Echinodermata			
Holothuroidea			
Heterocucumis steineni	20 (0–102)	133	7
Cucumaria georgiana	15 (0–50)	131	7

feeding score was simply the number of the individuals that were visible within a permanent recording quadrat ($1 \, \text{m}^2$) on the sea floor.

The feeding score for any given species was typically either 1 in summer or 0 in winter. Partial feeding scores were recorded occasionally in spring and autumn, and the start or end of feeding for any given season was defined as a feeding score of 0.5, the date of which was determined by linear interpolation (Fig. 1a). These start and end dates varied across the duration of the study. When data for all seasons were combined and pooled by month, feeding activity in a given species could be summarized into three categories: feeding, non-feeding, and transitional. These categories could then be summarized simply with a bar graph (Fig. 1b and Supplementary Appendix S1).
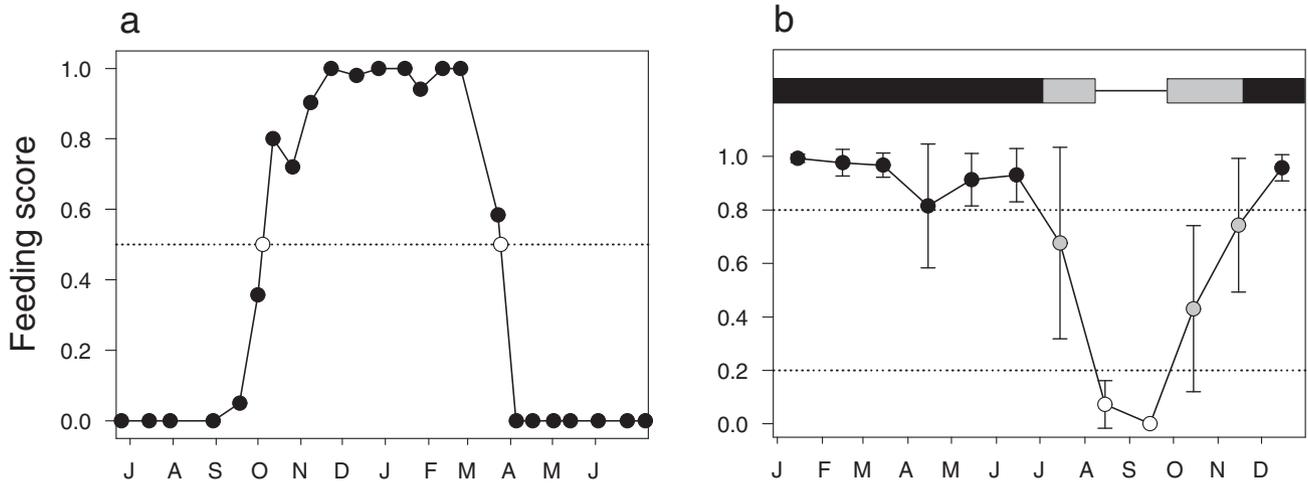
Fig. 1. Determination of feeding periods. (**a**) Feeding score for *Heterocucumis steineni* showing the determination of interpolated dates (open symbols) when feeding started and stopped (feeding score = 0.5, shown by the dotted line). Note that the abscissa runs from 01 July 1997 to 30 June 1998, so that the austral summer falls toward the center of the plot. (**b**) Monthly feeding scores (mean ± 95% confidence intervals) for *Isosecuriflustra tenuis*, data for 1997–2004 pooled by month and plotted from 01 January to 31 December, so that the austral winter falls in the center of the plot. The dotted lines show the threshold for feeding (0.8) and non-feeding (0.2), and the bars show the inferred duration of feeding (black bar and symbols), non-feeding (line and white symbols), and transition (gray bars and symbols).

Environmental background

The environmental data essential for interpreting the feeding data came from a long-term oceanographic study (the Rothera Time Series, RaTS), which started in 1997 and continues to this day. A CTD cast to the bottom (520 m) and a water sample at 15 m (the long-term mean depth of the chlorophyll maximum in Ryder Bay) are undertaken weekly in summer and every 2 weeks in winter, or when ice and weather conditions allow.

Because the different species studied take different sizes of prey, it was important to determine the seasonal variation in different size fractions of phytoplankton. The size fractions used were: microphytoplankton (> 20 μm), nanophytoplankton (20–5 μm), ultraphytoplankton (5–2 μm), and picophytoplankton (2–0.2 μm). These are the standard oceanographic size fractions for phytoplankton, but with an extra split at 5 μm.

The detailed methods, together with an analysis of the seasonal pattern of ice cover, mixed layer depth, chlorophyll biomass, and nutrient dynamics for the first 8 yr of the RaTS study, were presented by Clarke et al. (2008). Further details of the environmental background are given in the Supplementary Appendix S1.

