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Are abyssal scavenging amphipod assemblages linked to climate cycles?

Tammy Horton[a,*], Michael H. Thurston[a], Rianna Vlierboom[b,c], Zoe Gutteridge[b,d], Corinne A. Pebody[a], Andrew R. Gates[a], Brian J. Bett[a]

[a] *National Oceanography Centre, Southampton, European Way, Southampton SO14 3ZH, UK*
[b] *School of Ocean and Earth Science, University of Southampton Waterfront Campus, European Way, Southampton SO14 3ZH, UK*
[c] *Eurofins Aquasense, H.J.E. Wenckebachweg 120, 1114 AD Amsterdam-Duivendrecht, the Netherlands*
[d] *Environment Agency, Bromholme Lane, Brampton, Cambridgeshire PE28 4NE, UK*

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ABSTRACT

Scavenging amphipods are a numerically dominant and taxonomically diverse group that are key necrophages in deep-sea environments. They contribute to the detrital food web by scavenging large food-falls and provide a food source for other organisms, at bathyal and abyssal depths. Samples of this assemblage have been collected at the Porcupine Abyssal Plain Sustained Observatory (PAP-SO) in the North Atlantic (48°50′N 16°30′W, 4850 m) for > 30 years. They were collected by means of baited traps between 1985 and 2016, covering a period of well-characterised changes in the upper ocean. From the 19 samples analysed, a total of 16 taxa were identified from 106,261 specimens. Four taxa, *Abyssorchomene chevreuxi* (Stebbing, 1906), *Paralicella tenuipes* Chevreux, 1908, *P. caperesca* Shulenberger & Barnard, 1976, and *Eurythenes* spp., dominated catches and were present in all samples.

The dominant species varied in time with *P. tenuipes* typically dominant early in the time series (1985–1997) and its congener, *P. caperesca*, typically dominant later (2011–2016). Amphipod faunal composition exhibited a significant correlation with the Atlantic Multi-decadal Oscillation (AMO).

Amphipod diversity was significantly lower in years with higher estimated volumetric particle flux at 3000 m. Species richness varied significantly between AMO phases, with higher values during ‘cool’ phase.

Our results suggest a ‘regime shift’ in scavenging amphipod communities following a ‘regime shift’ in surface ocean conditions driven by a phase shift in Atlantic climate (from cool to warm AMO). This shift manifests itself in a remarkable change in dominant species, from obligate necrophages such as *Paralicella* spp., with semelparous reproduction to *Abyssorchomene* spp. which have a more varied diet and iteroparous reproduction, and are thus potentially more able to take advantage of greater or varied food availability from increased organic matter flux to the abyssal seafloor.

1. Introduction

Necrophagous amphipods are important components of the deep-sea ecosystem owing to their contribution to the detrital food web through the scavenging of large food-falls (Thurston, 1990; Nygard et al., 2012; Havermans et al., 2013; Duffy et al., 2013). Through the consumption and fragmentation of these large food-falls (e.g. marine mammals and fish), they recycle and disperse nutrients at the seabed (Horton et al., 2013). Large nekton falls are a sporadic source of nutrients, and studies of the feeding methods of scavenging amphipods have shown that many species are also capable of preying upon benthic organisms and consuming the export flux of detritus from the upper ocean (Havermans and Smetacek, 2018).

Scavenging amphipods provide a food source for other organisms, and are thus a vital component of secondary production cycles, acting as a link between scavenging and predatory food webs at abyssal and bathyal depths (Thurston, 1979; Stockton and DeLaca, 1982; Jones et al., 1998; Higgs et al., 2014). In abyssal habitats globally, necrophagous amphipods from the superfamilies Lysianassoidea and Alicelloidea dominate both numerically and taxonomically, and are readily sampled using baited traps (Wolff, 1971; Smith, 1985; Thurston, 1990; Janßen et al., 2000; De Broyer et al., 2004).

The importance of necrophagous amphipods in deep-sea food webs was not appreciated initially because of their rarity in benthic and suprabenthic trawl catches (Thurston, 1990; De Broyer et al., 2004). The presence of hundreds of individuals in a single trap sample led Thurston

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[*] Corresponding author.
E-mail address: tammy.horton@noc.ac.uk (T. Horton).

