

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

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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.

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. 2015; Carpenter-Kling et al. 2019). The PEIs form an archipelago that comprises Marion Island and Prince Edward Island, 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 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 (Stirnemann 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., 10s 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 and terrestrial species, as well as for the formulation of relevant guidelines for the conservation and management of this region.

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

MATERIAL 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 Prince Edward Island, 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 105–286 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 x 100 cm and a mesh size of 1 cm², 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, Bryozoans, Hydrozoans, 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.

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 Prince Edward Islands.

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

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 Prince Edward Islands.

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

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; $n = 3$), and year of collection (factor *Time*, 2016, 2017; $n = 2$) 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 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* and *Time* on the species richness, H' and J', using a factorial analysis of variance (ANOVA). Additionally, we tested for variations among regions in the abundances of the most ubiquitous taxa, which included ophiuroids, the polychaete *Lanice marionensis*, the brachiopod *Aerothyris kerguelensis*, and the serpulid polychaete *Serpula vermicularis*. 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 & 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*, 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* x *Region*, with samples from upstream- 2016 having a lower H' than upstream- 2017 (2.7 ± 0.2 vs. 3.7 ± 0.2), while no other significant effects were recorded for the other regions/years. Pielou's Evenness Index (J') averaged 0.9 ± 0.0 and did not vary as a function of year nor region ($p > 0.05$). 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*, the brachiopod *A. kerguelensis*, and several species of the colonial groups bryozoa (*Osthimosia bicornis*, *Reteporella flabellate*, *Tervia irregularis*), hydrozoa (*Staurotheca dichotoma*) and porifera (*Acanthella erecta*; Table S.1). The Ophiuroidea *Ophiocten amitinum* and *Ophioplinthus intorta* 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 one year in comparison to the next, linked for instance to variability in substratum type and/or 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 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 ophiuroids *Ophiolimna antarctica*. Generally, ophiuroids (i.e., *O. antarctica*, *Ophiosabine vivipara*, *Ophioplithus intorta*, *Ophiocten amitinum*) 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 (Table S.1, Fig S.2). The analyses indicated that there was no effect of the factor *Region* ($p > 0.05$), but a significant effect of *Year* ($p < 0.05$), with abundance generally increasing from 2016 to 2017. 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; Lager 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 focussing 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). As such substratum type can represent the main factor explaining the pattern observed.

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 of these 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.

Declarations

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Competing Interests

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.

Author contributions

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

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 DOI:10.25850/nioz/7b.b.mf.

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 Affairs of South Africa (now Department of Forestry, Fisheries, and the Environment).