Statistics and data availability

Ordinary least-squares linear regression and Pearson product–moment correlations (all data untransformed) were undertaken in Minitab (Minitab, Inc.). The feeding data are available to download from https://doi.org/gsp3. The background environmental data are available on request from the UK Polar Data Centre (https://www.bas.ac.uk/data/uk-pdc/).

Results

The focus of this study was seasonal and interannual variability in the feeding of a range of polar marine invertebrates. To interpret the results, however, we need to understand variability in the environment in which these organisms live.

Environmental background

The top of the water column in Ryder Bay is formed by Antarctic Surface Water. This exhibits a strong seasonality driven by solar insolation in summer and cooling in winter coupled with brine rejection during sea-ice formation. The maximum depth of the surface mixed layer in winter varied from ~30 to >140 m in different years. Below the Antarctic Surface, Water is modified Antarctic Circumpolar Deep Water, which extends to the bottom of the water column. These deeper waters exhibit little seasonality in temperature or salinity (Meredith et al. 2004) though they do experience an intense annual pulse of sedimenting phytodetritus (Clarke et al. 2008; Weston et al. 2013). All the species monitored in this study were living in the highly seasonal surface waters.

The duration of winter fast-ice in Ryder Bay is highly variable. From 1997 to 2019 (23 winter seasons), complete fast-ice cover ranged from 3 to 211 d and partial cover from 30 to 227 d. Median values were 66 d for complete cover and 97 d for partial cover (*see* Supplementary Appendix S1). Fast-ice could form at any time between May and late July, and typically blew out during a strong northerly wind following a period of warm weather. The feeding study covered the first 8 yr of the data, comprising three winters with > 100 d of complete fast-ice cover and five winters with < 75 d complete cover (*see* Fig. S2 in Supplementary Appendix S1).

The phytoplankton bloom in Ryder Bay is intensely seasonal (Fig. 2). It is confined to the surface mixed layer and the long-term maximum chlorophyll concentration is typically at 15 m (the depth of the water sample).

In winter, chlorophyll concentrations were very low (typically < 0.04 mg m^{-3}) and predominantly from small cells. Cell proliferation started in September, once photon flux exceeded ~15 μmol m^{-2} s^{-1}, the net photocompensation irradiance determined for Southern Ocean phytoplankton in the Bellingshausen Sea (Boyd et al. 1995). The timing of the subsequent development of the blooms in different size fractions was assessed by the date on which a threshold chlorophyll concentration was exceeded. The thresholds were 0.1 mg m^{-3} for microphytoplankton (> 20 μm) and 0.05 mg m^{-3} for the smaller size fractions (*see* Supplementary Appendix S1 for further details).

The bloom of larger phytoplankton (> 20 μm) developed in early November, reached peak concentration in February and then declined, returning to typical winter levels again in late May. This fraction comprised predominantly large solitary or chain-forming diatoms, though the species composition varied from season to season (Annett et al. 2010; van Leeuwe et al. 2020). Similar seasonality was shown by the smaller size factions, though here peak chlorophyll levels were an order of magnitude lower. These fractions were predominantly primnesiophytes and haptophytes (Rozema et al. 2017).

Summer peak values of total chlorophyll (all size fractions combined) were typically in the range 15–27 mg m^{-3}, although in four seasons it was < 10 mg m^{-3} (data for 1997 to 2016). This variation in peak concentration was driven predominantly by variation in the intensity of the diatom bloom

and was linked to the duration of fast-ice in the previous winter (Venables et al. 2013).

The timing of bloom development was highly variable across seasons. The nanophytoplankton bloom developed on average 15 d before the diatom bloom, and often when fast-ice was still present (11 of 18 seasons where the threshold date could be determined). The start dates of the two size fractions were highly correlated across seasons ($F_{1,15} = 40.7$, $p < 0.001$). The duration of the microphytoplankton and nanophytoplankton blooms also varied across the seasons, with the nanophytoplankton bloom lasting on average about 20 d longer. It might be expected that the phytoplankton bloom would be longer in season when the previous winter's fast-ice broke out earlier. Although data for the microphytoplankton bloom showed the expected relationship, this was not significant ($p \sim 0.2$). The duration of the nanophytoplankton bloom also showed no significant relationship with the timing of ice departure the previous winter ($p > 0.2$) (*see* Supplementary Appendix S1 for the full analysis).

Timing of feeding

The various groups of suspension feeders examined in this study take different food, capture that food in different ways, and exhibited different seasonal phenology. Within broader taxonomic groups, however, species generally exhibited similar patterns.