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(1979) to suggest that this apparent rarity was likely to be a result of their well-developed swimming ability (Laver et al., 1985; Sainte-Marie, 1986; Takeuchi and Watanabe, 1998; Ide et al., 2007), allowing them to evade slow-moving trawls and sledges. The use of baited traps in the deep sea has a long history. Traps were deployed as early as 1888 from the *Hirondelle* during an expedition of the Prince of Monaco, and between 1892 and 1912, 21 deployments of baited traps deeper than 3000 m were undertaken (Richard, 1934). After these early studies, it was not until the advent of more advanced technology, that the use of baited cameras revealed an active guild of mobile scavengers comprised largely of crustaceans and fish (Isaacs, 1969; Hessler et al., 1972). Baited traps are now used commonly to study the necrophagous guild in the deep sea, but despite this, few studies have analysed replicate baited trap samples for species composition at depths greater than 2000 m, especially over extended time series.

In the North Atlantic Ocean, Desbruyères et al. (1985) examined catches from 62 trap-sets from eight stations at depths of 230–4700 m in the Bay of Biscay, Thurston (1990) analysed 44 traps taken over a wide latitudinal and bathymetric range (8–50°N, 3144–5940 m), and reported a degree of faunal homogeneity across six abyssal plains. In contrast, Christiansen (1996) sampled three localities along longitude 20°W (34°, 47° and 59°N, ~3000–5100 m) and found the northern station to be isolated from those further to the south. Duffy et al. (2012) explored catches from eight traps set in the canyons off Portugal at 3194–4445 m, and Horton et al. (2013) studied the scavenging amphipod faunal composition at a single depth (2500 m) on the Mid-Atlantic Ridge, by fully analysing 12 trap samples taken over a 4-year time span. Other studies in the North Atlantic include those of Wickens (1983) and Jones et al. (1998).

Replicate baited traps from other regions have been analysed including the Mediterranean Sea (Albertelli et al., 1992, 6 traps at 1845–4505 m), the Gulf of Mexico (Escobar-Briones et al., 2010, 5 traps at 3308–3732 m), the South Atlantic Ocean (Duffy et al., 2016, 10 traps at 482–2073 m), the Arabian Sea (Janßen et al., 2000, 4 traps at 3190–4420 m; Treude et al., 2002, 5 traps at 1908–4420 m), the North Pacific Ocean (Shulenberger and Hessler, 1974, 2 traps at 5720 m; Shulenberger and Barnard, 1976, 2 traps at 5700 m; Hessler et al., 1978, 2 traps at 9605–9806 m; Ingram and Hessler, 1983, more than 20 traps at 5623–6018 m; Wilson et al., 1985, 27 traps at 1284–2970 m; France, 1993, 5 traps at 7218–9604 m; Shi et al., 2018, 4 traps at 6990–10840 m), the South Pacific Ocean (Thurston, 1999, 6 traps at 7800 m; Blankenship et al., 2006, 13 traps at 5515–10787 m; Jamieson et al., 2011, 7 traps at 4329–7966 m; Jamieson et al., 2013a, 2 traps at 6265–7000 m; Fujii et al., 2013, 5 traps at 4602–8074 m; Eustace et al., 2016, 5 traps at 4602–8074 m; Lacey et al., 2016, 43 traps at 1488–9908 m; Lacey et al., 2018, 31 traps at 1490–9908 m; Wilson et al., 2018, 7 traps, 6253–10817 m), the Arctic Ocean (Premke et al., 2006, 6 traps at 1468–2644 m) and the Southern Ocean (De Broyer et al., 2004, 31 traps at 171–3739 m; Cousins et al., 2013, 6 traps at 4161–4192 m). While replicate studies of scavenging amphipods have been carried out, often they have been limited in scope, aiming generally to make spatial comparisons between regions, or trenches, or across a depth range. Long-term studies of scavenging amphipods at a single abyssal site have never been undertaken.

