Marine Biology (2024) 171:70
https://doi.org/10.1007/s00227-024-04406-5

SHORT NOTES

Short-term temporal variability in offshore benthic biodiversity across hydrographic regions at a sub-Antarctic archipelago

Eleonora Puccinelli[1,2,3] · Renae Logston[4] · Cristina S. Russo[5] · Isabelle J. Ansorge[2] · Charles E. O. von der Meden[6]

Received: 22 August 2023 / Accepted: 31 January 2024 / Published online: 19 February 2024

Abstract
Community composition is one of the main factors influencing the ecological functioning of any given ecosystem, with a more diverse community providing a larger set of services. Benthic community composition can vary at spatial and temporal scales, with the dynamics of primary production and benthic food availability being key determinants of community structure of a given system. Studies have indicated shifts in benthic community composition at sub-Antarctic Islands over a period of 30 years, linked to variability in food availability driven by climate change. Here, we aim to evaluate possible short-term variability in benthic community composition at the sub-Antarctic archipelago Prince Edward Islands (PEIs), sampling stations across three hydrographically dynamic regions over two consecutive years, 2016–2017. The results indicated significantly higher species richness and abundance in 2017 than in 2016, with some taxa also showing variation among regions around the PEIs. Such effects can be linked to different substratum type or hydrographic regime. This study further contributes to understanding variability and changes in benthic communities in the near future, an essential information to develop efficient management strategies for this vulnerable marine system.

Keywords Southern Ocean · Biodiversity · Temporal scale · Benthos · Abundance · Species richness

Introduction

The Southern Ocean is known to be experiencing climate-induced bio-physical shifts, with future changes expected to involve primary production and benthic-pelagic links (e.g., Constable et al. 2014; Gutt et al. 2015; Trebilco et al. 2020; Cavanagh et al. 2021). It is now understood that benthic communities, even those of the deep abyssal zone, are susceptible to upper ocean changes and display relatively rapid responses to several factors, including variation in temperature, productivity, or introduction of new species (Glover et al. 2010; Sweetman et al. 2017). Hydrographic regime (e.g., eddies, water masses) is another main factor affecting species distribution and community composition (Treasure et al. 2019; Puerta et al. 2020). Ocean currents are responsible for the transport of nutrients and primary production (Sokolov and Rintoul 2007), including the mixing of coastal and offshore production (Puccinelli et al. 2016, 2018), making them a key factor influencing food availability, connectivity, and species distribution (Puerta et al. 2020; Mackenzie et al. 2022).

Over recent years, studies have highlighted the effects of climate-driven changes on marine environments (Doney et al. 2012), including the sub-Antarctic Prince Edward Islands (PEIs; von der Meden et al. 2017; Carpenter-Kling et al. 2019). The PEIs form an archipelago that comprises Marion Island and PEI, located in the Indian Sector of the Southern Ocean within the path of the Antarctic Circumpolar Current (ACC), with the Sub Antarctic Front (SAF) lying

Responsible Editor: C. Pansch-Hattich.

✉ Eleonora Puccinelli
eleonora.puccinelli@nioz.nl

1 Department of Coastal Systems, Royal Netherlands Institute for Sea Research (NIOZ), Texel, The Netherlands

2 Department of Oceanography, University of Cape Town, Rondebosch, Cape Town, South Africa

3 South African Institute for Aquatic Biodiversity (SAIAB), Makhanda, South Africa

4 Scripps Institute of Oceanography, San Diego, CA, USA

5 Department of Forestry, Fisheries and the Environment, Oceans and Coasts Research, V&A Waterfront, PO Box 52126, Cape Town 8000, South Africa

6 South African Environmental Observation Network (SAEON), Egagasini Node, Cape Town, South Africa

to the north and the Antarctic Polar Front (APF) to the south (Lutjeharms and Valentine 1984; Orsi et al. 1995). Although the SAF is generally found north of the PEIs, occasionally it is observed close to the islands (Lamont et al. 2019), which promotes the dominance of a flow-through system between the islands, with a simultaneous decrease in water retention in this area and in the frequency of conditions that promote local phytoplankton blooms (Stirnimann et al. 2021; Lamont et al. 2022). The proximity of the SAF to the PEIs and the influence of the eastward flow of the ACC allows the characterization of upstream (east of the islands), interisland (between the islands), and downstream (west of the islands) regions. This kind of hydrographic variability can lead to changes in marine communities (Pakhomov et al. 2000; von der Meden et al. 2017), most likely linked to shifts in the balance of food sources from autochthonous to allochthonous (Allan et al. 2013; Puccinelli et al. 2018). While temporal variability in benthos community composition has been observed over rather large temporal intervals (i.e., 10 s years; Allan et al. 2013; von der Meden et al. 2017), little is known about how sub-Antarctic communities may change over short time scales (weeks to 1–2 years).

The PEIs were declared a marine protected area in 2013 (Lombard et al. 2007) for their relevance in supporting a high abundance of marine species, including seabirds, penguins, and seals, several of which are classified as endangered (Reisinger et al. 2018; Rexer-Huber et al. 2019; Carpenter-Kling et al. 2020). The benthos directly or indirectly represents a major food source for many higher trophic levels and plays a fundamental role in ecosystem stability, resilience, and services (Pakhomov and Chown 2003; Puccinelli et al. 2018, 2020). As such, understanding the potential effects of spatio-temporal shifts in community composition and the variability associated with the benthos is of empirical importance, particularly for assessing potential effects on higher trophic level marine species, as well as for the formulation of relevant guidelines for the conservation and management of this region.

In this study, we aim to characterize short-term temporal variability in the benthic community composition across the three regions around the PEIs by looking at the variability over a 2-year period.

