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Seasonal variability in macrobenthos assemblage parameters in the highly disturbed Antarctic intertidal zone – Relatively rich biodiversity year around

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ABSTRACT

To understand the impact of anthropogenically induced transformations of biological communities, their naturally occurring fluctuation must be recognized first. Therefore, the aim of this study was to investigate the variability in Antarctic intertidal benthic assemblage faunal composition during an annual cycle (King George Island 62° S). Once a month, from December 2016 to November 2017, samples were collected at low-, mid- and high-tidal levels. Polychaetes were the most speciose group (15 species), followed by amphipods (12). Throughout the year, the most numerous taxa were gastropods (38% of the total number), followed by amphipods (23%) and bivalves (22%). The general pattern of the number of species and their abundance and biomass depended on the season and exhibited the highest values in austral autumn (April–June). Both species richness and abundance were highest in June and lowest in August. This study discovered that Antarctic intertidal macrofauna assemblages quickly respond to changes in environmental conditions and thus reflect seasonal climate fluctuations. The rapid development of these assemblages when the conditions are favourable proves their opportunistic and highly adaptable nature, which is potentially a good prognosis for survival in this ever-changing ecosystem.

1. Introduction

Strong seasonality is one of the basic ecological characteristics of Antarctic ecosystems. Seasonal changes in light conditions, air temperatures, precipitation, cyclical or permanent snow and ice cover, and glacier activity lead to strong fluctuations in primary productivity, e.g., long periods of limited food supplies, especially during the polar night (Vause et al., 2019). These highly variable environmental conditions of the Antarctic system are known to control both terrestrial and marine biota (Peck et al., 2006; Convey et al., 2014). In the case of benthic fauna, these environmental fluctuations could result in high temporal and spatial variability (Paiva et al., 2015). Organisms existing in Antarctic marine habitats seem to be fully adapted, yet their occurrence or distribution can be modified by many factors that are usually interrelated; thus, their effects are often difficult to separate. To understand the factors driving benthic assemblage occurrence and distribution, it is crucial to consider the differences between the impacts of biotic and abiotic processes such as recruitment and disturbance. Transport, settlement and larval growth are the initial processes of benthic assemblage

development (Kuklinski et al., 2017). They occur annually according to natural life cycles. Seasonally fluctuating environmental factors can limit these processes and drive benthos distribution patterns through post settlement mortality or dispersion (Barnes and Conlan, 2007). Predicted climate change is likely to reduce strong seasonal variations, leading to significant changes, also in winter (Vause et al., 2019). This may include changes such as a decreasing duration of winter sea ice caused by an increasingly warmer spring, thus lengthening the summer season (Schofield et al., 2017). Turbidity in the water column associated with increased glacial meltwater after sea-ice retreat can reduce phytoplankton, macroalgal and benthic microalgal production by suppressing underwater radiation (Kim et al., 2018; Deregibus et al., 2016; Hoffmann et al., 2019). In shallow coastal Antarctic ecosystems where benthic microalgae are the main primary producers, a significant reduction in the amount of light can shift benthic assemblages from an autotrophic to a heterotrophic state (Braeckman et al., 2021). Therefore, knowledge about physical and biological processes occurring all year around, including assemblage dynamics and structure, is essential for understanding contemporary adaptations of benthic organisms to

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extremely dynamic polar environments (Piepenburg, 2005). In comparison with the lower latitude environments, Antarctic marine and terrestrial habitats appear to represent the end point of the extremes available on the planet. Regardless, to date, most studies have given little attention to the interface between them. Despite intertidal areas being among the most intensely studied habitat types worldwide, the intertidal habitat around Antarctica is still poorly documented, which is understandable, as this region is among the least accessible to humans due to its remoteness causing logistical difficulties.

The Antarctic intertidal zone is one of the marine areas particularly affected by extreme environmental conditions, where the impact of seasonal factors is even more pronounced than that of the nearby subtidal habitats (Marcías et al., 2017). In harsh polar ecosystems, apart from high seasonality, there are additional factors that shape intertidal benthic assemblages. Their intensity is almost unique, especially in comparison to their counterparts from lower latitudes (Gutt, 2001; Barnes and Conlan, 2007). This includes ice-foot formation in winter, ice scouring in summer, exposure to air (desiccation, irradiation or freezing), extreme wave action and the resultant sediment turnover, as well as extreme changes in temperature, light and salinity caused by ice formation or meltwater runoff (Barnes, 1999; Peck et al., 2006; Gutt, 2001). Temperature ranges over seasonal time scales are experienced by Antarctic intertidal organisms, which are confronted with very variable thermal conditions, both on a daily and seasonal scale (Griffiths and Waller, 2016; Waller et al., 2017). Consequently, they must be eurythermal and more flexible in their response compared to organisms occurring in the nearby subtidal where the temperature range is relatively narrow and most Antarctic marine organisms seem to be highly stenothermic (Clarke, 1991; Peck, 2002; Peck et al., 2004). Generally, due to strong disturbances in the Antarctic intertidal zone, assemblages are considered rare and only exist in sheltered areas where there is no ice formation during the warm season (Wulff et al., 2009). Previous studies conducted in polar intertidal zones revealed that the number of species in intertidal and shallow subtidal assemblages is similar (Waller et al., 2006a), and a wide range of macrofauna were found inhabiting intertidal regions, especially in the protected lower layers of the cobble matrix (Waller et al., 2006a, 2006b; Griffiths and Waller, 2016). Therefore, it has been concluded that polar intertidal areas are not only habitats for vagrants but also for well-established and relatively diverse communities. However, studies of intertidal benthic assemblages in Antarctica have been carried out mostly during summer surveys (Waller et al., 2006a; Waller, 2008; Bick and Arlt, 2013; Liu et al., 2015; Martín et al., 2016; Aghmich et al., 2016). Research including annual cycle sampling or winter–summer comparisons is scarce. Nevertheless, some investigations have noted the ability of macrobiota to survive year-round temperature conditions in the Antarctic intertidal zone (see, e.g., Jazdzewski et al., 2001; Waller et al., 2006b).

In this context, the main objective of the present study was to establish solid knowledge on the diversity and abundance of macrobenthos assemblages inhabiting the Antarctic intertidal across vertical tidal transects from a seasonal point of view. Therefore, we will gain better insight into the ecology of the Antarctic intertidal for further and more thorough investigations of this rapidly changing ecosystem, enabling the detection of ongoing changes, including those driven by global warming.

2. Materials and methods

2.1. Study site

King George Island, the largest island in the South Shetland Archipelago, is located off the northern tip of the western Antarctic Peninsula (120 km) and separated from the Antarctic continent by the Bransfield Strait (Fig. 1). This region has a cold oceanic climate that is characteristic of maritime Antarctica. All seasons refer to the Southern Hemisphere annual cycle: summer (January–March), autumn (April–June),

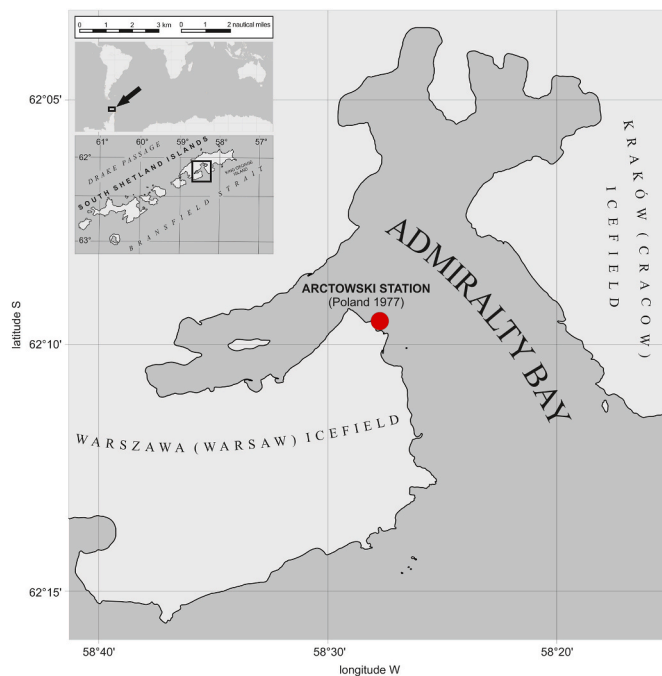


Fig. 1. Study area.