The three species of bryozoan studied all started to feed in October or November and continued until June, with only a short period (2 months or less) of non-feeding (Fig. 3a). The switch between feeding and non-feeding was rapid in any given year, typically occurring within 1 month, but differences in timing across years mean that when data for all years are pooled by month in the averaged plot these switches
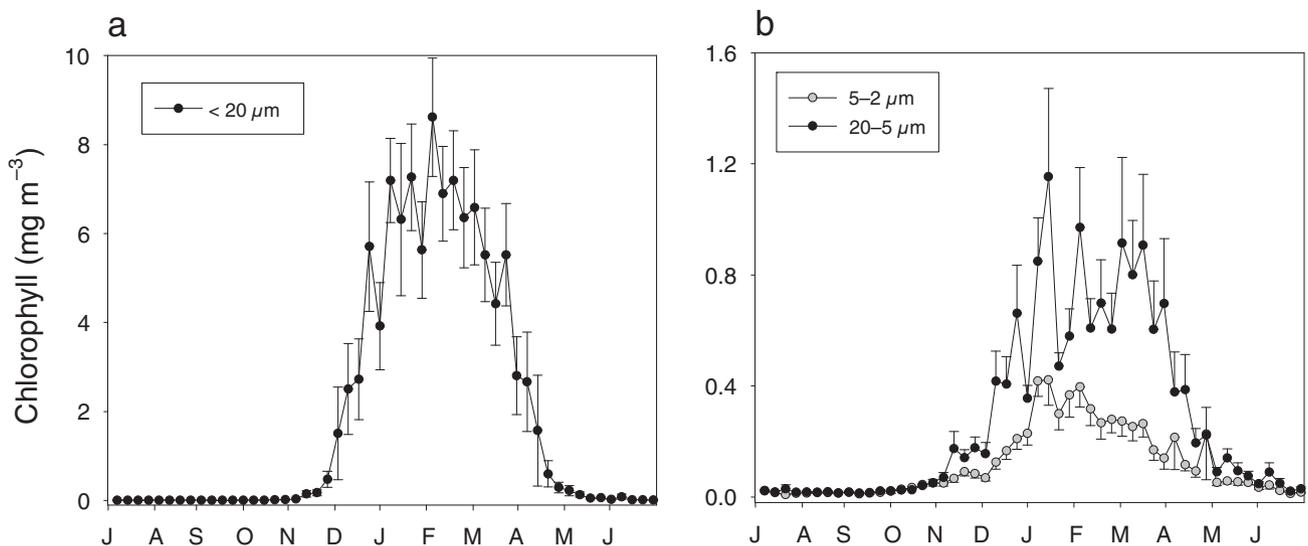

Fig. 2. Seasonal variation in chlorophyll biomass at 15 m at the RaTS station. Data are for the period 1997–2016, pooled by week, and plotted as mean and standard error (in winter the error bars were often smaller than the symbol size). Note that the abscissa runs from 01 July to 30 June, so that the austral summer falls toward the center of the plot. (**a**) Microphytoplankton (> 20 μm). (**b**) Nanophytoplankton (20–5 μm), and ultraphytoplankton (5–2 μm); note that some error bars have been omitted for clarity.
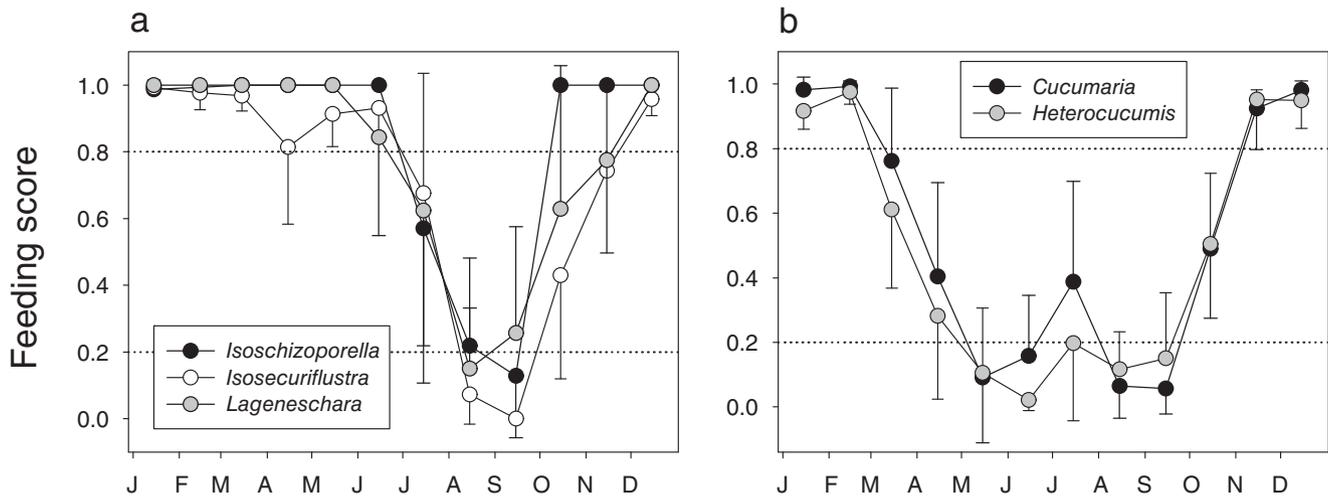
Fig. 3. Seasonal variation in feeding score for bryozoans and holothurians; data for each species pooled by month and plotted as mean ± 95% confidence intervals (note that some error bars have been omitted for clarity). Dotted lines show threshold feeding scores for determining feeding and non-feeding periods. (**a**) Three species of bryozoan. (**b**) Two species of dendrochirote holothurian.