The structure of scavenging amphipod assemblages is known to vary with water depth, latitude, and productivity regime (Christiansen, 1996; Christiansen and Martin, 2000; Blankenship et al., 2006; Jamieson et al., 2011; Duffy et al., 2012; Horton et al., 2013; Lacey et al., 2016). Latitudinal differences in the assemblage structure of scavenging amphipods at abyssal depths in the northeast Atlantic (Christiansen, 1996) reflected the trend reported for the ichthyofauna and the megafauna (Merrett, 1987; Thurston et al., 1995; Merrett and Fasham, 1998). These trends have been linked to the productivity of surface waters, with higher abundances and lower species diversities under eutrophic conditions when compared with oligotrophic areas. Surface productivity may have an indirect influence on the amount of food available to necrophages (Christiansen and Martin, 2000). Areas with high productivity are associated with a greater abundance of organisms in the upper ocean, which will likely result in a greater concentration of food-falls available to necrophages on the sea floor (Neilsen and Gosselin, 2011; Higgs et al., 2014). Increased discards from commercial fishing activities have also been postulated to have the potential to affect populations of scavengers at depth (Havermans and Smetacek, 2018). This increased availability of food to necrophages has been linked to higher abundances of scavengers at eutrophic sites. Drazen et al. (2012) showed a positive correlation between populations of scavenging deep-sea demersal grenadiers and pelagic Pacific hake populations, the latter being the target of the largest commercial fishery in the region.

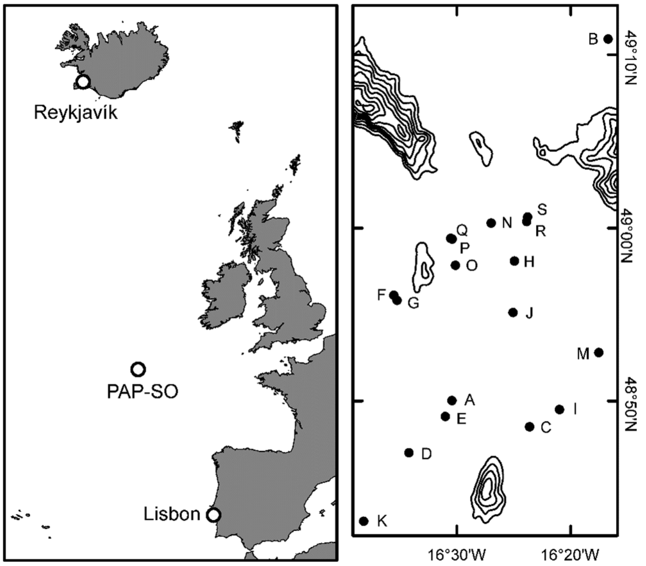

Fig. 1. Left, NE Atlantic, indicating position of the Porcupine Abyssal Plain Sustained Observatory (PAP-SO) and the monitoring sites for the Hurrell North Atlantic Oscillation Station-Based index (Lisbon, Reykjavik). Right, Estimated seafloor locations of amphipod traps deployed on the Porcupine Abyssal Plain, see Table 1 for sample detail by letter code (A-S). Abyssal hills in the area are indicated with 100 m-interval bathymetric contours, where 4800 m is the base contour. (WGS84 datum, Mercator projection).

The Porcupine Abyssal Plain Sustained Observatory (PAP-SO), situated in the subpolar Northeast Atlantic, at 48°50′N 16°30′W and a water depth of 4850 m (Fig. 1), is a key site for the long-term study of the deep ocean. Operations at the PAP-SO aim to reveal links between the atmosphere (e.g. CO_2), the upper ocean (phytoplankton and zooplankton), the deep ocean (carbon flux), and the deep-sea floor, including its resident animal population (Hartman et al., 2012). The PAP-SO site has been subject to long-term observations since it was first sampled in 1985 (Thurston, 1986). Subsequently, sampling at the site became more frequent through the Joint Global Ocean Flux Study (JGOFS) in 1989 (Lampitt et al., 2010a), and was intensively researched during the EU "High-resolution temporal and spatial study of the BENthic biology and Geochemistry of a northeastern Atlantic abyssal Locality" project (BENGAL, Billett and Rice, 2001) which focussed on temporal changes in benthic biology and geochemistry. Since 1989, this abyssal study site has become a major focus for international and interdisciplinary scientific research and monitoring including water column biogeochemistry, physics and benthic biology. It forms part of several collaborative efforts to enhance broader scale ocean observing (e.g. the OceanSITES component of the Global Ocean Observing System (GOOS)) and is a key site in the Integrated Carbon Observing System (ICOS) and European Multidisciplinary Seafloor and water column Observatory (EMSO), both European Research Infrastructure Consortia (ERIC). This region of the North Atlantic has been noted for interannual and seasonal variations in the carbon flux reaching the abyssal seafloor (Lampitt et al., 2010b). The PAP-SO study area is predominantly a relatively uniform abyssal plain environment, punctuated by the presence of abyssal hills. These features can have a strong influence on food availability and therefore species abundance and biomass (Durden et al., 2015; Durden et al., this issue).