winter (July–September) and spring (October–December) (Holland, 2014). King George Island is located at relatively low latitudes (62° 10' S), which is a factor determining the potential influx of solar radiation. The average duration of a day in June and December is 5.1 and 19.5 h, respectively (Kejna et al., 2013). The study site was selected in Admiralty Bay in the direct vicinity of the Arctowski Polish Antarctic Station (62° 09.41' S; 58° 28.10' W). The location of the bay in relation to the Bransfield Strait and the distribution of the prevailing wind direction (SW, Plenzler et al., 2019) provide relatively good shelter from short-lasting dynamic ocean inflows. The wave movement in this area is mainly caused by the local wind field (Pruszek, 1980). The average wind speed in Admiralty Bay is approximately 6.4 m/s in winter and 4 m/s in summer (Echeverria and Paiva, 2006). Tides have a regular diurnal pattern with an average tidal range of 1.4 m but can reach up to 2.1 m (Catewicz and Kowalik, 1983). In Admiralty Bay, the average water temperature and salinity range from -0.8 °C and 34.4 in winter and 2.3 °C and 33.5 in summer, respectively. The differences between these two parameters are due to the rising atmospheric temperature and the freshwater inflow from melting ice during austral summer. Both temperature and salinity are comparatively stable throughout the bay due to vertical mixing. In winter, the intertidal zone is usually covered by ice for several weeks or even months (crew of the Arctowski Polish Antarctic Station, personal communication). During summer, growlers, i.e., small icebergs (<2 m across), frequently cover the intertidal and subtidal zones (Fig. 2). The substratum in the study area is primarily composed of cobbles and pebbles packed and embedded in a sandy sediment.

2.2. Sampling

Three intertidal zones, low (LT) 62° 09.467' S, 58° 28.453' W, mid (MT) 62° 09.476' S, 58° 28.474' W and high (HT) 62° 09.483' S, 58° 28.486' W, were selected according to the vertical gradient of the tides. At each of the selected intertidal levels, temperature-light intensity loggers were installed in well-ventilated (openwork) openings of the concrete slabs (100 × 70 × 20 cm) to protect them from ice, tides and wave action. Loggers took measurements throughout the year every 5 min.

Seasonal sampling of intertidal macrofauna was carried out once a

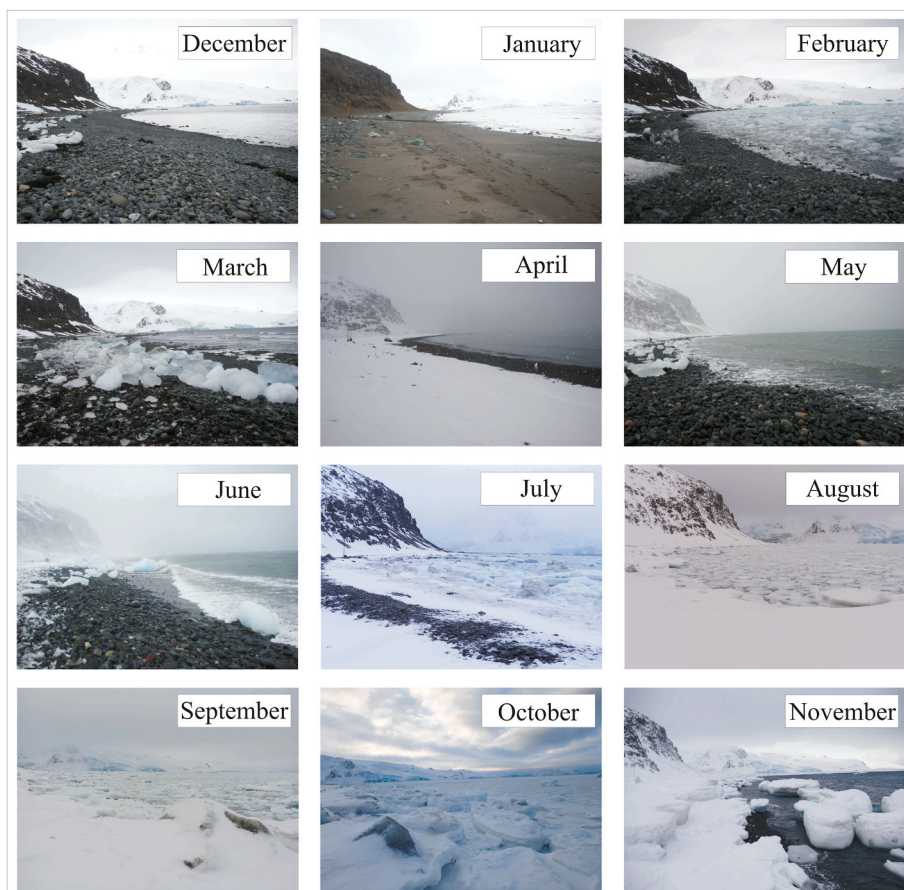


Fig. 2. Examples of environmental conditions in the investigated intertidal zone throughout the year.

month from December 2016 to November 2017 (Table 1). The intertidal zone was suitable for sampling only 2–3 days a month during extreme low (spring) tides. In September and October, due to the total coverage of the tidal zone with ice foot, no macrofauna samples were collected (Fig. 2). Each time, three replicate (0.25 m²) quadrats were haphazardly selected from each of the three intertidal zones. Samples were collected manually using a 50 × 50 cm frame and preserved in 4% formaldehyde diluted in seawater. Rocks with encrusting fauna were collected from each quadrat to identify and estimate the abundance of epifaunal taxa present. Animal colonies such as Bryozoa were recorded as one unit. All macrofauna (>0.5 mm in size) were identified to the lowest taxonomic level possible, typically species, counted and weighed in the laboratory of the Institute of Oceanology Polish Academy of Sciences in Sopot, Poland. Biomass is presented as wet mass values for each species.

2.3. Statistical analysis

Species richness (S), abundance (N), biomass (B), Shannon–Wiener's diversity (H') and Pielou's evenness (J') were calculated for each month and tidal level. Differences in the structure of the intertidal community between months and tidal heights were compared using PERMANOVA main and *post hoc* pairwise tests $p < 0.05$ (using the *adonis* function in the R package *vegan*, Herve, 2020). To visualize these data, non-metric multidimensional scaling (nMDS) ordination was performed using the Bray–Curtis similarity matrices of intertidal taxa abundance (square-root transformed) at each month within each tidal level. Patterns of change in macrofauna assemblages over time at different tidal levels were visualized using nMDS on the distances among relevant centroids (Anderson, 2017). Temporal trajectories for different tidal levels were examined in separate ordination plots, with segmented bubbles showing S , N , J' and H' . The statistical significance is based on 9999 permutations

of the variance components. All statistical analyses were performed in the R statistical environment (R Core Team, 2020), except for the nMDS plots of temporal trajectory, which were performed using PRIMER Ver. 6.1.5 package (Clarke and Warwick, 2001).