appear to be slower. The three species were very similar in the pattern of shut-down in feeding, but differed in the timing of when they started to feed. Limited data were also obtained for two species of bryozoan not plotted in Fig. 3a. *Reteporella frigida* was found only in deeper water and could not be observed on every SCUBA dive. It was monitored intermittently for 70 months during which time feeding was continuous and did not cease even in the depths of winter. In *Arachnopusia inchoata*, monitored intermittently for 22 months there was a break in feeding of ~3 months in both winters but the length of this non-feeding period could be determined only roughly.

The two holothurians showed very similar dynamics, but differed from the bryozoans in having a shorter feeding period (November to March) and a longer winter non-feeding period (May to October) (Fig. 3b). The switch from feeding to non-feeding or vice versa was typically rapid, but there was considerable year to year variability in the timing of these, which lead to an apparently slower transition when data were averaged across all years. A particularly interesting aspect of the holothurian feeding was the re-emergence of tentacles in some individuals in mid-winter (July). This was more evident in *Cucumaria* than in *Heterocucumis*, and only involved a few individuals. This behavior has also been noted in some individuals maintained in flow-through aquaria in the laboratory aquarium at Rothera (J. Marlow pers. comm.) and is also evident in data from a year-round study of feeding in *Cucumaria frondosa* in the Bay of Fundy (Singh et al. 1999).

The two polychaetes studied were very different in size and hence how far into the water column they could feed. They also differed in the extent of variability across individuals, leading to an offset in the averaged plots and a difference in the duration of the winter non-feeding period (Fig. 4a). The

spirorbid *Paralaeospira* was feeding from December to March but the non-feeding period was only 2 months (August and September). By contrast in the sabellid *Perkinsiana*, the winter non-feeding period was 7 months (April to October) and at no time were all of the individuals found to be feeding.

The two gorgonian soft-corals also differ in their morphology. The sea-whip *Primnoella* had a summer feeding period extending from December to April and a 4-month winter non-feeding period (Fig. 4b). As with other species in this study, the switch between feeding and non-feeding in any given year was swifter than implied by the averaged picture. *Alcyonium* has a lower profile, and although the overall shape of the averaged feeding score was similar, there was marked variability across individuals and the summer feeding period appeared to be shorter (Fig. 4b). There was a clearly defined winter non-feeding period from August to October.

The two hydroids showed very similar patterns of seasonal feeding activity. In both *Ptychogena* and *Antarctoscyphus*, feeding activity was continuous from January to July, and even in the winter months some individuals could be found with their tentacles extended (Fig. 5a). The feeding period was even longer in the two actinian species, both of which could be observed with their tentacles extended throughout the year (Fig. 5b).