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Figures

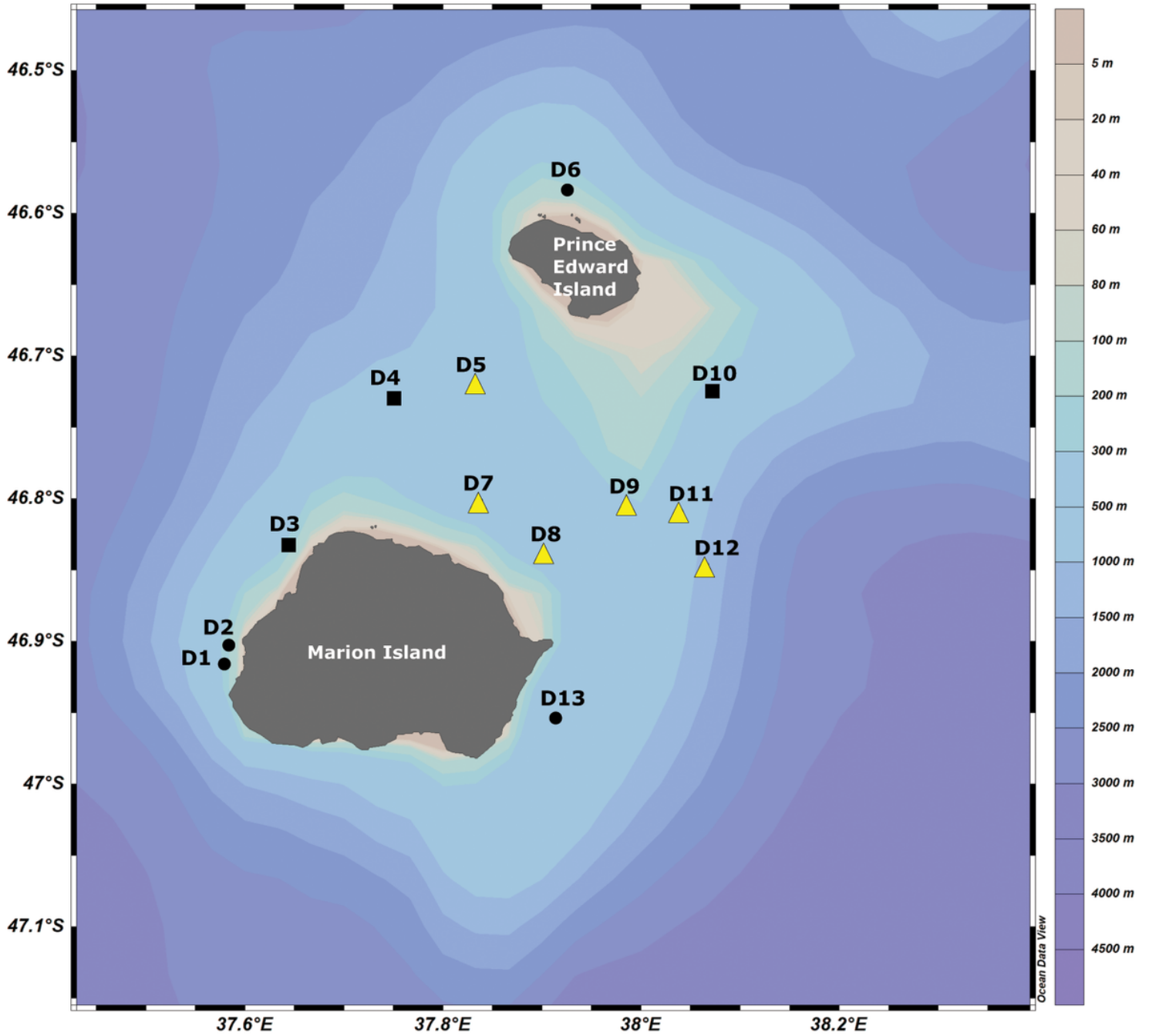


Figure 1

Map of the study area indicating the location of the dredge stations sampled in the proximity to the Prince Edward Islands. The shape of the symbols indicates the year of collection: 2016 only (black circle), 2017 only (black square), and both years (yellow triangle).