Materials and methods

Sampling was conducted aboard the R/V *S.A. Agulhas II* during the annual relief voyages to the PEIs (46.77° S, 37.85° E), in April–May 2016 and 2017, as part of the South African National Antarctic Programme. Marion Island and PEI, the two islands forming the PEIs archipelago, are 22 km apart and separated by a shallow (mean depth ~ 180 m) interisland plateau that rapidly falls to approximately 3000 m (Fig. 1). Sampling was conducted at 13 stations with depths between 105 and 286 m, six of which were located in the upstream region (D1–D6), three in the interisland region (D7–D9), and four in the downstream region (D10–D13) (Table 1). Samples were collected using a dredge, with a mouth opening of 30 × 100 cm and a mesh size of 1 cm^2, which was towed behind the vessel at 1 knot for 20 min. Six of the 13 stations were sampled in both years (D5, D7, D8, D9, D11, D12), while four (D1, D2, D6, D13) and three (D3, D4, D10) were unique stations for 2016 and 2017, respectively (Fig. 1). The content of each dredge was quantified, and a known portion was stored in ethanol for identification. All organisms > 0.5 mm were counted and identified using an Olympus SZX16 stereomicroscope to the highest taxonomic level possible using taxonomic keys (Branch et al. 1991, 1993b; Branch 1994; Hibberd and Moore 2009). Colonial organisms, including Porifera, Bryozoa, Hydrozoa, and Octocorallia, were categorized according to their volume and measured in milliliters (mL). In contrast, all the non-colonial taxonomic groups were individually counted according to species.

Data analysis

Abundance data were transformed using a ranking system following Branch et al. (1993a). The colonial volumetrically measured species were ranked according to the following scheme: rank 0 = absent; rank 1 = 1–5 mL; rank 2 = 6–25 mL; rank 3 = 26–75 mL; rank 4 = 76–250 mL; rank 5 = 251–500 mL. The non-colonial species were ranked according to the following scheme: rank 0 = absent; rank 1 = 1–5 individuals; rank 2 = 6–15 individuals; rank 3 = 16–30 individuals; rank 4 = 31–50 individuals; rank 5 = 51–100 individuals; rank 6 = 101–300 individuals; rank 7 = 301–1000 individuals.

A multivariate permutational analysis (PERMANOVA; Anderson 2001) was performed to test for differences among regions (factor *Region*, upstream, interisland, downstream; $n = 3$), year of collection (factor *Time*, 2016, 2017; $n = 2$) and substratum type (factor *Substratum*, partial rock-sand, mud; $n = 2$) in the community composition around the PEIs. Each term in the PERMANOVA analysis was tested using > 9999 permutations as the relevant permutable units (Anderson and Braak 2003). In the event of significant results, PERMANOVA pairwise tests were performed. Shannon (H′) and

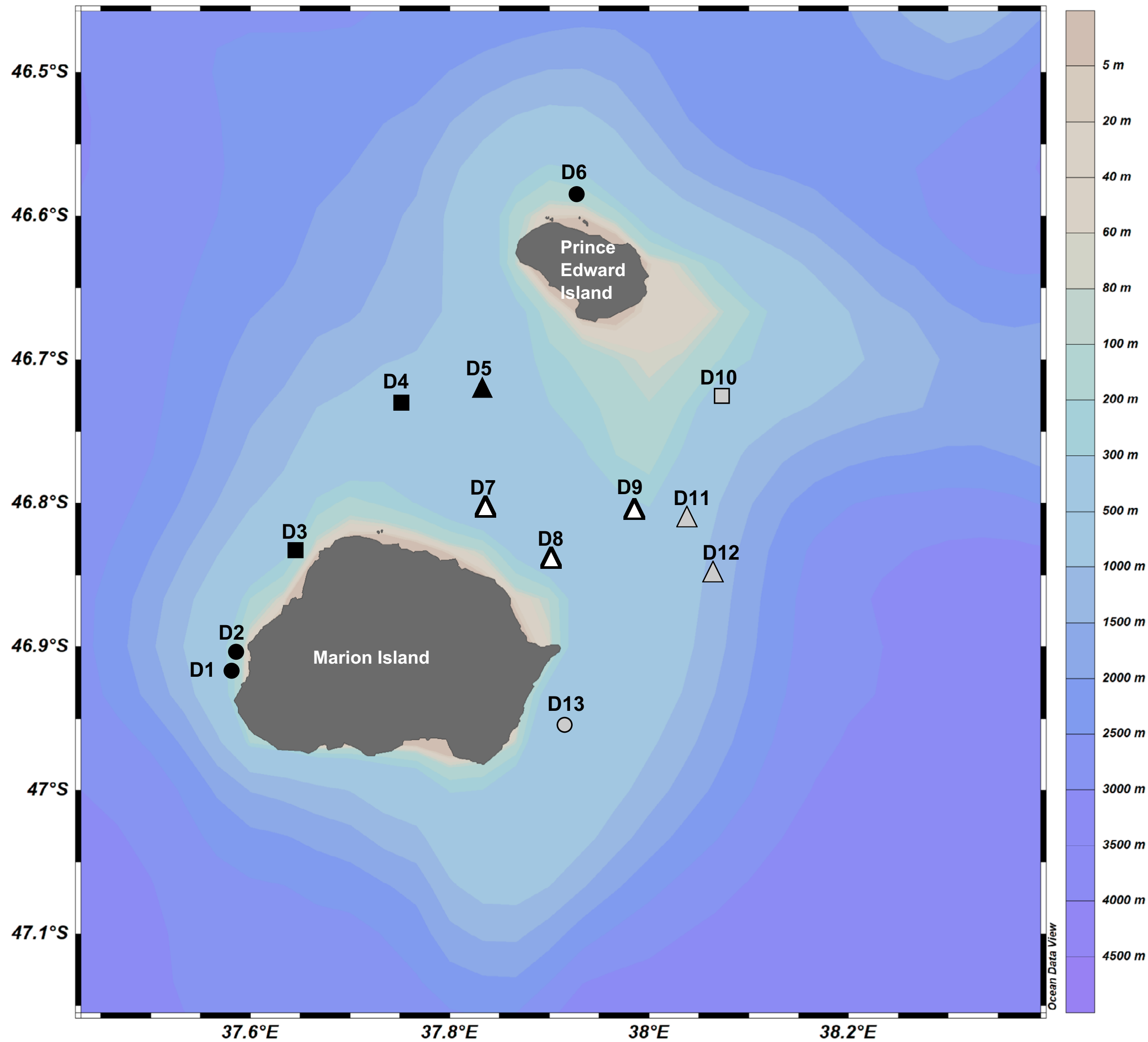

Fig. 1 Map of the study area indicating the location of the dredge stations sampled in the proximity to the Prince Edward Islands (PEIs): D1–D6 upstream (black), D7–D9 interisland (white), D10–D13 downstream (grey). The shape of the symbols indicates the year of collection: 2016-only (circle), 2017-only (square), and both years (triangle) (color figure online)