Previous time-series studies at the PAP-SO have noted widespread, substantial changes in the abundance, biomass, diversity and ecosystem functioning of the meio- (protist and metazoan), macro-, and megafaunal components of the benthos (Billett et al., 2001, 2010; Gooday et al., 2010; Kalogeropoulou et al., 2010; Soto et al., 2010). This change was initially most evident among two small holothurian species, *Amperima rosea* (Perrier, 1886) and *Ellipinion molle* (Théel, 1879), and was thought to be linked to inter-annual or longer-term change in the flux of organic matter to the seafloor (Billett et al., 2001). The former species subsequently provided a name for this temporal change in the benthos, an "*Amperima* event", the initial event having been noted in data from 1996, with a subsequent event suggested in 2002 data (Billett et al., 2010). Again, a potential link to temporal change in the quantity or quality (biochemical composition) of detrital flux to the abyssal plain was suggested, with possible supporting evidence derived from studies of holothurian reproduction and nutritional biochemistry (Kiriakoulakis et al., 2001; Wigham et al., 2003a, b; Ramirez-Llodra et al., 2005; FitzGeorge-Balfour et al., 2010). In a joint assessment of long-term time-series observations at the PAP-SO and similar studies at Station M in the NE Pacific (Smith et al., 2020), Smith et al. (2009) indicated the potential for climate-driven change in surface ocean communities to have a rapid impact on the abyssal benthos. The latter authors suggested connections between climate indices, the Northern Oscillation Index (NOI) at Station M and the North Atlantic Oscillation (NAO) index at PAP-SO, deep water column fluxes of organic matter, and temporal change in deep-seafloor communities. Smith et al. (2009) further noted the doubling in abundance of the scavenging macrourids *Coryphaenoides armatus* (Hector, 1875) and *C. yaquinae* Iwamoto and Stein, 1974 at Station M and potential linkage with changing epipelagic carrion supply as influenced by commercial fishing and climate variation (Bailey et al., 2006; Drazen et al., 2008).

Given the established major changes in the benthos of the PAP-SO (*Amperima* events) and their possible connection to temporal variations in the flux of organic matter to the seafloor, and the potential occurrence of similar responses in the scavenging fish population at Station M, here we examine (a) long-term change in the PAP-SO scavenging amphipod assemblage, and corresponding change in (b) the flux of organic matter to the seafloor and (c) potentially related climate indices. The amphipod dataset represents the longest duration biological observation series at the PAP-SO, having been initiated in 1985 (Thurston, 1986) and continuing to the present day (Hartman, 2019), it may therefore have the greatest power to detect climate-driven secular change at the abyssal seafloor.

2. Material and methods

2.1. Study area

All samples were collected from the Porcupine Abyssal Plain Sustained Observatory (PAP-SO) area (Hartman et al., 2012) having a nominal central location of 48°50′N 16°30′W and water depth of 4850 m (Billett and Rice, 2001; Fig. 1). Full station information for the scavenging amphipod samples used in this contribution is provided in Table 1. The centroid of the sampled locations was 48°56′N 16°28′W, with all samples recovered from within 32 km of that position, and the majority (15 of 19) from within 15 km of the centroid. Recorded water depth at time of trap deployment ranged from 4839 to 4851 m, consistent with the level-bottom seafloor environment of the abyssal plain in this area. Fig. 1 shows the estimated seafloor locations of the amphipod traps and the general bathymetry of the area.