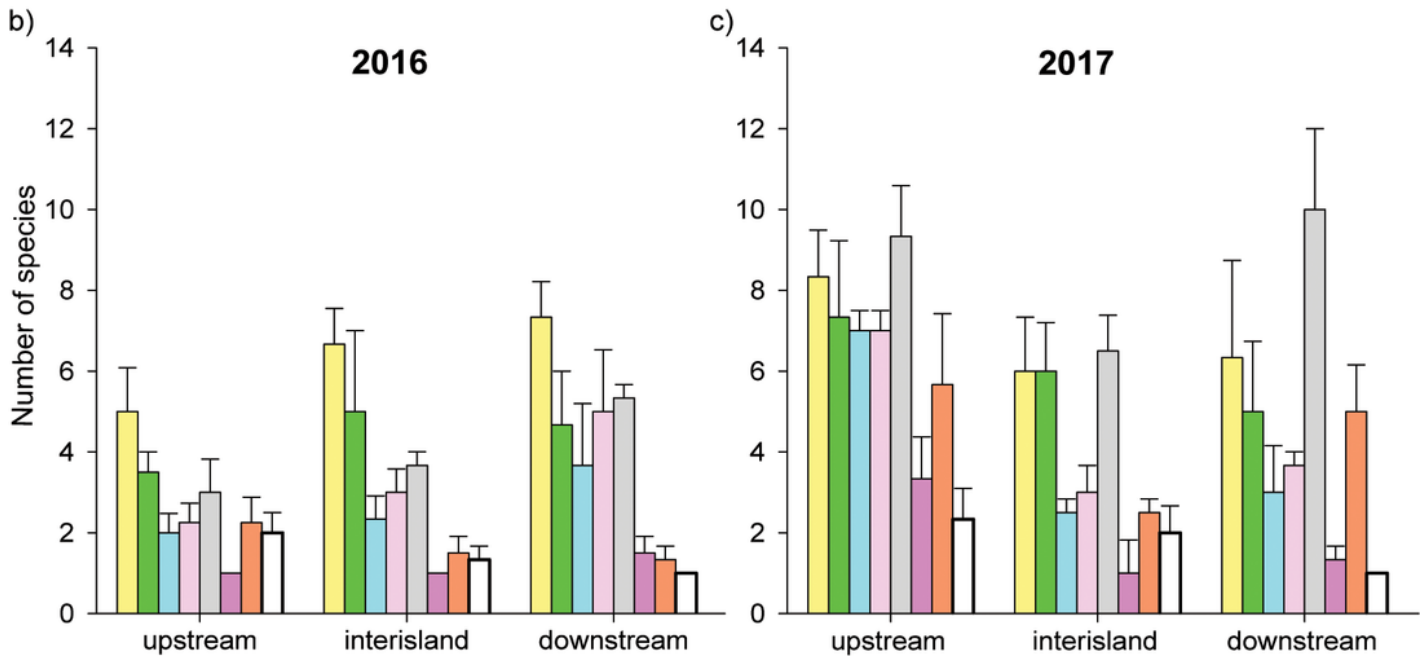
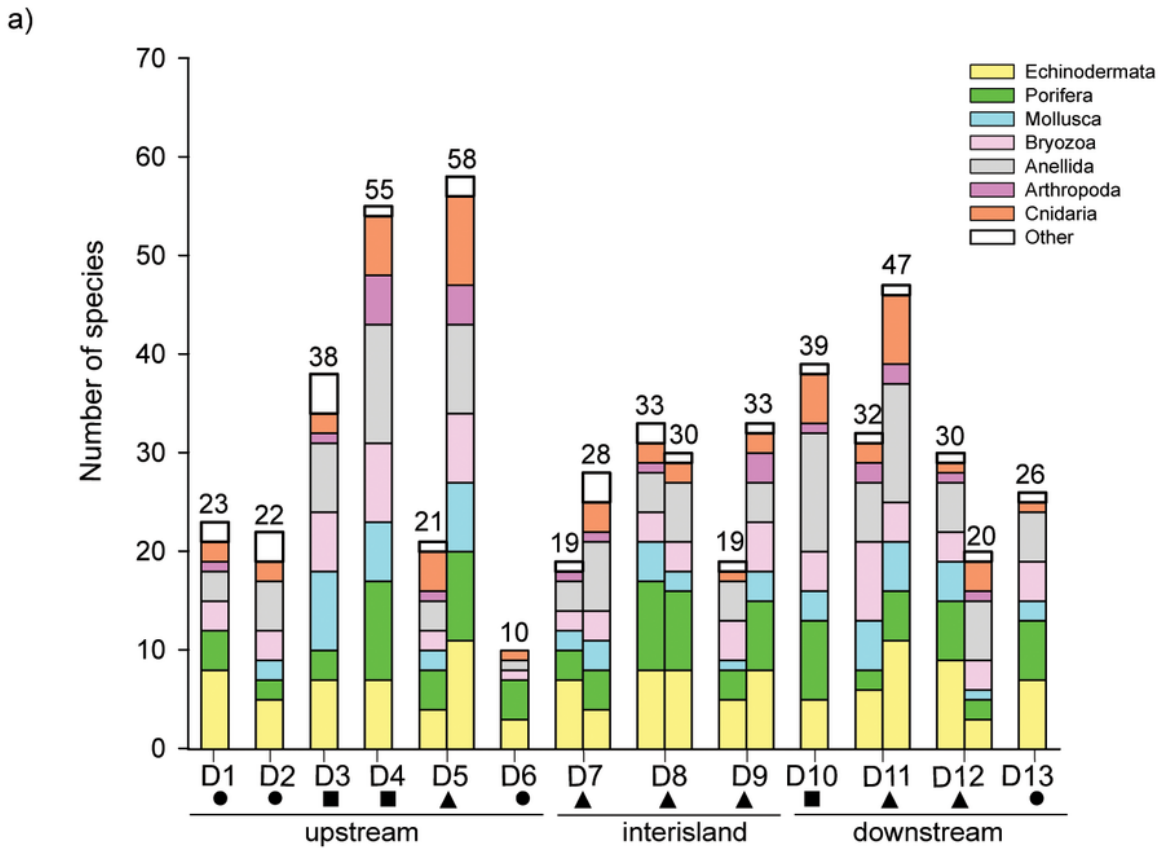


Figure 2

Number of species of the most abundant phyla collected from stations located in the upstream, interisland, and downstream regions of the Prince Edward Islands in 2016 and 2017. Values represent abundance for 500 m² 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 \pm standard error of number of species

from the most abundant phylum 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.