3. Results

3.1. Vertical and seasonal changes in temperature

The average temperature fluctuations depended on the season and tidal height (Fig. 3). In the summer (January–March), the largest temperature fluctuations were recorded at high tide (HT) and ranged from -1.45 °C to $+17.95$ °C. In the mid-tidal (MT) zone, the temperature ranged from -1.34 °C to $+12.19$ °C, while at low tide (LT), it ranged from -1.25 °C to $+9.47$ °C. In the autumn (April–June), temperatures ranged from -4.11 °C to $+3.55$ °C (HT), -3.32 °C to $+3.43$ °C (MT), and -2.1 °C to $+1.87$ °C (LT); in the winter (July–September), temperatures ranged from -15.2 °C to $+1.15$ °C (HT), -9.92 °C to $+1.1$ °C (MT), and -4.94 °C to $+0.7$ °C (LT); and in the spring (October–December), temperatures ranged from -6.48 °C to $+10.12$ °C (HT), -4.81 °C to $+8.23$ °C (MT), and -1.96 °C to $+6.16$ °C (LT). The warmest month was January, when the average temperatures were 4.94 ± 2.1 °C (\pm standard deviation) (HT), 2.65 ± 1.8 °C (MT) and 2.4 ± 1.5 °C (LT). The coldest month was August, with average temperatures of -10.2 ± 4.2 °C (HT), -6.2 ± 1.9 °C (MT) and -1.5 ± 0.5 °C (LT).

3.2. Seasonal changes in macrofauna species diversity, abundance and biomass

Throughout the year, a total of 35,235 specimens belonging to 40 taxa were recorded. Polychaetes were the most diverse taxon, with 15

Table 1
Numerical abundance of macrofauna taxa expressed as the mean \pm standard deviation (in brackets) in a particular month. In bold -the most numerous taxa in each month. Sampling dates in the table header rows.

Taxa	Species	December	January	February	March	April	May	June	July	August	November
		02.12.2016	03.01.2017	01.02.2017	02.03.2017	01.04.2017	03.05.2017	02.06.2017	02.07.2017	05.08.2017	02.11.2017
Amphipoda	<i>Bovallia gigantea</i>		0.11 (0.33)	0.22 (0.44)		0.44 (0.88)	0.44 (0.73)	0.77 (1.09)			
	<i>Cheirimedon femoratus</i>		0.55 (1.01)		14.88 (37.01)	17.66 (43.19)	17.11 (40.55)	24.11 (50.93)	1 (1.32)	0.55 (0.88)	0.88 (1.16)
	<i>Eurymera monticulosa</i>	0.44 (1.01)	0.77 (1.71)					0.44 (0.73)			
	<i>Gondogeneia antarctica</i>	1.66 (2.69)	2.55 (4.36)	6.22 (9.07)	68 (103.31)	80.55 (118.67)	87.22 (126.12)	106.88 (148.97)	8.44 (8.34)	0.88 (1.36)	5.55 (5.45)
	<i>Ischyrocerus camptonyx</i>					0.22 (0.66)	0.33 (0.50)	0.44 (0.73)			
	<i>Lepidepcreum cingulatum</i>	0.55 (0.72)	0.88 (1.53)	0.44 (0.73)	2.88 (5.11)	2.66 (3.97)	2.22 (4.02)	3.11 (5.06)			
	<i>Orchomenella denticulata</i>	0.33 (0.50)		4.33 (8.88)	0.44 (1.33)	0.33 (0.71)	0.44 (0.73)	1.22 (1.78)			1.33 (1.58)
	<i>Orchomenella rotundifrons</i>	0.55 (0.72)	0.22 (0.66)	0.22 (0.44)	0.55 (0.88)	0.44 (0.88)	0.33 (0.50)	0.77 (0.97)			0.22 (0.66)
	<i>Paramoera edouardi</i>	15.11 (15.19)	12.88 (13.64)	27.22 (40.96)	57.33 (84.01)	74.11 (112.17)	76 (109.76)	117.33 (160.84)	8.55 (8.68)	1.22 (1.99)	10.22 (9.65)
	<i>Phoxocephalidae</i> indet.			0.33 (0.50)	0.22 (0.44)						
	<i>Probolisca ovata</i>	2.88 (4.25)	6.88 (10.62)	0.66 (0.71)	3.11 (5.51)	2.55 (4.03)	2.22 (3.89)	3.44 (5.25)			0.88 (1.17)
	<i>Prostebbingia gracilis</i>				0.22 (0.44)	0.33 (0.71)		0.44 (0.53)			
	<i>Spinoserolis beddardi</i>		0.11 (0.33)	0.11 (0.33)	0.22 (0.44)	0.44 (0.73)		0.33 (0.71)			
	Isopoda	<i>Salvatoria rhopalophora</i>	2.55 (3.74)	5.11 (9.36)	2.88 (6.19)	2.11 (4.40)	3.22 (4.71)	2.88 (4.14)	4 (5.22)	0.77 (1.09)	
<i>Capitella capitata</i>		0.55 (0.72)	1 (1.65)	1.44 (2.60)	0.44 (0.73)	0.88 (0.93)	1.77 (1.85)	2.44 (2.40)	0.44 (0.73)		0.88 (1.05)
Polychaeta	<i>Capitella capitata antarctica</i>	0.33 (0.50)	0.66 (1.11)	1.33 (1.80)	1.11 (2.31)	1.11 (1.61)	1.77 (2.86)	2.55 (3.57)	1.11 (1.54)	0.22 (0.44)	0.88 (1.36)
	<i>Capitella perarmata</i>	0.11 (0.33)			0.77 (1.56)	0.55 (0.73)	0.55 (0.88)	0.33 (0.50)			
	<i>Ceratonereis</i> sp.		0.11 (0.33)								
	<i>Eteone sculpta</i>	1.11 (1.26)	2.77 (3.89)	7.22 (9.64)	0.88 (1.69)	1.22 (1.56)	1.77 (2.22)	3.33 (3.24)	2.11 (2.31)	0.22 (0.44)	1.77 (2.39)
	<i>Eulalia varia</i>	3.66 (5.54)	4.88 (8.86)	3.88 (6.69)	1.33 (2.50)	4.66 (6.06)	4.44 (6.91)	5.22 (8.04)	1.55 (2.88)		1.11 (1.61)
	<i>Exogone</i> sp.		0.44 (1.01)								
	<i>Genetyllis polyphylla</i>		0.22 (0.44)	0.55 (1.01)	0.55 (1.33)	0.66 (1)	0.77 (1.09)	0.55 (0.88)			
	<i>Levinsenia gracilis</i>							0.22 (0.66)			
	<i>Maldanidae</i> indet.				0.11 (0.33)						
	<i>Micronereis antarctica</i>		0.22 (0.66)	0.22 (0.66)		0.33 (0.50)					
	<i>Polycirrus macintoshi</i>		0.33 (0.50)	0.33 (1)							
	<i>Aphelochaeta cincinnata</i>					0.33 (0.71)					
	<i>Tharyx</i> sp.	2.11 (2.85)	1.55 (2.74)	7.11 (11.42)	9.11 (13.31)	14.55 (16.93)	18 (21.66)	25.66 (33.18)			2.44 (3.05)
	Oligochaeta	<i>Lumbricillus</i> sp.	4 (5.15)	6.33 (10.50)	39.44 (44.66)	21.11 (30.25)	26 (30.56)	25 (34.80)	32 (40.32)	3.55 (4.03)	
Oligochaeta gen. sp. indet.		3.66 (4.38)	4.88 (6.60)	7.22 (9.61)	10.66 (12.80)	18.33 (19.63)	21.33 (22.19)	25.77 (25.28)	4.11 (4.59)	0.44 (0.73)	3.44 (4.19)
Gastropoda	<i>Nacella concinna</i>	1 (1.58)	4.55 (7.38)	3.22 (4.99)	2.33 (3.43)	3.88 (5.16)	3.44 (4.87)	5 (6.34)	0.44 (0.73)		0.44 (0.73)
	<i>Laevilacunaria antarctica</i>	17.77 (22.15)	30.66 (39.32)	33.44 (45.56)	44 (53.41)	48.88 (63.89)	59.66 (73.40)	67.66 (83.29)	3.33 (3.12)	0.66 (1.11)	5.55 (5.13)
	<i>Laevilitorina caliginosa</i>	19.88 (22.91)	44.55 (37.36)	64 (89.47)	98.66 (123.01)	111.33 (140.83)	120.22 (152.43)	144.55 (176.71)	5.66 (5.41)	0.66 (1.11)	6.55 (7.18)
	<i>Margarella antarctica</i>	0.77 (2.33)	6.44 (9.35)	2.77 (4.55)	7.33 (11.13)	9.44 (13.01)	11.22 (15.75)	16.77 (19.60)	0.66 (1.41)		
	<i>Onoba</i> sp.	31.22 (37.99)	46.55 (56.57)	13.55 (13.02)	90.55 (136.76)	99.44 (139.04)	100.77 (141.59)	120.33 (157.18)	4.77 (5.38)	0.44 (0.73)	3.22 (3.42)
Bivalvia	<i>Altenaeum charcoti</i>	13.33 (14.61)	27.11 (33.03)	42.66 (83.86)	148.33 (200.24)	153.11 (197.04)	145.44 (181.22)	166.55 (215.31)	5.44 (4.98)	0.33 (0.71)	5.44 (5.41)
	<i>Mysella antarctica</i>	4.77 (6.79)	6 (9.09)	15.33 (23.87)	24.22 (48.44)	29.22 (49.84)	30 (53.43)	39.77 (69.15)	1.11 (1.36)	0.22 (0.44)	1.44 (1.51)
Platyhelminthes	Platyhelminthes gen. sp. indet.	7.55 (7.79)	32.22 (27.15)	16.11 (16.96)	14.22 (21.62)	23.77 (27.27)	22.44 (26.77)	23.22 (26.60)	3 (3.81)	0.44 (0.73)	3.22 (3.46)
Nemertini	Nemertini gen. sp. indet.	1.88 (2.47)	2 (2.83)	6.11 (6.73)	10 (9.35)	11.77 (10.77)	10.55 (10.54)	12.11 (10.81)	2.77 (4.52)	0.33 (0.71)	2.22 (2.59)
Bryozoa	Bryozoa gen. sp. indet.		0.55 (0.53)		0.33 (0.71)	0.55 (0.73)	0.22 (0.44)	0.55 (0.88)			0.22 (0.44)