Table 1 Coordinates, bottom depth, and substratum type for the stations sampled in 2016 and 2017 in three regions (upstream, interisland, downstream) in proximity to the PEIs

Station #	Year	Region	Depth (m)	Latitude	Longitude	Substratum type
D1	2016	Upstream	150	−46.9149333	37.5794667	Partial Rock-Sand
D2	2016	Upstream	200	−46.9031333	37.58445	Partial Rock-Sand
D3	2017	Upstream	109	−46.83235	37.6444	Partial Rock-Sand
D4	2017	Upstream	286	−46.7286583	37.7506167	Partial Rock-Sand
D5	2016–2017	Upstream	285	−46.7180833	37.8321333	Partial Rock-Sand
D6	2016	Upstream	105	−46.58295	37.9232167	Mud
D7	2016–2017	Interisland	172	−46.80175	37.8366	Mud
D8	2016–2017	Interisland	146	−46.838	37.9015833	Mud
D9	2016–2017	Interisland	134	−46.8038333	37.98505	Mud
D10	2017	Downstream	185	−46.7231833	38.0695	Mud
D11	2016–2017	Downstream	258	−46.8086	38.0383333	Mud
D12	2016	Downstream	180	−46.84705	38.065	Mud
D13	2016	Downstream	142	−46.9524333	37.9137833	Sand

Pielou's (J′) indexes were computed to determine species diversity and evenness between years and among regions. Analyses were based on Bray–Curtis dissimilarities and were conducted using the PERMANOVA + add-on package of PRIMER v6 (Clarke and Gorley 2006; Anderson et al. 2008).

We tested the effects of the factor *Region*, *Time* and *Substratum* on the species richness, H′ and J′, using a factorial analysis of variance (ANOVA). In addition, we tested for variations among regions in the abundances of the most ubiquitous taxa, which included ophiuroids, the polychaete *Lanice marionensis* Branch, the brachiopod *Aerothyris kerguelensis* Davidson, and the serpulid polychaete *Serpula vermicularis* Linnaeus. In the event of significant results, Tukey HSD post hoc tests were conducted. Analyses were performed using R version 3.6.3. (R Core Team, 2020).

Results and discussion

In this study, we aimed to provide information on short-term variability in the benthic community composition of the shelf surrounding the PEIs. The analyses indicated that species richness varied between years regardless of *Region* or *Substratum*, which did not significantly affect species richness in either year, with generally a higher number of species in 2017 compared to 2016 ($p < 0.01$, Fig. 2). Analyses conducted on Shannon Diversity Index (H′) indicated a significant effect of the interaction *Time* × *Region*, with samples from upstream—2016 having a lower H′ than upstream—2017 (2.7 ± 0.2 vs. 3.7 ± 0.2; Table 2), while no other significant effects were recorded for the other regions/years/substratum types. Pielou's Evenness Index (J′) averaged 0.9 ± 0.0 and did not vary as a function of year, nor region or substratum type ($p > 0.05$; Table 2). Annelida had the highest number of species (12 at station D4), followed by Echinodermata and Porifera (11 and 10 both at station D5) (Fig. S.1). Among those, the tube-forming polychaete *L. marionensis* was present at every station in both years, followed by the echinoid *Pseudechinus marionis* Mortensen, the brachiopod *A. kerguelensis*, and several species of the colonial groups bryozoa (*Osthimosia bicornis* Busk, *Reteporella flabellata* Busk, *Tervia irregularis* Meneghini), hydrozoa (*Staurotheca dichotoma* Allman) and porifera (*Acanthella erecta* Carter). The Ophiuroidea *Ophiocten amitinum* Lyman and *Ophioplinthus intorta* Lyman were also present at most stations in both years. A likely reason for the variation in species richness and diversity observed between years could be linked to the causality of sampling a higher number of species and/or individuals in 1 year in comparison to the next, linked for instance to the inability to sample the exact same location. While we sampled the same station in both years, in offshore/deep-sea research, it is difficult to sample the exact same location over consecutive sampling events (Gage and Bett 2005). Variability in benthic community composition can occur at different spatial scales, from large to micro (Murray et al. 2002; Ingels and Vanreusel 2013). At local and small scales (0.1–100 m and 0.1–10 cm, respectively), benthic communities are influenced by food and oxygen availability, sediment type, bioturbation or seafloor topography (Glover et al. 2010; Haley et al. 2017; Rosli et al. 2018; Román et al. 2019), leading