2.2. Sample collection

Nineteen samples, collected using a variety of freefall trap-rigs set between the years 1985 and 2016, were selected for this study. These include samples from purpose-designed amphipod trap systems and from opportunistic additions of traps to other benthic lander systems (section 2.2.1). Additional necrophagous amphipod samples have been collected from the PAP-SO area during this period. For the purposes of this study we rejected samples on two conditions: (i) deployments returning with very low numbers of specimens on the grounds that they would not adequately represent species diversity or species composition; in the present study the minimum number of individuals per deployment was 208 (sample R; Table 3a); (ii) deployments of exceptionally long durations (referred to as soak times), on the grounds that within-trap predation, and/or temporal succession may have resulted in substantial modification of diversity and composition characteristics. In the present study the maximum soak time was 104 h (sample G; Table 1). All of the samples included in the present analyses were derived from baited traps (Section 2.2.1), deployed on a ballasted seafloor-landing frame, equipped with an acoustic release unit and buoyancy to enable subsequent recovery of the trap system (see e.g. Jamieson et al., 2013b; Jamieson, 2016).

2.2.1. Trap types

The earliest trap design, employed at the PAP-SO in 1985 and 1986 and described as the *Cyana* amphipod trap (Thurston, 1986), was a system of two benthic traps (only one trap used in 1986) in a rectangular frame about 1000 mm long by 800 mm wide by 800 mm high. The system delivered pumped odour-laden seawater to the traps. One of the two traps contained the bait container (Table 1; Thurston, 1986; Roe, 1987). The benthic traps measured 500 × 500 × 200 mm, had a solid top and bottom, and four walls each with a large rectangular window into which was fitted a 500 µm mesh funnel with a 40 × 40 mm aperture (Fig. 2A, denoted MAR). In operation, the trap apertures would be located within 50 cm of the seafloor. A cylindrical bait container of 10 mm mesh was located centrally in the trap. Bait consisted of two whole mackerel (*Scomber scombrus*) one of which was wrapped in muslin.

For samples collected in 1991, 1994, 1996, and 1997, the *Cyana* amphipod trap system was reconfigured and renamed the DE-rated Mark And Recapture system (denoted DEMAR in Table 1; Fig. 2A), with the addition of a suprabenthic trap with apertures located 100 cm from the seafloor in operation. The suprabenthic trap consisted of a cylinder, 725 mm in length and 300 mm internal diameter, with mesh funnel entrances (45 mm diameter final aperture) at each end and was baited with a single muslin wrapped mackerel.

In 1997, in addition to the DEMAR traps, deployments were made using traps attached to a Royal Netherlands Institute for Sea Research (NIOZ) benthic lander (Rice, 1997; Witbaard et al., 2000). These comprised three simple baited pipe traps attached to the lander at 50, 100, and 200 cm above the seafloor in operation. The traps were cylindrical, 40 cm in length and 7 cm in internal diameter, with slot like apertures of order 15 × 60 mm.

Since 2011, a new amphipod trap system has been in use (denoted AMPHIPOD TRAP in Table 1; Fig. 2B) comprising four traps on one rig; two benthic and two suprabenthic traps set at 90°to each other. Each trap is a cylinder, 500 mm in length and 290 mm internal diameter, with a double funnel entrance (45 mm then 35 mm apertures) at one end, baited with a single mackerel. This system was successfully deployed at the PAP-SO in 2011, 2012, 2013, and 2016 (Table 1; Ruhl, 2012; Lampitt, 2013; Lampitt, 2014; Stinchcombe, 2017).

The trap systems were launched, buoyancy first, with the frame hung over the stern on a crane and released with a slip hook. Ideally the system was left *in situ* for 24 h, but soak times varied widely (6–104 h) owing to ship schedule constraints and weather conditions. There is a large gap from 1997 until 2011 during which no trap samples were

Table 1
Station data for scavenging amphipod samples collected from the Porcupine Abyssal Plain Sustained Observatory area between 1985 and 2016. Samples are coded A-S, with locations shown in Fig. 1.