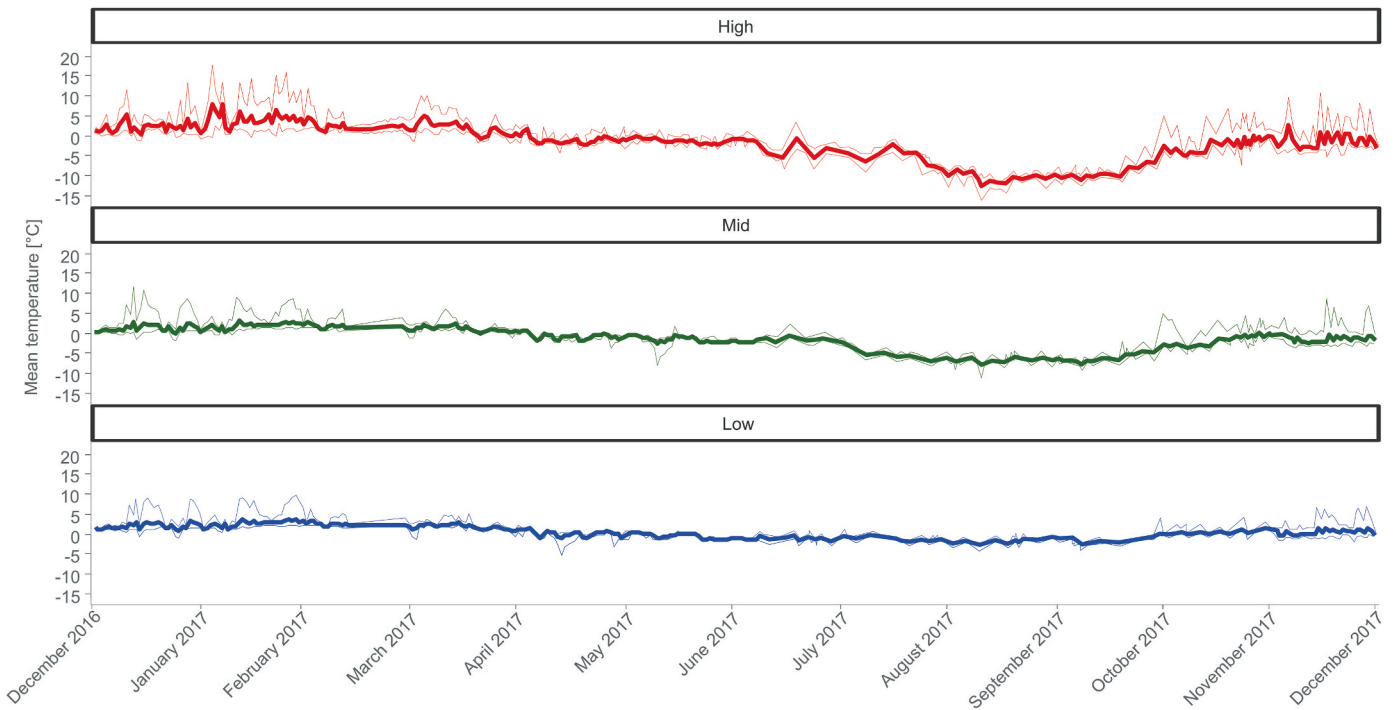


Fig. 3. Mean temperatures (thick line) and minimum–maximum values (thin line) in the high- (red), mid- (green) and low- (blue) tidal zones during the 12 months. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

species (approximately 40% of the total species number found), followed by amphipods (12 species, 35%). Gastropods were less diverse (5 species, 15%), followed by bivalves and oligochaetes, with 2 species each (6%). The most abundant taxa were gastropods (38% of total),

followed by amphipods (23%) and bivalves (22%).

Changes in species richness recorded in the current study are summarized in Fig. 4, showing the extent of temporal and vertical variability. The highest mean richness occurred in June (LT) 29 ± 1 species