The two infaunal species studied have very different feeding ecologies, *Laternula* being a suspension feeding bivalve and *Edwardsiella* a predatory actinian (sea anemone). Both exhibited a strong seasonality in feeding activity with a similar decline in the number of individuals feeding from a summer peak in January and February to low, but still detectable, winter levels. The return to full summer feeding activity occurred earlier in *Laternula* than in *Edwardsiella* (Fig. 6).
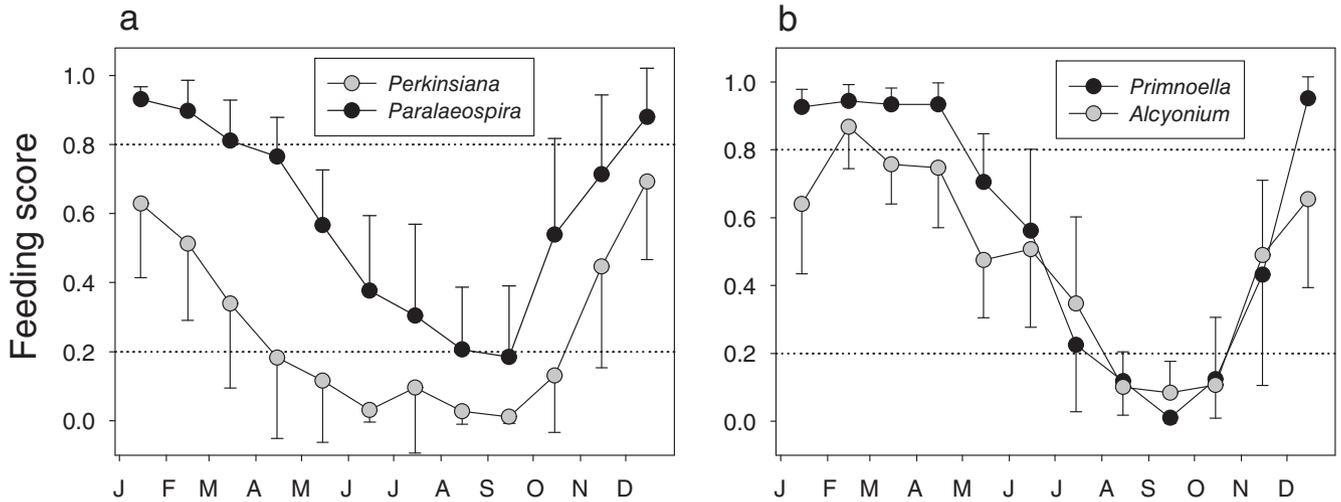
Fig. 4. Seasonal variation in feeding score for polychaetes and gorgonians; presentation as for Fig. 3. (**a**) Two species of polychaete. (**b**) Two species of gorgonian (octocoral).
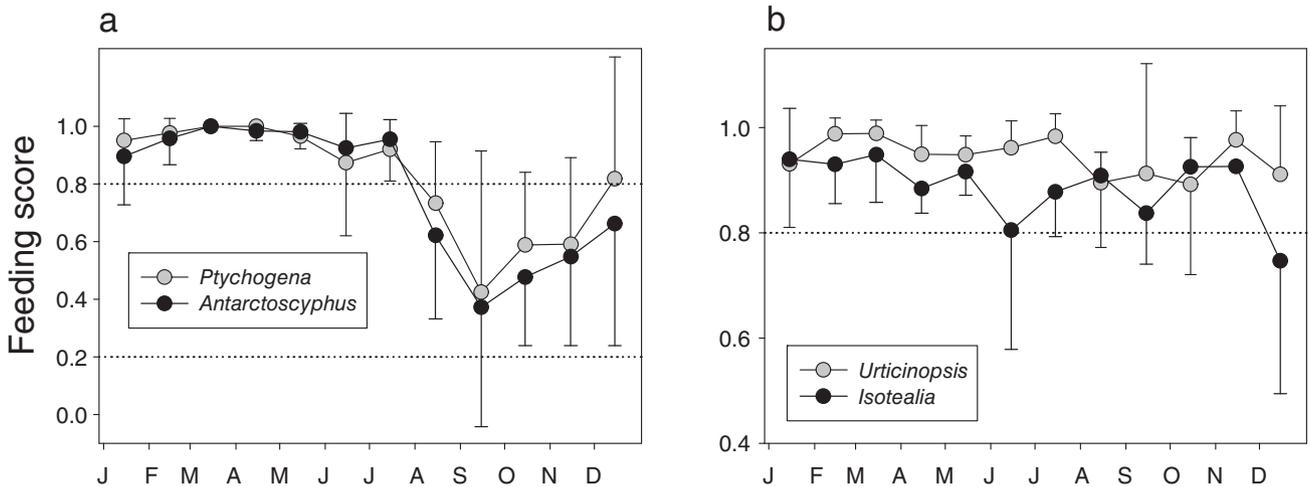

Fig. 5. Seasonal variation in feeding score for hydroids and actinians; presentation as for Fig. 3. (**a**) Two species of hydroid. (**b**) Two species of actinian (sea anemone).

Discussion

The patterns of seasonal feeding in the various species can be most easily compared by summarizing the data in bar graphs. These divide the annual cycle into feeding and non-feeding periods and periods when the species was sometimes found to be feeding and sometimes not as the population switched between feeding and non-feeding (Fig. 1b, and Supplementary Appendix S1).

The three groups that feed predominantly on phytoplankton showed very different seasonal patterns (Fig. 7). In bryozoans, particles are captured by the lophophore using a combination of ciliary currents and tentacle flicks, and unsuitable material is discarded before ingestion (Bullivant 1968; Strathmann 1982; Riisgård and Larsen 2010). The size of food

item ingested is related to mouth size and bryozoans feed predominantly on the nanophytoplankton (Winston 1977). The species studied at Rothera could all be found feeding throughout most of the year, with only short winter non-feeding periods. All three species ceased feeding in August, and the mean non-feeding period ranged from 17 d in *Lagenschara* to 52 d in *Isosecuriflustra*. In 10 species studied over 2 yr at Signy Island, the winter non-feeding period was broadly similar but tended to be slightly longer, ranging from 26 d in *Alloeflustra tenuis* and *Nematoflustra flagellata* to over 100 d in *Beania erecta, Celleporella bougainvillea*, and *Escharoides tridens* (Barnes and Clarke 1994, 1995).