Sample Code	Station Number	Date	Latitude	Longitude	Water depth (m)	Soak time (h)	Bait type	Trap type
A	52216#5	23/06/1985	48° 50.0′ N	016° 30.4′ W	4842	35	Chopped fish (unspecified)	Mark & Recapture System[c]
B	52403#20	08/12/1986	49° 10.9′ N	016° 16.7′ W	4849	17	1 × Abyssal grenadier[a]	Mark and Recapture System[c]
C	52701#35	22/05/1991	48° 48.5′ N	016° 23.6′ W	4843	20	2 × Mackerel[b] (in mesh cage)	DEMAR design[c]
D	53201#18	12/04/1994	48° 47.0′ N	016° 34.2′ W	4846	15	2 × Mackerel[b] (in mesh cage)	DEMAR design[c]
E	53201#25	14/04/1994	48° 49.1′ N	016° 31.0′ W	4844	26	2 × Mackerel[b] (in mesh cage)	DEMAR design[c]
F	12930#83	18/09/1996	48° 56.1′ N	016° 35.5′ W	4839	14	2 × Mackerel[b] (in mesh cage)	DEMAR design[c]
G	13077#4	14/03/1997	48° 55.8′ N	016° 35.2′ W	4844	104	3 × Mackerel[b] (3 traps)	Pipe traps on NIOZ Lander
H	13077#35	19/03/1997	48° 58.1′ N	016° 24.9′ W	4845	84	3 × Mackerel[b] (3 traps)	Pipe traps on NIOZ Lander
I	13077#92	27/03/1997	48° 49.5′ N	016° 21.0′ W	4844	21	2 × Mackerel[b] (in mesh cage)	DEMAR design[c]
J	13078#14	01/04/1997	48° 55.1′ N	016° 25.1′ W	4845	13	2 × Mackerel[b] (in mesh cage)	DEMAR design[c]
K	13078#22	03/04/1997	48° 43.0′ N	016° 38.2′ W	4842	6	2 × Mackerel[b] (in mesh cage)	DEMAR design[c]
L	JC062#063	08/08/2011	49° 05.3′ N	016° 40.0′ W	4848	27	1 × Mackerel[b] per trap (4 total)	AMPHIPOD TRAP
M	JC062#072	10/08/2011	48° 52.8′ N	016° 17.5′ W	4851	30	1 × Mackerel[b] per trap (4 total)	AMPHIPOD TRAP
N	JC071#020	04/05/2012	49° 00.3′ N	016° 27.0′ W	4847	17	1 × Mackerel[b] per trap (4 total)	AMPHIPOD TRAP
O	JC071#034	05/05/2012	48° 57.8′ N	016° 30.1′ W	4846	40	1 × Mackerel[b] per trap (4 total)	AMPHIPOD TRAP
P	JC085#010	21/04/2013	48° 59.4′ N	016° 30.5′ W	4840	23	1 × Mackerel[b] per trap (4 total)	AMPHIPOD TRAP
Q	JC085#019	22/04/2013	48° 59.4′ N	016° 30.4′ W	4843	62	1 × Mackerel[b] per trap (4 total)	AMPHIPOD TRAP
R	DY050#27	25/04/2016	49° 00.4′ N	016° 23.8′ W	4850	26	1 × Mackerel[b] per trap (4 total)	AMPHIPOD TRAP
S	DY050#100	02/05/2016	49° 00.6′ N	016° 23.8′ W	4850	24	1 × Mackerel[b] per trap (4 total)	AMPHIPOD TRAP

[a] *Coryphaenoides armatus*.
[b] *Scomber scombrus*.
[c] Considered to be the same in subsequent analyses.

collected. This gap represents the retirement of one of the authors (MHT), and a later continuation of the time series. There are some replicate samples (years 1994, 1997, 2011, 2012, 2013, 2016), with the current aim being to collect two replicate samples each year.

2.2.2. *Sample processing*

On recovery of the trap samples, specimens were fixed in either 100% ethanol or borax-buffered 4% formaldehyde. Formaldehyde-fixed material was transferred to 80% industrial methylated spirit solution on return to the laboratory. All amphipod specimens were identified to the species level except for specimens in the genus *Eurythenes*. As detailed by Horton et al. (2020a, this issue) the genus *Eurythenes* is now known to comprise four distinct species at the PAP-SO. *Eurythenes* species are therefore enumerated at the genus level. Species names and authorities have been checked with the World Amphipoda Database (Horton et al., 2020b). Specimens without binomial names are given a code to facilitate later referencing.