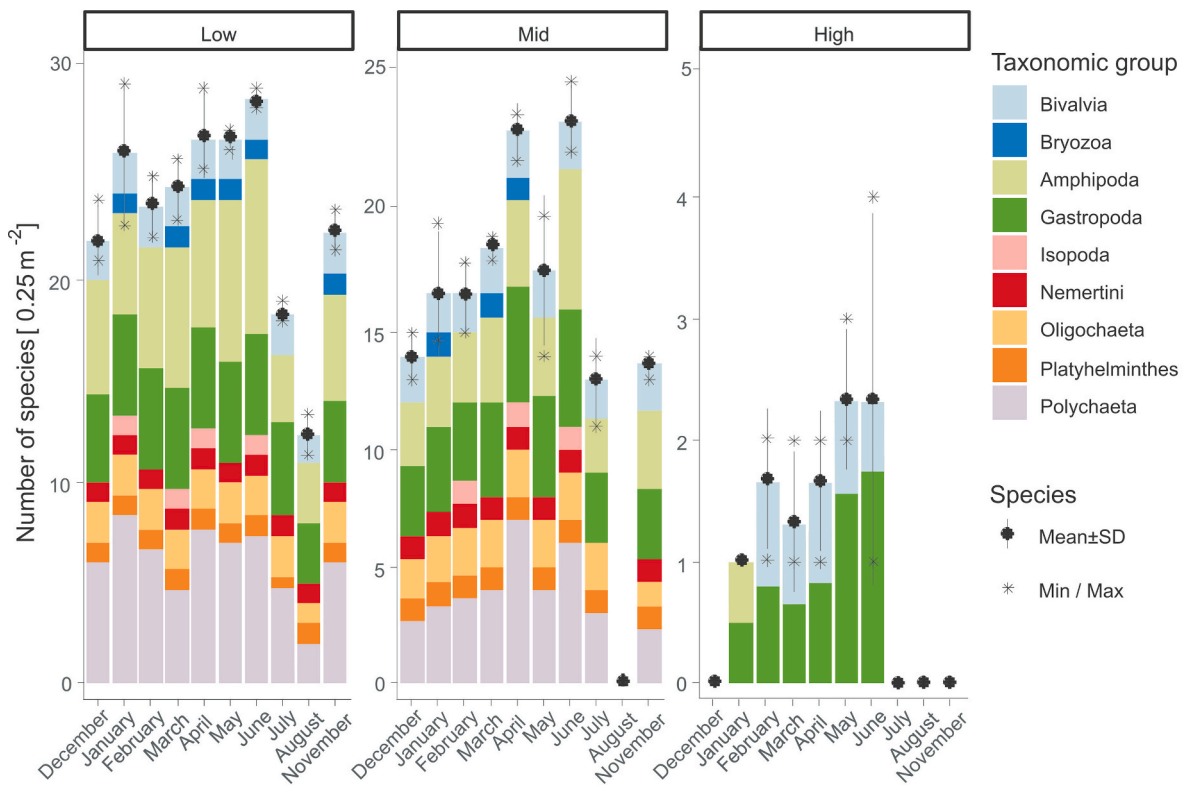


Fig. 4. Mean values of richness (number of species 0.25 m^{-2}) for all macrofauna at particular tidal heights throughout the year. Black bars represent \pm standard deviations, and asterisks = minimum–maximum values. Colours represent different macrofaunal groups expressed as the means. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

0.25 m⁻² (mean ± standard deviation), followed by May (LT) 27 ± 1 species 0.25 m⁻² and April (LT) 27 ± 3 species 0.25 m⁻², with the lowest species number recorded in August (LT) 12 ± 2 species 0.25 m⁻². Each month, the low-tidal zone had the highest species richness (Fig. 4), with the average number ranging from 12 to 29 species 0.25 m⁻². The mid-tidal zone was characterized by a lower mean species richness ranging from 0 to 23 species 0.25 m⁻². The poorest species was the high-tidal zone, with only 0–5 species recorded 0.25 m⁻², such as the gastropods *Laevitorina caliginosa* and *Onoba* sp., as well as the bivalve *Altenaeum charcoti*.

Abundance across seasons followed the same trend in all tidal zones. The highest mean abundance occurred in the autumn season (Fig. 5): June (LT) 2470 ± 2355 individuals 0.25 m⁻², followed by May (LT) 2017 ± 1967 ind. 0.25 m⁻² and April (LT) 1945 ± 1732 ind. 0.25 m⁻². The fewest individuals were found in August (LT) (21 ± 32 ind. 0.25 m⁻²). Again, the fauna of the low-tidal zone was the most abundant (Fig. 5), with the average number of individuals ranging from 21 to 2470 ind. 0.25 m⁻². In the mid zone, 0–356 ind. 0.25 m⁻² were found, while in the high-tidal zone, 0–6 ind. 0.25 m⁻² were recorded.

Similar to abundance, the highest mean biomass occurred in June (LT) 16.92 ± 5.14 g 0.25 m⁻² (Fig. 6) but also in January (LT) 13.52 ± 7.45 g 0.25 m⁻². The lowest value was recorded again in August (LT) 0.25 ± 0.03 g 0.25 m⁻². Biomass values were highest in the low-tidal zone (Fig. 6), with the average value ranging from 0.25 to 16.92 g 0.25 m⁻². In the mid zone, it ranged from 0 to 1.83 g 0.25 m⁻², while in the high-tidal zone, it ranged from 0 to 0.013 g 0.25 m⁻². The gastropod *Nacella concinna* had the highest mean biomass among all recorded species, 0–11.83 g 0.25 m⁻² (LT), and constituted the highest part of the obtained values (0–88% of total, Fig. 6).

The multidimensional scaling (nMDS) plot revealed strong differences in assemblage structure among the tidal heights and seasons (Fig. 7). The assemblages of the low- and mid-tidal zones were revealed to be more similar to each other than the assemblages from the high-tidal zone. The nMDS also indicated that the assemblages of the low-tidal zone had considerably more variability than those of the higher zones, as expressed by the more scattered samples on the plot. The season was a significant factor that explained assemblage composition and abundance. The nMDS clearly differentiated the samples according to month (Fig. 7). The most similar groups were found in March, April,

May and June, which are mainly the autumn months when the greatest amount of life was recorded. The PERMANOVA test confirmed significant differences in all of the assemblage parameters (*S*, *N*, *B*, *H'*, and *J'*) between the tidal heights within each month (Table 2).

The highest values of the Shannon–Wiener diversity index were in January and February, ranging from 2.55 to 2.71 (Fig. 8). In the majority of cases (7 out of 10), assemblages in the low-tidal zone were the most diverse, except for April, May and June, when the mid zone had a higher *H'* value. In the case of Pielou's evenness, a different pattern was recorded. The highest values ranging from 0.67 to 0.74 were in November, July and August (Fig. 8). Between tidal heights, the evenness results corresponded with the Shannon–Wiener diversity index.

The shape of the seasonal trajectories of macrofauna assemblages varied for each of the tidal levels (Fig. 8). The most diverse and numerous low-tidal zone (Fig. 8a) had several dominant species. Species such as the bivalve *Altenaeum charcoti*, gastropod *L. caliginosa*, as well as amphipods *Gondogeneia antarctica* and *P. edouardi* increased gradually from March to June, but species evenness remained high. The mid-tidal zone (Fig. 8b) assemblage was numerically dominated by the molluscs *A. charcoti*, *L. caliginosa* and *Onoba* sp., maintaining high species diversity and evenness. The poorest was the high-tidal zone (Fig. 8c), with one dominant species, the gastropod *L. caliginosa*. The points in this plot were the most concentrated, indicating the lowest variability. The temporal trajectory of changes in macrofauna assemblages in the higher-tidal zones was analogous to that of the low-tidal zones, i.e., the highest peak in the number of organisms was in the period from March to June.

4. Discussion

This study revealed that the intertidal zone of Admiralty Bay is characterized by relatively rich biodiversity for most of the year. The seasonal pattern of intertidal assemblage parameters (number of species, abundance, and biomass) was as follows: autumn > summer > spring > winter. These patterns are consistent with those obtained by Jazdzewski et al. (2001) in the same intertidal area. This finding confirms that this is an interannual trend. Strong variability in the environmental parameters (temperature and ice presence) in the study area are undoubtedly the driving factors for the observed seasonal changes in the macrofauna assemblage structure. Additionally, our results confirm previous general