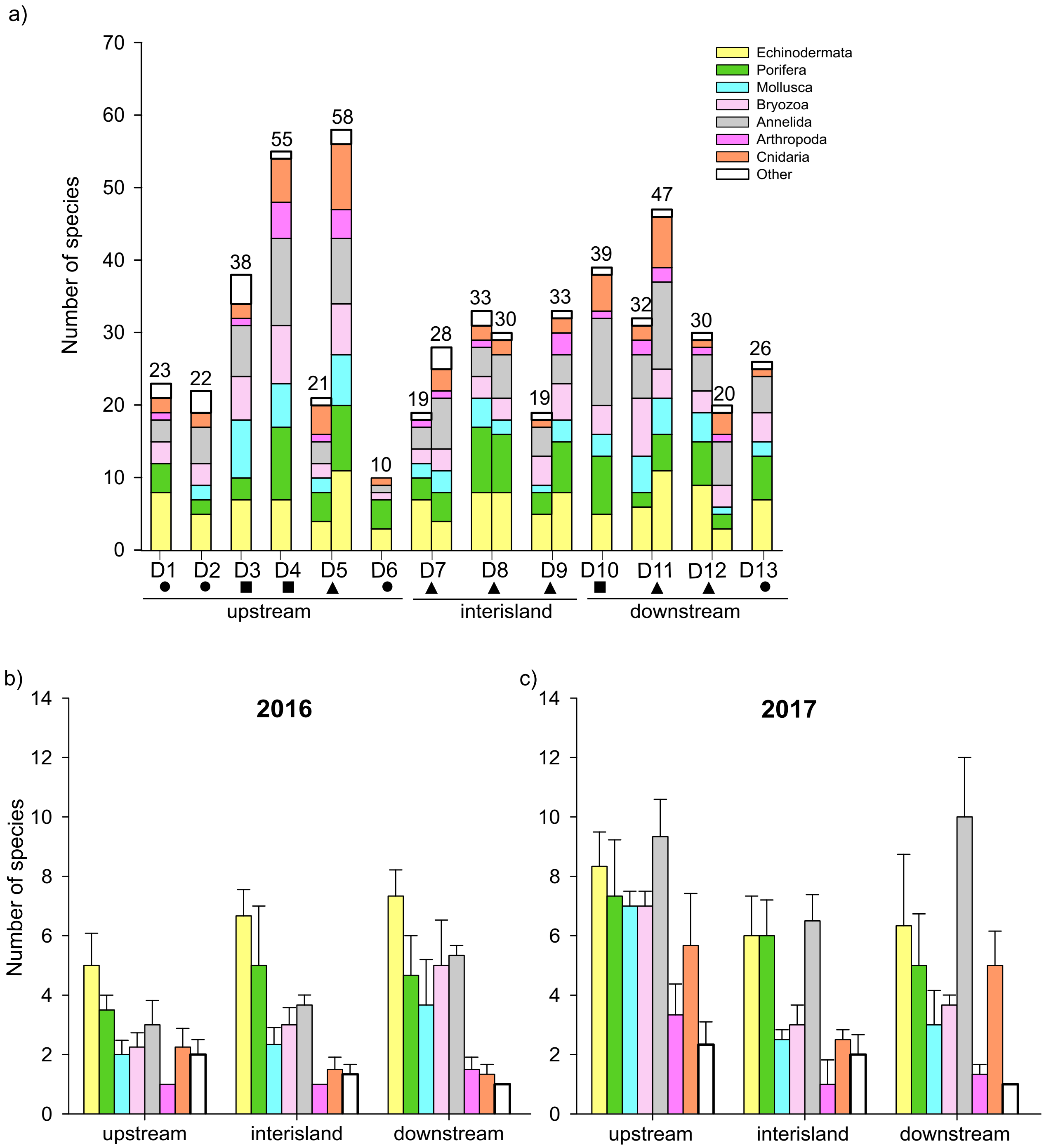

Fig. 2 Number of species of the most abundant phyla collected from stations located in the upstream, interisland, and downstream regions of the PEIs in 2016 and 2017. Values represent abundance for 500 m^2 of seafloor dredged. **a** The number above each column indicates the total number of species found at the selected station. Symbols indicate stations that were sampled in 2016-only (circle), 2017-only (square), and both years (triangles). **b**, **c** Mean ± standard error of number of species from the most abundant phyla collected in the upstream, interisland, and downstream regions for years 2016 and 2017, respectively. Yellow = Echinodermata, green = Porifera, light blue = Mollusca, pink = Bryozoa, grey = Annelida, dark pink = Arthropoda, orange = Cnidaria, white = others (color figure online)

Table 2 Species richness, Pielou evenness (J′), and Shannon diversity (H′) indices for samples collected in 2016 and 2017 at stations located in three regions (upstream, interisland, downstream) in proximity to the PEIs

Station #	Year	Region	Species richness	Pielou Index (J′)	Shannon Index (H′)
D1	2016	Upstream	23	0.934	2.930
D2	2016	Upstream	22	0.941	2.908
D5	2016	Upstream	21	0.955	2.907
D6	2016	Upstream	10	0.939	2.161
D7	2016	Interisland	19	0.914	2.690
D8	2016	Interisland	33	0.953	3.332
D9	2016	Interisland	19	0.940	2.768
D11	2016	Downstream	32	0.951	3.296
D12	2016	Downstream	30	0.942	3.205
D13	2016	Downstream	26	0.928	3.023
D3	2017	Upstream	38	0.951	3.460
D4	2017	Upstream	54	0.953	3.802
D5	2017	Upstream	58	0.954	3.875
D7	2017	Interisland	28	0.944	3.145
D8	2017	Interisland	30	0.948	3.226
D9	2017	Interisland	33	0.947	3.309
D10	2017	Downstream	39	0.950	3.503
D11	2017	Downstream	47	0.952	3.624
D12	2017	Downstream	20	0.940	2.815

to local seafloor patchiness of both the habitat and the resident communities, resulting in correspondingly patchy patterns of abundance and species composition.

When focusing on species abundance, *L. marionensis* and *A. kerguelensis* had the highest rank (7), together with the polychaete *S. vermicularis* and the ophiuroid *Ophiolimna antarctica* Lyman. Generally, ophiuroids (i.e., *O. antarctica*, *Ophiosabine vivipara* Ljungman, *O. intorta* Lyman, *O. amitinum* Lyman) were abundant at most stations and in both years, particularly at stations D3, D4, D5 in 2017 and D6, D12 in 2016 with ranks > 5 (Fig. 3). The analyses indicated that there was no effect of the factor *Region* or *Substratum* ($p > 0.05$), but a significant effect of *Year* ($p < 0.05$), with abundance generally increasing from 2016 to 2017 (Fig. S.2). The increment in abundance between the two sampling events could be linked to the life cycles of the benthos. Some species are known to be fast-growing with rapid sexual maturation and a short lifespan, having a life cycle of just a few years (Arendt 1997; Metcalfe and Monaghan 2003; Lagger et al. 2021), while others can reproduce quickly, especially when asexual reproduction is involved (e.g., Ophiuroidea; McGovern 2002). However, species reproduction output naturally varies over the years (Olive et al. 1997; López et al. 1998; Grange et al. 2004), and further, interannual samples would be needed to clearly assess short-term temporal variation on species abundance at the PEIs.