Growth in both the erect bryozoan *Cellarinella watersi* at Signy and the encrusting bryozoan *Fenestrulina rugula* at Rothera is correlated with the duration of the summer nanophytoplankton
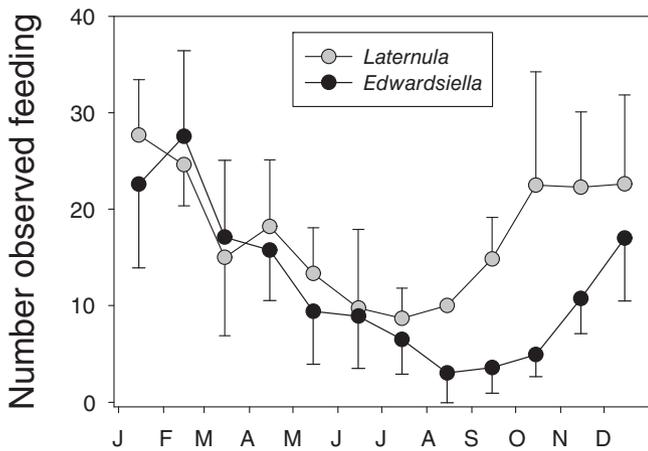
Fig. 6. Seasonal variation in feeding activity in two infauna, the filter-feeding bivalve *Laternula elliptica* and the burrowing actinian *Edwardsiella* sp. Data for each species are the number of individuals observed feeding within the study quadrat, pooled by month and plotted as mean ± 95% confidence intervals; note that some error bars have been omitted for clarity.
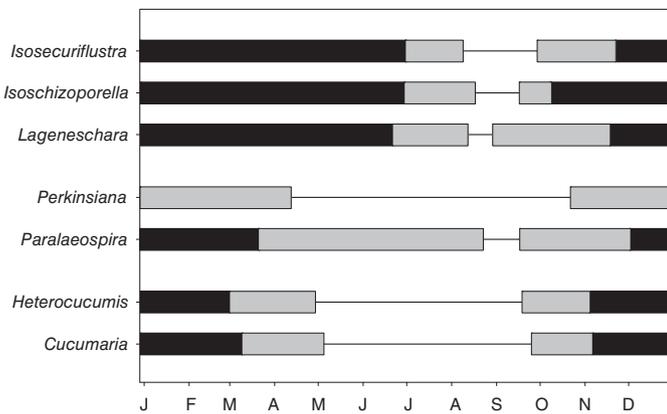

Fig. 7. Summary of averaged feeding periods of suspension feeding bryozoans (upper three species), polychaetes (middle two species), and dendrochirote holothurians (lower two species) in Ryder Bay, Antarctica. The black bars represent periods when that species was always feeding, the line shows when that species was never observed feeding and the gray bars mark the periods when that species was sometimes feeding and sometimes not.

(Barnes 1995, 2017). On average, the nanophytoplankton bloom at Rothera starts a little earlier and dies away later than at Signy (Clarke et al. 1988, 2008), and so it is interesting that Barnes and Arnold (2001) found that the annual growth of three species of bryozoan increased polewards along the western Antarctic Peninsula. This is a counter-intuitive result in the sense that the generally accepted pattern is one where the length of the summer feeding period and hence annual growth in suspension feeders both decline polewards (*see* for example Harrington 1987). It indicates that while realized growth in Antarctic suspension feeders is influenced strongly by the time available for feeding (that is,

seasonality) other factors also play a role (Barnes and Clarke 1998; Barnes and de Grave 2002; Barnes 2013).

Sabellid fan-worms capture particles with a tentacular crown, using currents generated by cilia (Nicol 1930; Fauchald and Jumars 1979). Captured particles are moved by the cilia to the base of the tentacles, where they are sorted and the smaller cells selected. The feeding mechanism in spirorbids is believed to be similar (Fauchald and Jumars 1979) but the seasonal patterns in the two groups at Rothera were quite different. Although bryozoans and sabellid polychaetes both feed on smaller cells, their seasonal feeding patterns are quite different. Bryozoans have short non-feeding periods, whereas the sabellid fan-worm *Perkinsiana* had a long winter non-feeding period (~190 d), although in *Paralaeospira* this was only ~24 d, similar to that observed at Signy (Barnes and Clarke 1995).