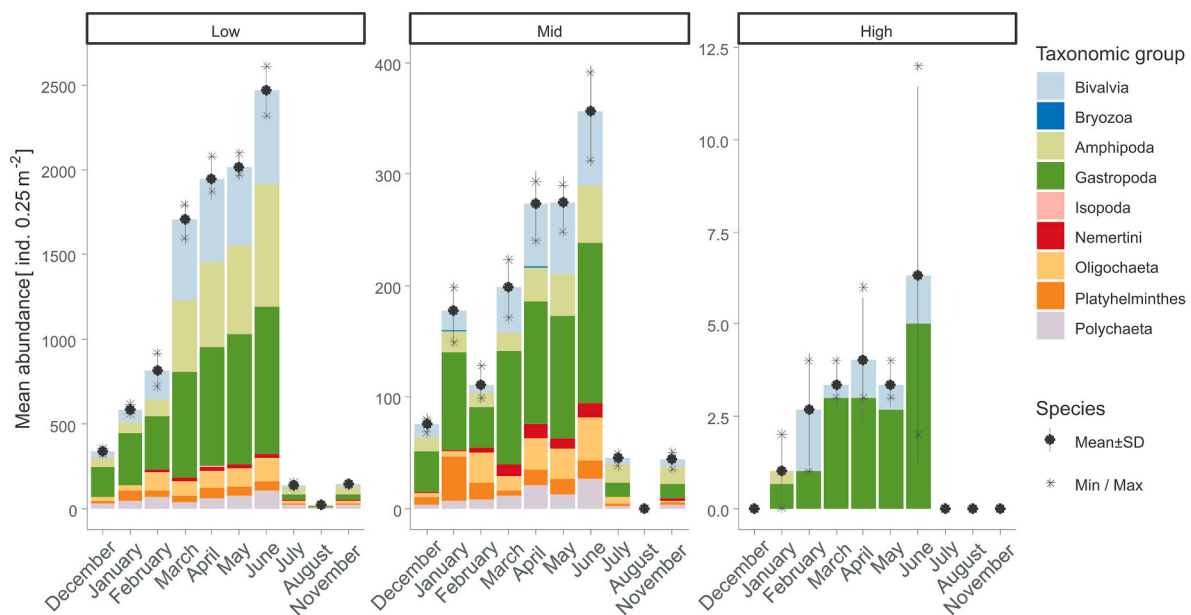


Fig. 5. Mean values of abundance (individuals 0.25 m⁻²) for all macrofauna at particular tidal heights throughout the year. Black bars represent ± standard deviations, and asterisks = minimum–maximum values. Colours represent different macrofaunal groups expressed as the means. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

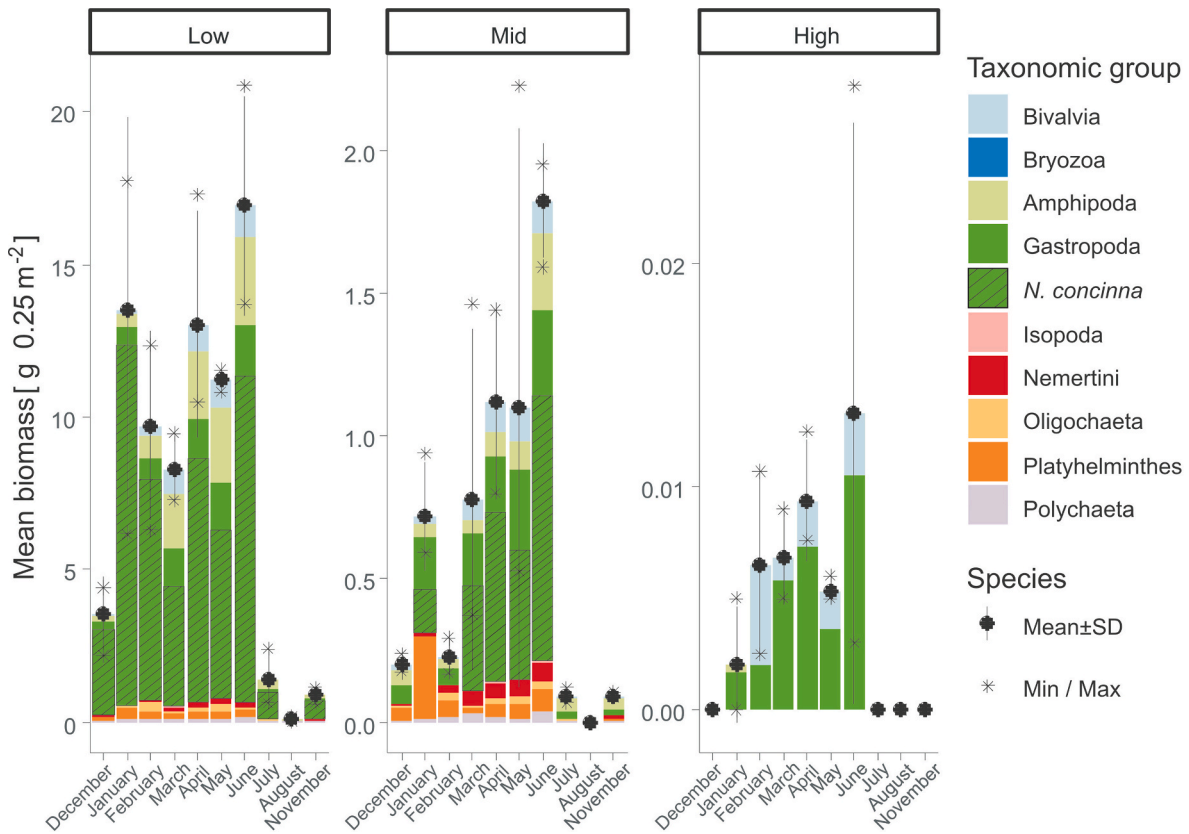


Fig. 6. Mean values of biomass ($\text{g } 0.25 \text{ m}^{-2}$) for all macrofauna at particular tidal heights throughout the year. The black hatched box shows the contribution of *N. concinna* to the total biomass of gastropods. Black bars represent \pm standard deviations, and asterisks = minimum–maximum values. Colours represent different macrofaunal groups expressed as the means. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

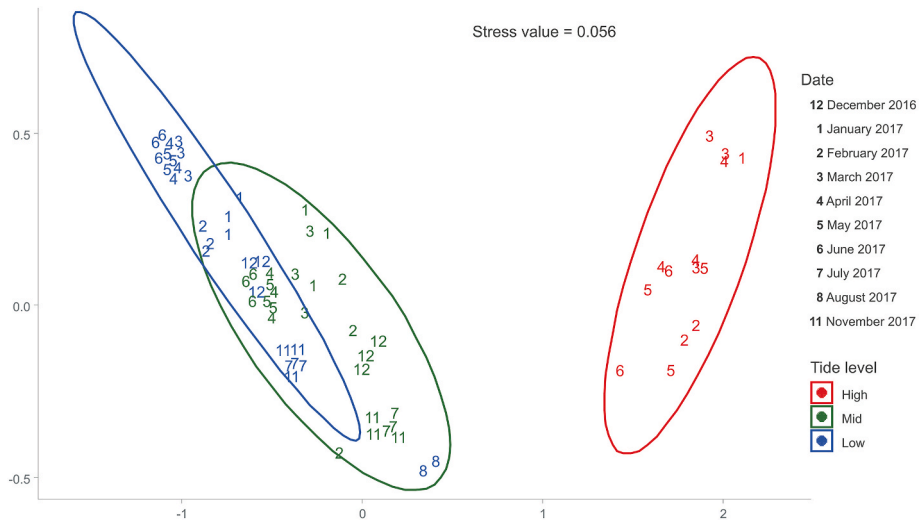


Fig. 7. Non-metric multidimensional scaling (nMDS) ordination of community composition using zones and months as variables. Bray–Curtis similarities are calculated on square root transformed data of abundances of species.

observations (Chelchowski et al., 2021), i.e., a clear vertical zonation, with changes in species composition and assemblage structure (species richness and abundance) among the three intertidal levels. This study clearly indicates that vertical zonation with a decrease in macrofaunal number of species, abundance and biomass along increasing tidal height is a pattern observed during all investigated months.

Intertidal assemblages, even during austral summer, were exposed to

a very high degree of variability in physical parameters such as ice scour, high ultraviolet radiation and occasionally lower salinity values due to freshwater runoff (snow melting). In addition, it was the period with the highest amplitude of temperatures in the year ranged from $-1.45 \text{ }^\circ\text{C}$ up to $+17.95 \text{ }^\circ\text{C}$ in the high-tidal zone and from $-1.25 \text{ }^\circ\text{C}$ to $+9.47 \text{ }^\circ\text{C}$ in the low-tidal zone (Fig. 3). Nevertheless, our data clearly show that it is possible for the intertidal zone on King George Island to support

Table 2

PERMANOVA results for differences in macrofauna assemblages to species richness (*S*), abundance (*N*), biomass (*B*), Shannon–Wiener's diversity (*H'*) and Pielou's evenness (*J'*) data between tidal heights each month. ≠ - statistically significant differences between tidal heights each month (*post hoc* pairwise comparison $p < 0.05$).