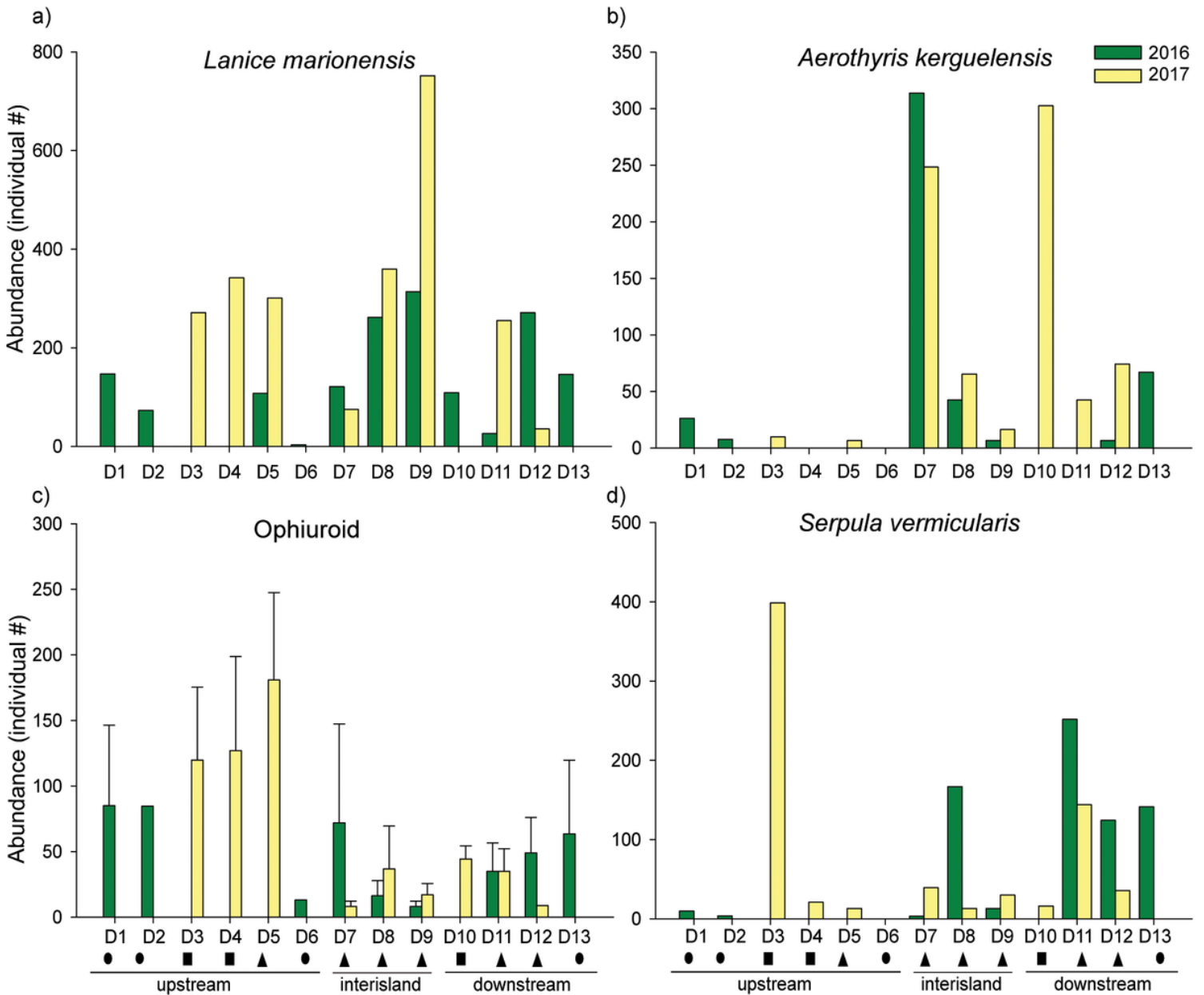


Figure 3

Abundance of the polychaete a) *Lanice marionensis*, brachiopod b) *Aerothyris kerguelensis*, c) ophiuroids (i.e., *O. 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 Prince Edward Islands in 2016 and 2017. Values represent abundance for 500 m² 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.

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