Suspension feeding dendrochirote holothurians capture food particles with sticky papillae on the tentacles (Fankboner 1978, 2009) and food is removed when the tentacle is inserted into the mouth. *Heterocucumis steineni* maintained at Signy Island in aquaria with through-flowing natural seawater produced fecal pellets that contained predominantly diatom frustules (Clarke unpubl.), indicating an ability to capture the larger phytoplankton size-fractions. The two species studied at Rothera were observed feeding from November through to early March, and the winter non-feeding periods averaged ~140 d, very similar to the non-feeding period observed at Signy (Barnes and Clarke 1995). The function of the temporary extension of feeding tentacles in the depths of winter when food availability is at a seasonal minimum is unclear, though it has been noted in all three species of dendrochirote holothurians for which seasonal feeding data are available.

The remaining three groups studied at Rothera are all cnidarians, equipped with nematocysts on their tentacles and thus able to capture animal prey (Ozbeck 2011). Gorgonians (octocorals) have been found to take a range of prey items including phytoplankton, nauplii, eggs, and low mobility zooplankton, generally less than ~200 μm in size (Roushdy and Hansen 1961; Sebens and Koehl 1984; Coma et al. 1994). Experimental work on Antarctic sea-whips showed that *Primnoisis antarctica* ingested predominantly the diatom *Fragillariopsis*, but also dinoflagellates and ciliates, whereas an unidentified *Primnoella* species took predominantly dinoflagellates with smaller quantities of ciliates and centric diatoms (Orejas et al. 2003). Stable isotope studies showed that Antarctic sea-whips may also consume phytodetritus in autumn when the phytoplankton bloom is fading (Elias-Piera et al. 2013).

Hydroids are traditionally regarded as carnivorous, but studies of Antarctic species have revealed a wide range of diets. The arborescent *Oswaldella antarctica* on the high Antarctic shelf at Kapp Norvegica was found to take mainly diatoms, whereas the smaller and lower-growing *Tubularia ralphii* took predominantly copepods (Orejas et al. 2001) and *Silicularia rosea* from the intertidal at Potter Cove (King George Island) fed principally on resuspended benthic diatoms (Gili
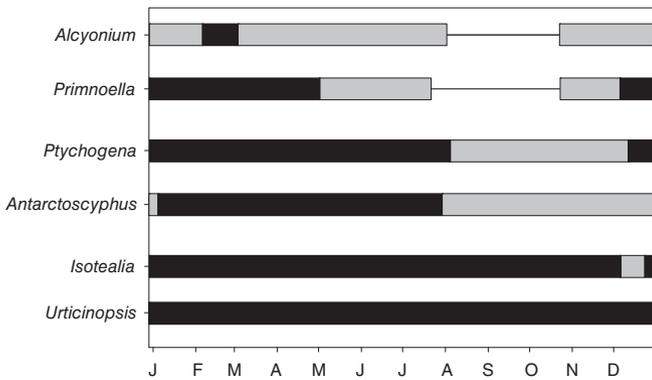
Fig. 8. Summary of averaged feeding periods of three groups of cnidarians in Ryder Bay, Antarctica: Gorgonians (upper two species), hydroids (middle two species), and actinians (lower two species). Presentation as for Fig. 7.
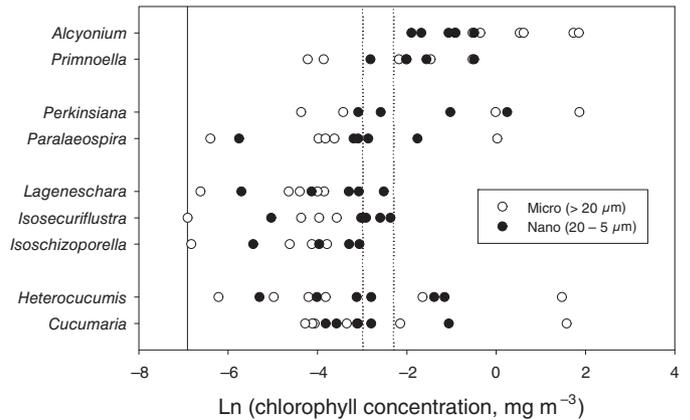

Fig. 9. Chlorophyll concentrations at start of feeding in nine species of suspension feeding marine benthos at Ryder Bay, Antarctica. Data are shown separately for microphytoplankton (> 20 μm, white symbols) and nanophytoplanton (20–5 μm, black symbols) fractions; each data point represents a different austral summer. Note the logarithmic scale for chlorophyll concentration. The solid line shows the minimum detection threshold (0.001 mg m^{-3}) and the two dotted lines the threshold concentrations used to define the development of the bloom in the two size fractions (0.1 mg m^{-3} for microphytoplankton, 0.05 mg m^{-3} for nanophytoplankton).

et al. 1996). Hydroids as a group clearly take a wide range of food, and in both the species studied at Rothera individuals could be found with their tentacles extended throughout the year. Feeding activity was most intense from January through to July, but some individuals continued to extend their tentacles through the entire winter (Fig. 8). At Signy, hydroids (believed to be a species of *Tubulopora*) fed throughout the year, apart from a short non-feeding period of about 1 month in August (Barnes and Clarke 1995). Actinians (sea anemones) take larger prey items, including gelatinous zooplankton, crustaceans, and small fish (Ivanova and Grebelnyi 2016). Both species studied at Rothera could be found with extended tentacles all year.