Assemblage parameter	<i>F</i>	<i>p</i>	Pairwise <i>post hoc</i>
<i>S</i>	212.35	0.001	low ≠ mid low ≠ high mid ≠ high
<i>N</i>	40.81	0.001	low ≠ mid low ≠ high mid ≠ high
<i>B</i>	7.04	0.001	low ≠ mid low ≠ high mid ≠ high
<i>H'</i>	180.47	0.001	low ≠ mid low ≠ high mid ≠ high
<i>J'</i>	174.62	0.001	low ≠ mid low ≠ high mid ≠ high

relatively species-rich and abundant assemblages (Table 1). Unexpectedly, the most intensive increase in all assemblage parameters (*S*, *N* and *B*) occurred in the last month of austral summer (i.e., March) and lasted until the end of autumn (June, Figs. 4–6). Perhaps this was related to the stability of environmental conditions after the summer peak freshwater runoff from melting snow, ice and surrounding glaciers (Pugh and Davenport, 1997; Waller, 2008). During the peak diversity period (June), the temperature was high enough to protect the sea fringe from freezing, which could be a contributing driver to the observed pattern (Fig. 7). Another important factor for seasonal organism distribution might be the presence of a basic food source, i.e., algal detritus produced by the rich algal community of Admiralty Bay. Most of these algae accumulate in the intertidal zone during summer, with a peak in April (Jazdzewski et al., 2001). Additionally, microphytobenthos peaks in March and is present for several months (February–June, Brêthes et al., 1994). Another possibly important food source for intertidal organisms may be epilithic, epenthic and epiphytic diatoms. A number of diatoms have been recorded underwater (Majewska et al., 2015) and on the shores of Admiralty Bay (Ligowski, 1993b). Epilithic diatoms found directly on the shore occur in spring and summer but disappear in winter. Abundant epiphytic diatoms on macroalgae are present year round and occur on stranded algae. From August to October, shore-ice diatoms have also been recorded (Ligowski, 1993a). Important development of diatom assemblages in spring and summer has been frequently observed in the upper sublittoral zone in East and West Antarctica. According to Momo (1995), the total number of amphipods, *Gondogeneia antarctica*, in Hope Bay (the tip of the Antarctic Peninsula) was positively correlated with the microalgal biomass, the peaks of which occurred, on average, 24 days prior to the maximum density of the amphipods.

Winter, with its low temperature and permanent ice presence, may be a challenge for the survival of intertidal macrofauna in the Antarctic. Our results indicate that all parameters, including species richness, abundance and biomass, declined. The winter temperature variation was from -15.2 °C to $+1.15$ °C in the high-tidal zone and from -4.94 °C to $+0.7$ °C in the low-tidal zone (Fig. 3). However, according to Waller et al. (2006b), some species of the Antarctic intertidal zone, such as *N. concinna*, *L. caliginosa* or *M. antarctica* (species also present in our study area), have cold-tolerance characteristics that are significantly lower (i.e., below -5 °C). Observations of Jazdzewski et al. (2001) suggest that the sharp decreases in Antarctic benthic organism abundance that occur during winter are related not only to lowered water temperature but also to the devastating sea-ice presence. Echeverria and Paiva (2006) showed that shifts in benthic communities in Admiralty

Bay were mainly related to sea-ice impacts and storminess levels. In our study, strong ice disturbances were observed in July, which could have resulted in a significant reduction in the number of species and abundance at each tidal level (Figs. 4 and 5). Ice scour is caused by floating ice grounding and scraping on the substratum, leading to intertidal denudation (Barnes, 1999). The first significant cooling occurred in August, when the air temperature dropped to -14.2 °C (Fig. 3), which was closely followed by a lengthy and marked decrease in air temperature variability. As a result, winter fast ice connected to the shore formed an ice foot that covered the entire intertidal zone in September and October (Fig. 2). Such a temporal pattern in temperature suggests that the ice foot formed after the first pronounced seasonal drop in temperature and that, after the subsequent rise to positive values, the ice foot broke down, exposing the intertidal zone again. The ice foot may have positive effects on benthic assemblages when it is stable during the coldest periods of the year. It provides protection against extreme temperature drops and protects the shore from erosion and waves (Gutt, 2001). Brêthes et al. (1994) concluded that assemblages that remain in the intertidal zone during winter could take advantage of ice algae inhabiting the underside of the ice foot and fast ice. In their study, the ice algae started and peaked in growth in August, decreasing rapidly after ice melt. This was confirmed by Waller et al. (2006b) in a study on Adelaide Island. In September 2004, they found a total of 17 macrofauna species under the top layer of cobbles during an ice-foot duration. However, in our study, directly after the ice foot broke down, we noticed only a small number of mobile organisms, such as the limpet *Nacella concinna*, which could have migrated from the adjacent subtidal zone. The ice foot may stimulate physical disturbance during thawing, as ice fragments can remove benthic organisms from the substrate through scouring (Gutt, 2001). At our study site, boulder pavements that resemble boulder lag deposits are poorly formed, and boulder packing is not well developed. Perhaps such cobble pavement did not provide a sufficiently protected microhabitat that would enable assemblages to survive. Nevertheless, the results of both Waller et al. (2006b) and our study (before ice foot formation) indicate that a range of taxa have the ability to survive year-round temperature conditions in the Antarctic intertidal zone. Survival strategies such as tolerance to ice formation in extracellular fluids as well as lowered freezing points well below that of the surrounding seawater have been adopted by their inhabitants (Sinclair et al., 2004; Waller et al., 2006b; Leeuwis and Gamperl, 2022).

Our results showed that for most of the year, the intertidal macrofauna is dominated by gastropods, followed by amphipods and bivalves. This is not surprising, as generally in the Antarctic shallow marine environment, the dominant macrobenthic groups in terms of abundance and biomass are molluscs and amphipods, which also dominate the intertidal zone (Jazdzewski et al., 2001; Martín et al., 2016). Species reported in this study also exist in nearby shallow subtidal areas and are able to adapt to adverse environments (Sicinski et al., 2011). The taxonomic composition of the macrofauna was similar to that recorded in a previous summer survey of the intertidal in Admiralty Bay (Chelchowski et al., 2021), confirming that such taxonomic composition is an interannual pattern. In 2016–2017 (present study), the bivalve *Altenaeum charcoti* was the most numerous (Table 1). This species has a wide geographic distribution, with a larger number of records from western Antarctica, particularly around the Antarctic Peninsula and subantarctic islands (Domaneschi et al., 2002). Additionally, in the shallow subtidal area of Admiralty Bay, it is the most abundant species among bivalves (Sicinski et al., 2011). *Altenaeum charcoti* can be considered a highly specialized brooding species. Domaneschi et al. (2002) described the ability of *A. charcoti* to survive digestion by *Notothenia coriiceps* (Nototheniidae: Pisces) and their incubation habit. Resistance passage through the gastrointestinal tract of fishes enables these bivalves to passively disperse and colonize new habitats or recolonize shallow-water substrates severely affected by ice.