Although benthic and suprabenthic traps have been used, the specimen numbers for each of the traps in each trap-set were combined to produce a single count for each station.

The samples collected in 2011 (samples L and M) contained some four to five times as many specimens as the next largest sample (Table 3a) and were considered too large to sort in totality. These samples were split using a MOTODA plankton splitter (Motoda, 1959). In each case 1/8th (2 × 1/16th) of the original sample was enumerated and used to calculate the total sample size according to the methods in Dahiya (1980) and Griffiths et al. (1984). Specimens of *Eurythenes* could be identified easily by their large size when compared to other amphipod specimens present in the sample (Supplementary Fig. 7). Such a disparity in size could affect the performance of the splitter by causing the sample to clump (Griffiths et al., 1984). Prior to sample splitting, all *Eurythenes* spp. specimens were removed, and fully enumerated, to avoid the potential interference of these large specimens in the splitting process. Specimens are stored in the Discovery Collections at the National Oceanography Centre (DISCOLL, NOC, UK; https://www.gbif.org/grscicoll/institution/74ae2bc3-e5a8-443f-bc8b-89cc223500d1). The raw data can be downloaded from the Ocean Biogeography Information System (OBIS) at: http://ipt.iobis.org/obis-deepsea/resource?r=pap_scavenging_amphipods.

2.3. *Assessment of species diversity and composition*

Amphipod trap sample diversity was examined by the rarefaction and extrapolation of Hill numbers ^0D, ^1D, and ^2D, respectively species richness, the exponential form of the Shannon index, and the inverse

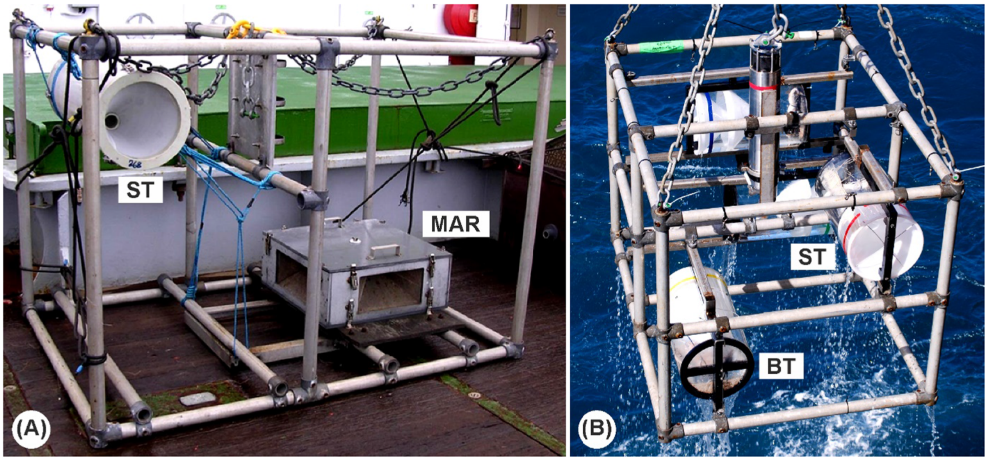

Fig. 2. Amphipod trap type. (A) DE-rated Mark & Recapture (DEMAR) system, carrying original mark and recapture trap (MAR) and suprabenthic trap (ST) used for samples collected between 1991 and 1997. (B) Currently operated AMPHIPOD TRAP system used since 2011, carrying two benthic traps (BT) and two suprabenthic traps (ST) set at 90° to each other.

form of Simpson's index (Hill, 1973; Chao et al., 2014). The analyses were carried out using the methodology described by Hsieh et al. (2016) as implemented in the R computing environment (version 3.6.0; R Core Team, 2019) using the iNEXT package (version 2.0.19; Hsieh et al., 2019). Diversity measures and corresponding 95% confidence intervals, were calculated for samples rarefied, or extrapolated, to expected values for 500 and 1000 specimens. In addition, corresponding values were calculated for sample data aggregated to the year of sampling. Note that the time between deployments within a given year spans only 1–20 days, i.e. within a single cruise, (see Table 1).