The summary bar graphs indicate that, with the exception of the two polychaetes, species within broader taxonomic groups (bryozoans, hydroids, and so on) tend to be similar and different from those in other groups; compare, for example, bryozoans and holothurians in Fig. 7. This suggests that species within broader groups are often responding to similar cues to start or stop feeding although correlations between species within taxonomic groups in the timing of the start or end of feeding across years were statistically significant only for bryozoans ($p < 0.01$; for the full analysis, *see* the Supplementary Appendix S1).

Timing of feeding in relation to the phytoplankton bloom

Individuals will feed only when the energetic benefits outweigh the metabolic or other fitness costs of feeding. Thus for a species feeding on phytoplankton it might be expected that when the bloom develops later, feeding would also start later; and hence, there would be a correlation across years between the timing of feeding and the phytoplankton boom. However, in none of the species feeding on phytoplankton (bryozoans, polychaetes, holothurians) was there a significant correlation between the onset of feeding and the threshold date for bloom development (all $p > 0.05$; *see* Supplementary Appendix S1).

The only species in which the correlation was statistically significant was the gorgonian *Alcyonium*, although it was nearly significant in the other gorgonian studied, *Primnoella*. This in turn suggests that these two gorgonians rely on the phytoplankton for their food, at least early in the season.

Part of the reason for the lack of correlation could be that feeding often starts at chlorophyll concentrations well below the threshold values used to define the start of bloom development; indeed Sanderson et al. (1994) showed that in *Himantozoum antarcticum* feeding saturates at a lower level and is more effective at low temperatures than in temperate bryozoans. Although there is considerable variability in the data (Fig. 9), some patterns are discernible. Firstly feeding in bryozoans and dendrochirote holothurians started at very low chlorophyll concentrations, whereas in gorgonians the start of feeding coincided with considerably higher chlorophyll levels. Secondly some species within groups behaved similarly (e.g., bryozoans), whereas in others they differed markedly (e.g., gorgonians). (Full summary statistics are given in the Supplementary Appendix S1.)

Feeding of several taxa (bryozoans, holothurians, hydroids) started unusually late in the 1998/1999 austral summer when a dense bloom of benthic filamentous algae developed, covering the sea floor for several weeks. Clearly the onset of feeding is influenced by a number of factors, and variability in these will obscure any underlying relationship with the phenology of the bloom that might exist.

Concluding remarks

Polar regions are highly seasonal environments. Phytoplankton cell proliferation starts at low light levels, often with winter fast-ice still present, and the duration of winter fast-ice

influences the intensity and species composition of the subsequent phytoplankton bloom though not its phenology. Benthic suspension feeders taking phytoplankton showed a strong seasonality in feeding activity, though the winter non-feeding period could be quite short. Species taking a wider spectrum of food, or those specializing in large prey items, showed little seasonality of feeding activity. All the species with seasonal feeding showed interannual variability in their phenology but correlations with the timing of winter fast-ice or the summer phytoplankton bloom were weak, indicating that feeding in polar suspension feeders is influenced by a suite of environmental factors.

The western Antarctic Peninsula is experiencing a period of rapid regional environmental change (King and Harangozo 1998; Turner et al. 2005; Clarke et al. 2007). As yet, however, secular warming of the upper ocean in the study area is not evident against the background of strong interannual variability (Clarke et al. 2008). Variability in the duration of winter sea-ice affects the benthos directly through increased ice-scour by icebergs (Smale et al. 2008; Barnes and Souster 2011) but also from changes in the taxonomic composition of the phytoplankton (Annett et al. 2010; van Leeuwe et al. 2020). Studies elsewhere in Antarctica have demonstrated changes in the population dynamics of benthos in response to oceanographic factors operating over decadal or longer time-scales (Dayton et al. 2013, 2019) and also to the collapse of ice-shelves (Fillinger et al. 2013; Gutt et al. 2013), emphasizing the importance of long-term studies to determine the effects of environmental change in Antarctica.

Data availability statement
The feeding data are available to download from https://doi.org/gsp3. The background environmental data are available on request from the UK Polar Data Centre (https://www.bas.ac.uk/data/uk-pdc/).

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Conflict of interest

The authors declare no conflicts of interest.