The dominant taxon among Gastropoda, *Laevittorina caliginosa*, is known to have a high tolerance to desiccation and adaptations to survive

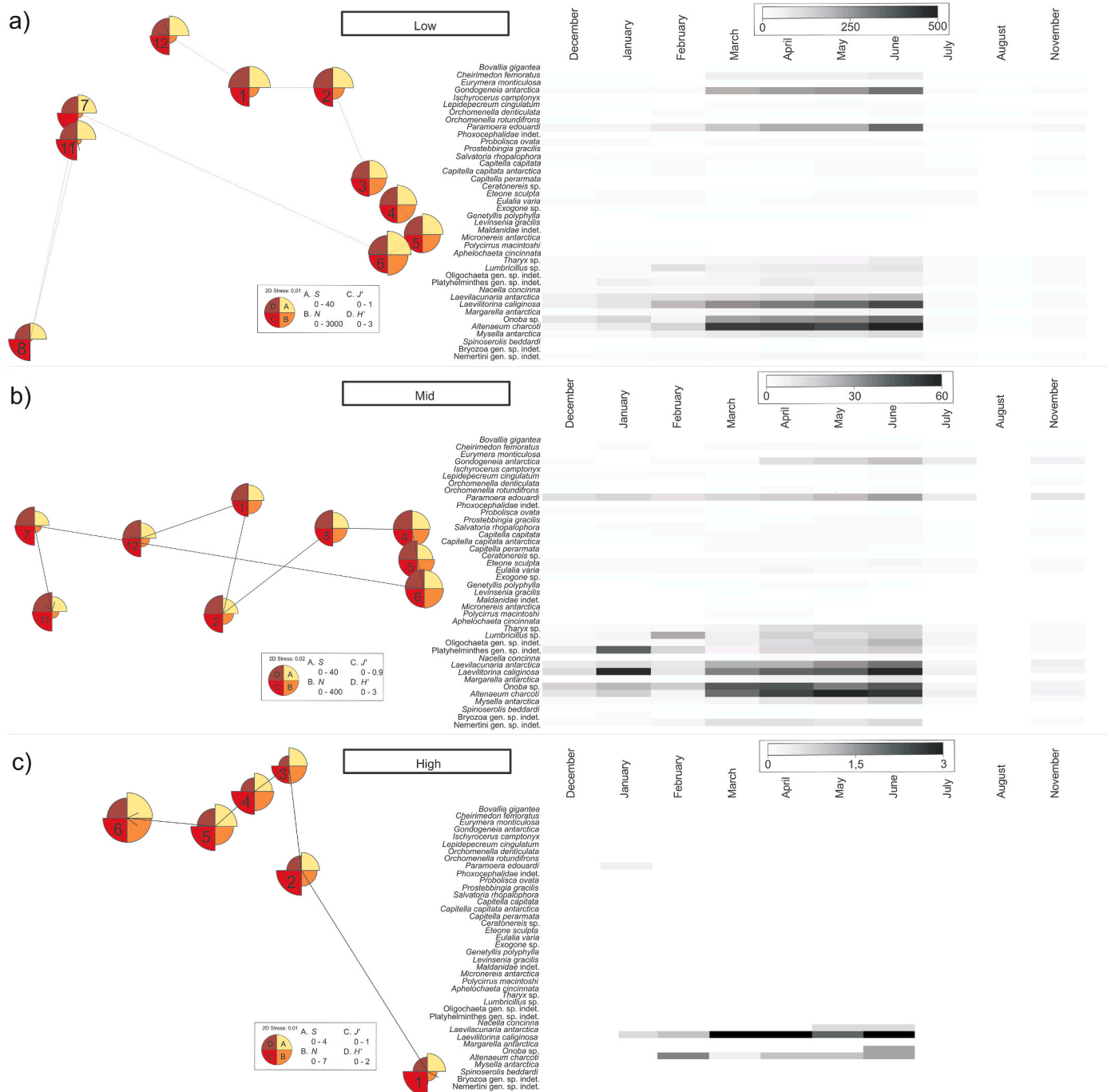


Fig. 8. Non-metric MDS plots of macrofauna assemblages at low- (a), mid- (b) and high- (c) tidal levels calculated on the basis of Bray–Curtis dissimilarities after a transformation using dispersion weighting of average abundances, with temporal trajectory connecting the points through time and overlying bubbles with data for species richness (S, yellow), abundance (N, orange), Pielou’s evenness (J’) and Shannon–Wiener’s diversity (H’, brown). Each plot has a corresponding shade plot of the underlying data matrix. The larger the entry in a specific cell is, the darker the shade plotted; white representing the absence of that species, and full black representing the largest entry in the whole matrix. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

under prolonged air exposure. Davenport and Macalister (1996) found that *L. caliginosa* (family Littorinidae) could occur in a thermal range from $-11\text{ }^{\circ}\text{C}$ to $+28\text{ }^{\circ}\text{C}$, an adaptation that shows its successful survival in Antarctic intertidal zones throughout the year but also on the upper shore. Another factor that may play an important role in the survival of these gastropods on the upper shore is colour, which affects the absorption and reflection of heat. Vermeij (1973) stated that a light-coloured surface absorbs less radiation from visible light, preventing thermal stress (Pandey and Thiruchitrambalam, 2019). The

majority of *L. caliginosa* collected from the higher-tidal levels were pale yellow or light brown in colour. In our study, Rissoidea was the second most abundant family of gastropods and is well adapted to demanding environmental conditions. *Onoba* sp. – numerous in the low-tidal zone – were also the dominant members of the mid-tidal assemblages. They have also been recorded formerly as a common species in the South Shetland Archipelago, occurring even down to a 200 m depth and deeper (Güller and Zelaya, 2017). The key Antarctic species, the gastropod *N. concinna*, represented the greatest proportion of biomass

(Fig. 6). Limpets accounted for up to 88% of the total biomass (LT), a result comparable to that on Adelaide Island (74%, Waller et al., 2006a). *N. concinna* was found both in the mid- and low-tidal zones. However, the significantly greater numbers on the lower shore make it unambiguous that they prefer this zone for food and optimum survival conditions, such as to avoid predation by kelp gulls (Suda et al., 2015).

Amphipod species that can be recognized as typical dwellers of this stony sublittoral fringe are primarily the pontogeneids *Paramoera edouardi* and *G. antarctica*. They are known as omnivorous species, mainly herbivorous on microalgae, but also eating small crustaceans and detritus (Jazdzewski et al., 2001). Therefore, the peak of their abundance probably coincided with the high accumulation of summer/autumn algal biomass washed ashore in Admiralty Bay by surf waves.

Different responses to seasonal disturbances (i.e., temperature variability and ice presence) were noted when different aspects of diversity, such as species richness and evenness, were examined. Our results show that a decline in species richness was not attended by a decrease in evenness, expressed by the Pielou index (Fig. 8). Species diversity (measured by the Shannon–Wiener index), which combines both species richness and evenness, decreased as a result of the decline in species richness (Fig. 8). Magurran (2003) found that disturbance is not always attended by a decline in evenness and that species richness measures are better indicators of a perturbation than evenness or species diversity metrics, which is also confirmed in our study.

Throughout the year, there was a clear gradient in assemblage biodiversity and relative abundance from the low-to high-tidal zones, with the lowest values of those always in the highest-tidal area (Fig. 8). The observed vertical assemblage patterns were undoubtedly due to the high variability in environmental conditions and differences in environmental stress that occurred at different tidal heights in the study area (Menge and Branch, 2001; Kuklinski and Balazy, 2014; Chelchowski et al., 2021). It is well known that abiotic stressors increase from the low-to high-tidal zone, which is strongly exposed to physical factors such as emersion, desiccation and salinity changes (Menge and Branch, 2001; Scrosati and Heaven, 2007). The distribution of organisms along tidal heights depends on their environmental preferences, i.e., physiological needs related to physical stress and biological interactions, allowing them to survive in a given zone (Benedetti-Cecchi et al., 2000).

In this study, the distribution of organisms across the tidal heights shows that the dominant species that occur year around are also the most abundant at higher-tidal levels (Table 1 and Fig. 8). In the context of ongoing Antarctic ecosystem transformations, such as air temperature increases or glacial retreat, intertidal species with a wide physiological tolerance, such as *L. caliginosa*, *Onoba* sp. or *A. charcoti*, would gain an advantage from this and would likely dominate in these conditions. Considering that intertidal macrofauna assemblages quickly respond to changes in environmental conditions and thus may reflect environmental fluctuations, more studies are suggested for these habitats in terms of seasonal and interannual changes, which might help us to understand the impact of global warming on Antarctic assemblages.

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CRediT authorship contribution statement

Maciej Chelchowski: Writing – original draft, Investigation, Formal analysis. **Piotr Balazy:** Writing – review & editing, Visualization, Supervision, Methodology. **Piotr Kuklinski:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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