When focusing on the most abundant taxa, we observed a significant difference among regions, with the upstream and interisland regions having the highest abundance in the case of ophiuroids and *L. marionensis*, respectively ($p < 0.05$). In contrast, abundance of *A. kerguelensis* and *S. vermicularis* was higher in the interisland and downstream regions compared to the upstream ($p < 0.05$; Fig. 3). Depth typically influences patterns of benthic life (Cartes et al. 2004; Ramirez-Llodra et al. 2010; Long and Baco 2014; Puccinelli et al. 2018). However, it cannot explain these patterns since all stations in the present study were within the same approximate depth range. Rather, differences may relate to the predominant substratum type(s) occurring within the respective regions. Substratum characteristics are known to be a key factor determining the composition of benthic communities (Haley et al. 2017; von der Meden et al. 2017). Upstream stations were mostly composed of partial rock and sand, while the interisland and downstream stations by mud (Table 1). It is known that polychaetes *S. vermicularis* and *L. marionensis* are usually associated with a soft substratum environment (Branch 1994) and that the brachiopod *A. kerguelensis* is ubiquitous (Branch et al. 1991), while ophiuroids are usually ubiquitously present but with higher abundances in partial rock/sand substratum (Branch et al. 1993b). Here, *A. kerguelensis* and *S. vermicularis* were significantly more abundant in mud stations, while ophiuroids in partial rock-sand stations ($p < 0.01$), while no clear pattern was observed for *L. marionensis*. These results suggest that substratum type represents an important factor determining pattern of distribution of deep-sea benthos.

A clear temporal variation in offshore benthic community composition at the PEIs has been observed over a long time period (i.e., decades (von der Meden et al. 2017)), and this study highlights the occurrence of short temporal variability in species richness and abundance, as well as the likely underlying influence of substratum type. Both aspects need to be considered when interpreting the results of long-term studies. While the present study looked at the differences over two consecutive years only, a better understanding of short-term variability will come from consecutive interannual studies that also account for the life cycles and periodicity of key benthic taxa. The information we provide here is essential to comprehend long-term changes in benthic communities and related consequences for higher trophic levels that rely on them for survival. Understanding how benthic communities may change in the near future is essential to develop efficient management and conservation strategies for this vulnerable ecosystem.

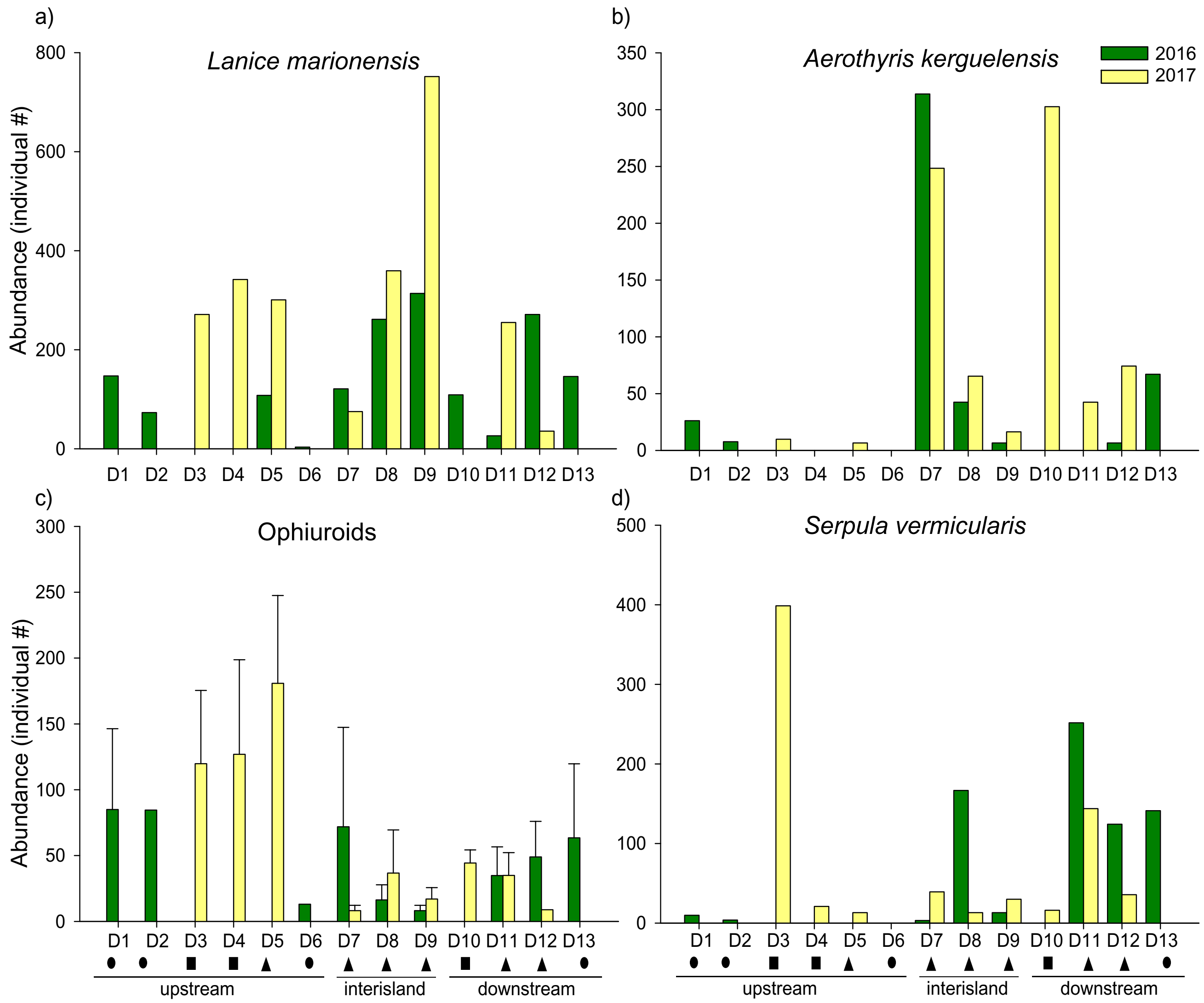

Fig. 3 Abundance of the polychaete **a** *Lanice marionensis*, brachiopod **b** *Aerothyris kerguelensis,* **c** ophiuroids (average ± standard error of *Ophiolimna antarctica*, *Ophiosabine vivipara, Ophioplinthus intorta, Ophiocten amitinum*) and polychaete **d** *Serpula vermicularis* from samples collected at stations located in the upstream, interisland and downstream regions of the PEIs in 2016 and 2017. Values represent abundance for 500 m^2 of seafloor dredged. Symbols indicate stations that were sampled in 2016-only (circle), 2017-only (square), and both years (triangles). Note that a different scale is used in each panel

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-024-04406-5.

Acknowledgements Special thanks go to Captain Syndercombe, Captain Bengu, and the R/V SA Agulhas II officers and crew for their assistance at sea. We would also like to thank Robyn Adams, Sarah Asdar, Tahlia Henry, Holly Nel, Sandi Smart, Kirrin Reid, Luca Stirnimann, Marcel van den Berg, and Grant van der Heever for their help with sample collection. We are very grateful to Christopher Mah (Smithsonian Institution) and Jennifer Olbers (WildTrust) for their help with sample identification.

Author contributions EP conceived the ideas and designed the methodology. EP and RL collected the data. EP, RL, CR, and CVDM analyzed the data. IA provided the funding and resources to support the work. EP led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

Funding Open access funding provided by University of Cape Town. This work was supported by funding from the South African Department of Environmental Affairs (now Department of Forestry, Fisheries, and the Environment), the National Research Foundation, and the South African National Antarctic Program (SANAP) through grant 110719 to Prof Isabelle Ansorge.

Data availability The authors declare that all data relative to this work are available in the public repository Data Archive System (DAS) of NIOZ with the https://doi.org/10.25850/nioz/7b.b.mf.

Declarations

Conflict of 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.

Ethics approval All applicable international, national and/or institutional guidelines for sampling, care and use of invertebrates for this study were followed. In addition, the permit to work at the Prince Edward Islands was obtained by the Department of Environmental Affair of South Africa (now Department of Forestry, Fisheries, and the Environment).

References

Allan LE, Froneman WP, Durgadoo JV, McQuaid CD, Ansorge IJ, Richoux NB (2013) Critical indirect effects of climate change on sub-Antarctic ecosystem functioning. Ecol Evol 3:2994–3004. https://doi.org/10.1002/ece3.678

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Anderson M, Braak CT (2003) Permutation tests for multi-factorial analysis of variance. J Stat Comput Simul 73:85–113. https://doi.org/10.1080/00949650215733

Anderson M, Gorley R, Clarke K (2008) PERMANOVA + for PRIMER: guide to software and statistical methods. PRIMER-E

Arendt JD (1997) Adaptive intrinsic growth rates: an integration across taxa. Q Rev Biol 72:149–177. https://doi.org/10.1086/419764

Branch ML (1994) The Polychaeta of subantarctic Marion and Prince Edward Islands: illustrated keys to the species and results of the 1982–1989 University of Cape Town surveys. S Afr J Antarct Res 24:3–52

Branch ML, Arnaud PM, Cantera J, Gianakouras D (1991) The benthic Mollusca and Brachiopoda of subantarctic Marion and Prince Edward Islands: 1) Illustrated keys to the species 2) Records of the 1982–1989 University of Cape Town surveys

Branch GM, Attwood CG, Gianakouras D, Branch ML (1993a) Patterns in the benthic communities on the shelf of the sub-Antarctic Prince Edward Islands. Polar Biol 13:23–34. https://doi.org/10.1007/BF00236580

Branch ML, Jangoux M, Alva V, Massin C, Stampanato S (1993b) The Echinodermata of subantarctic Marion and Prince Edward Islands. S Afr J Antarct Res 23:37–70

Carpenter-Kling T, Handley JM, Connan M, Crawford RJM, Makhado AB, Dyer BM, Froneman W, Lamont T, Wolfaardt AC, Landman M, Sigqala M, Pistorius PA (2019) Gentoo penguins as sentinels of climate change at the sub-Antarctic Prince Edward Archipelago, Southern Ocean. Ecol Indic 101:163–172. https://doi.org/10.1016/j.ecolind.2019.01.008

Carpenter-Kling T, Pistorius P, Reisinger R, Cherel Y, Connan M (2020) A critical assessment of marine predator isoscapes within the southern Indian Ocean. Mov Ecol 8:29. https://doi.org/10.1186/s40462-020-00208-8

Cartes JE, Maynou F, Moranta J, Massutí E, Lloris D, Morales-Nin B (2004) Patterns of bathymetric distribution among deep-sea fauna at local spatial scale: comparison of mainland vs. insular areas. Prog Oceanogr 60:29–45. https://doi.org/10.1016/j.pocean.2004.02.001

Cavanagh RD, Melbourne-Thomas J, Grant SM, Barnes DKA, Hughes KA, Halfter S, Meredith MP, Murphy EJ, Trebilco R, Hill SL (2021) Future risk for Southern Ocean ecosystem services under climate change

Clarke KR, Gorley RN (2006) Primer V6: user manual—tutorial. Plymouth Marine Laboratory

Constable AJ, Melbourne-Thomas J, Corney SP, Arrigo KR, Barbraud C, Barnes DKA, Bindoff NL, Boyd PW, Brandt A, Costa DP, Davidson AT, Ducklow HW, Emmerson L, Fukuchi M, Gutt J, Hindell MA, Hofmann EE, Hosie GW, Iida T, Jacob S, Johnston NM, Kawaguchi S, Kokubun N, Koubbi P, Lea M-A, Makhado A, Massom RA, Meiners K, Meredith MP, Murphy EJ, Nicol S, Reid K, Richerson K, Riddle MJ, Rintoul SR, Smith WO Jr, Southwell C, Stark JS, Sumner M, Swadling KM, Takahashi KT, Trathan PN, Welsford DC, Weimerskirch H, Westwood KJ, Wienecke BC, Wolf-Gladrow D, Wright SW, Xavier JC, Ziegler P (2014) Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. Glob Change Biol 20:3004–3025. https://doi.org/10.1111/gcb.12623

Doney SC, Ruckelshaus M, Emmett Duffy J, Barry JP, Chan F, English CA, Galindo HM, Grebmeier JM, Hollowed AB, Knowlton N, Polovina J, Rabalais NN, Sydeman WJ, Talley LD (2012) Climate change impacts on marine ecosystems. Annu Rev Mar Sci 4:11–37. https://doi.org/10.1146/annurev-marine-041911-111611

Gage JD, Bett BJ (2005) Deep-sea benthic sampling. In: Methods for the study of marine benthos. John Wiley & Sons, Ltd. pp 273–325

Glover AG, Gooday AJ, Bailey DM, Billett DSM, Chevaldonné P, Colaço A, Copley J, Cuvelier D, Desbruyères D, Kalogeropoulou V, Klages M, Lampadariou N, Lejeusne C, Mestre NC, Paterson GLJ, Perez T, Ruhl H, Sarrazin J, Soltwedel T, Soto EH, Thatje S, Tselepides A, Van Gaever S, Vanreusel A (2010) Chapter one—Temporal change in deep-sea benthic ecosystems: a review of the evidence from recent time-series studies. In: Lesser M (ed) Advances in marine biology. Academic Press, London, pp 1–95

Grange LJ, Tyler PA, Peck LS, Cornelius N (2004) Long-term interannual cycles of the gametogenic ecology of the Antarctic brittle star *Ophionotus victoriae*. Mar Ecol Prog Ser 278:141–155. https://doi.org/10.3354/meps278141

Gutt J, Bertler N, Bracegirdle TJ, Buschmann A, Comiso J, Hosie G, Isla E, Schloss IR, Smith CR, Tournadre J, Xavier JC (2015) The Southern Ocean ecosystem under multiple climate change stresses—an integrated circumpolar assessment. Glob Change Biol 21:1434–1453. https://doi.org/10.1111/gcb.12794

Haley C, von der Meden C, Atkinson L, Reed C (2017) Habitat associations and distribution of the hyperbenthic shrimp, *Nauticaris marionis*, around the sub-Antarctic Prince Edward Islands. Deep

Sea Res Part Oceanogr Res Pap 127:41–48. https://doi.org/10.1016/j.dsr.2017.07.005
Hibberd T, Moore K (2009) Field identification guide to Heard Island and McDonald Islands benthic invertebrates: a guide for scientific observers aboard fishing vessels. Australian Antarctic Division and Fisheries Research and Development Corporation (Australia), Kingston
Ingels J, Vanreusel A (2013) The importance of different spatial scales in determining structural and functional characteristics of deep-sea infauna communities. Biogeosciences 10:4547–4563. https://doi.org/10.5194/bg-10-4547-2013
Lagger C, Neder C, Merlo P, Servetto N, Jerosch K, Sahade R (2021) Tidewater glacier retreat in Antarctica: the table is set for fast-growing opportunistic species, is it? Estuar Coast Shelf Sci 260:107447. https://doi.org/10.1016/j.ecss.2021.107447
Lamont T, van den Berg MA, Tutt GCO, Ansorge IJ (2019) Impact of deep-ocean eddies and fronts on the shelf seas of a sub-Antarctic archipelago: the Prince Edward Islands. Cont Shelf Res 177:1–14. https://doi.org/10.1016/j.csr.2019.03.001
Lamont T, Tutt GCO, Barlow RG (2022) Phytoplankton biomass and photophysiology at the sub-Antarctic Prince Edward Islands ecosystem in the Southern Ocean. J Mar Syst 226:103669. https://doi.org/10.1016/j.jmarsys.2021.103669
Lombard AT, Reyers B, Schonegevel LY, Cooper J, Smith-Adao LB, Nel DC, Froneman PW, Ansorge IJ, Bester MN, Tosh CA, Strauss T, Akkers T, Gon O, Leslie RW, Chown SL (2007) Conserving pattern and process in the Southern Ocean: designing a marine protected area for the Prince Edward Islands. Antarct Sci 19:39–54. https://doi.org/10.1017/S0954102007000077
Long DJ, Baco AR (2014) Rapid change with depth in megabenthic structure-forming communities of the Makapu'u deep-sea coral bed. Deep Sea Res Part II Top Stud Oceanogr 99:158–168. https://doi.org/10.1016/j.dsr2.2013.05.032
López S, Turon X, Montero E, Palacín C, Duarte CM, Tarjuelo I (1998) Larval abundance, recruitment and early mortality in *Paracentrotus lividus* (Echinoidea). Interannual variability and plankton-benthos coupling. Mar Ecol Prog Ser 172:239–251. https://doi.org/10.3354/meps172239
Lutjeharms JRE, Valentine HR (1984) Southern ocean thermal fronts south of Africa. Deep Sea Res Part Oceanogr Res Pap 31:1461–1475. https://doi.org/10.1016/0198-0149(84)90082-7
Mackenzie CL, Kent FEA, Baxter JM, Gormley KSG, Cassidy AJ, Sanderson WG, Porter JS (2022) Genetic connectivity and diversity of a protected, habitat-forming species: evidence demonstrating the need for wider environmental protection and integration of the marine protected area network. Front Mar Sci 9:1
McGovern TM (2002) Patterns of sexual and asexual reproduction in the brittle star *Ophiactis savignyi* in the Florida Keys. Mar Ecol Prog Ser 230:119–126. https://doi.org/10.3354/meps230119
Metcalfe NB, Monaghan P (2003) Growth versus lifespan: perspectives from evolutionary ecology. Exp Gerontol 38:935–940. https://doi.org/10.1016/S0531-5565(03)00159-1
Murray JMH, Meadows A, Meadows PS (2002) Biogeomorphological implications of microscale interactions between sediment geotechnics and marine benthos: a review. Geomorphology 47:15–30. https://doi.org/10.1016/S0169-555X(02)00138-1
Olive PJW, Porter JS, Sandeman NJ, Wright NH, Bentley MG (1997) Variable spawning success of *Nephtys hombergi* (Annelida: Polychaeta) in response to environmental variation: a life history homeostasis? J Exp Mar Biol Ecol 215:247–268. https://doi.org/10.1016/S0022-0981(97)00047-6
Orsi AH, Whitworth T III, Nowlin WD Jr (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. Deep Sea Res Part Oceanogr Res Pap 42:641–673. https://doi.org/10.1016/0967-0637(95)00021-W
Pakhomov EA, Chown SL (2003) The Prince Edward Islands: Southern Ocean Oasis†. Ocean Yearb Online 17:348–379. https://doi.org/10.1163/221160003X00140
Pakhomov EA, Ansorge IJ, Froneman PW (2000) Variability in the inter-island environment of the Prince Edward Islands (Southern Ocean). Polar Biol 23:593–603. https://doi.org/10.1007/s003000000125
Puccinelli E, McQuaid CD, Noyon M (2016) Spatio-temporal variation in effects of upwelling on the fatty acid composition of benthic filter feeders in the Southern Benguela Ecosystem: not all upwelling is equal. PLoS ONE 11:e0161919. https://doi.org/10.1371/journal.pone.0161919
Puccinelli E, McQuaid CD, Ansorge IJ (2018) Factors affecting trophic compositions of offshore benthic invertebrates at a sub-Antarctic archipelago. Limnol Oceanogr 63:2206–2228. https://doi.org/10.1002/lno.10934
Puccinelli E, Smart SM, Fawcett SE (2020) Temporal variability in the trophic composition of benthic invertebrates in the Indian sub-Antarctic ocean. Deep Sea Res Part Oceanogr Res Pap 163:103340. https://doi.org/10.1016/j.dsr.2020.103340
Puerta P, Johnson C, Carreiro-Silva M, Henry L-A, Kenchington E, Morato T, Kazanidis G, Rueda JL, Urra J, Ross S, Wei C-L, González-Irusta JM, Arnaud-Haond S, Orejas C (2020) Influence of water masses on the biodiversity and biogeography of deep-sea benthic ecosystems in the North Atlantic. Front Mar Sci 7
Ramirez-Llodra E, Brandt A, Danovaro R, De Mol B, Escobar E, German CR, Levin LA, Martinez Arbizu P, Menot L, Buhl-Mortensen P, Narayanaswamy BE, Smith CR, Tittensor DP, Tyler PA, Vanreusel A, Vecchione M (2010) Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. Biogeosciences 7:2851–2899. https://doi.org/10.5194/bg-7-2851-2010
Reisinger RR, Raymond B, Hindell MA, Bester MN, Crawford RJM, Davies D, de Bruyn PJN, Dilley BJ, Kirkman SP, Makhado AB, Ryan PG, Schoombie S, Stevens K, Sumner MD, Tosh CA, Wege M, Whitehead TO, Wotherspoon S, Pistorius PA (2018) Habitat modelling of tracking data from multiple marine predators identifies important areas in the Southern Indian Ocean. Divers Distrib 24:535–550. https://doi.org/10.1111/ddi.12702
Rexer-Huber K, Veale AJ, Catry P, Cherel Y, Dutoit L, Foster Y, McEwan JC, Parker GC, Phillips RA, Ryan PG, Stanworth AJ, van Stijn T, Thompson DR, Waters J, Robertson BC (2019) Genomics detects population structure within and between ocean basins in a circumpolar seabird: the white-chinned petrel. Mol Ecol 28:4552–4572. https://doi.org/10.1111/mec.15248
Román S, Lins L, Ingels J, Romano C, Martin D, Vanreusel A (2019) Role of spatial scales and environmental drivers in shaping nematode communities in the Blanes Canyon and its adjacent slope. Deep Sea Res Part Oceanogr Res Pap 146:62–78. https://doi.org/10.1016/j.dsr.2019.03.002
Rosli N, Leduc D, Rowden AA, Probert PK (2018) Review of recent trends in ecological studies of deep-sea meiofauna, with focus on patterns and processes at small to regional spatial scales. Mar Biodivers 48:13–34. https://doi.org/10.1007/s12526-017-0801-5
Sokolov S, Rintoul SR (2007) On the relationship between fronts of the Antarctic Circumpolar Current and surface chlorophyll concentrations in the Southern Ocean. J Geophys Res Oceans 112:C07030. https://doi.org/10.1029/2006JC004072

Stirnimann L, Bornman TG, Verheye HM, Bachèlery M-L, van der Poel J, Fawcett SE (2021) Plankton community composition and productivity near the Subantarctic Prince Edward Islands archipelago in autumn. Limnol Oceanogr 66:4140–4158. https://doi.org/10.1002/lno.11949

Sweetman AK, Thurber AR, Smith CR, Levin LA, Mora C, Wei C-L, Gooday AJ, Jones DOB, Rex M, Yasuhara M, Ingels J, Ruhl HA, Frieder CA, Danovaro R, Würzberg L, Baco A, Grupe BM, Pasulka A, Meyer KS, Dunlop KM, Henry L-A, Roberts JM (2017) Major impacts of climate change on deep-sea benthic ecosystems. Elem Sci Anthr 5:4. https://doi.org/10.1525/elementa.203

Treasure AM, Ruzicka JJ, Pakhomov EA, Ansorge IJ (2019) Physical transport mechanisms driving sub-Antarctic island marine ecosystems. Ecosystems 22:1069–1087. https://doi.org/10.1007/s10021-018-0326-1

Trebilco R, Melbourne-Thomas J, Constable AJ (2020) The policy relevance of Southern Ocean food web structure: Implications of food web change for fisheries, conservation and carbon sequestration. Mar Policy 115:103832. https://doi.org/10.1016/j.marpol.2020.103832

von der Meden CEO, Atkinson LJ, Branch GM, Asdar S, Ansorge IJ, van den Berg M (2017) Long-term change in epibenthic assemblages at the Prince Edward Islands: a comparison between 1988 and 2013. Polar Biol 40:2171–2185. https://doi.org/10.1007/s00300-017-2132-1