Variations in amphipod species composition between samples and years were visualised using non-metric multidimensional scaling (NMDS) ordination of Bray-Curtis dissimilarity based on sample-standardised data (i.e. percentage abundance of a species within a sample; see e.g. Clarke, 1993). This was followed by SIMPER analysis to identify characteristic species and ANOSIM to assess the significance of the environmental factors. The sample set contains variable ‘soak-times’ and trap designs, which could influence the sample composition so the catch size and diversity measures were tested against these factors using Spearman’s rank correlation, prior to subsequent analyses. The possible influence of seasonality was investigated by classifying each sample to seabed phytodetritus present and absent periods of the year, based on the prior observations reported by Bett et al. (2001), i.e. present May–September (8 samples), absent October–April (11 samples). Catch size, all diversity measures (S total, and ^0D, ^1D, and ^2D for 500 and 1000 individuals), and MDSx as a summary of species composition, were compared between these seasons using Mood's median test.

2.4. Environmental factors

2.4.1. Organic matter flux

Sediment traps (McLane Parflux, 21, 0.5 m^2 aperture; Honjo and Doherty, 1988) have been operated at the PAP-SO, or near vicinity (Lampitt et al., 2001), on a subsurface mooring from 1989 to the present day (Lampitt et al., 2010b). For this study we accessed available data (April 1989–April 2018) from traps deployed at c. 3000 m water depth (1850 m above bottom). Individual sample collection periods varied from 4 to 70 days, with a median of 14 days. Trap operation, sample handing, and flux parameter determination followed established protocols (Knap et al., 1996; Lampitt et al., 2000; Salter, 2007) and best practice (Pebody and Lampitt, 2016). In this contribution we reference three measures of organic matter flux: estimated volumetric flux (EVF, mL m^{-2} d^{-1}), dry weight flux (DW, mg m^{-2} d^{-1}), and organic carbon flux (CORG, mg C m^{-2} d^{-1}). To establish a conventional time-series dataset, the original variable interval trap data were converted to fortnightly values, using a duration-weighted average where necessary. The resultant data were subject to modelling / interpolation via a ‘seasonal decomposition of time series by LOESS’ (STL) method (Cleveland et al., 1990). These analyses were carried out in the R computing environment (version 3.6.0; R Core Team, 2019) using the ‘stlplus’ package (version 0.5.1; Hafen, 2016). The STL-derived ‘predicted’ fortnightly values were then averaged for the years corresponding to amphipod trap catches where some original organic matter flux data were available for that year (EVF and DW 1994–2016; CORG 2011–2016; Fig. 3; Table 2). All diversity parameters ($n = 500$ and $n = 1000$ D_0, D_1, and D_2) were correlated against the flux parameters at 3000 m (EVF, DW, and CORG).

2.4.2. Climate indices

Two climate indices were used as environmental factors in co-analyses with the amphipod sample data. Firstly, the Hurrell North Atlantic Oscillation (NAO) index (Station-Based) (Hurrell et al., 2003); accessed 22 March 2020, https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based. The winter index, December–March, is employed here, based on the difference of normalized sea level pressures between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland (Fig. 4, Table 2). Typically, a positive NAO brings stormy westerlies, cool summers, and mild and wet winters while negative NAO values are associated with suppressed westerlies and cold dry winters. For our analyses ‘positive’ and ‘negative’ values of the index were used as a categorical variable.

Secondly, the Atlantic Multi-decadal Oscillation (AMO) index (Trenberth and Shea, 2006); data provided by the Climate Analysis Section, NCAR, Boulder, USA, accessed 22 March 2020, https://climatedataguide.ucar.edu/climate-data/atlantic-multi-decadal-oscillation-amo. Note that those data only cover the period to 2010, consequently, additional data were sourced from https://www.esrl.noaa.gov/psd/data/timeseries/AMO/, and were processed using a 77-month, centred, running mean to generate values for the years 2011–2016 (Fig. 4; Table 2). The AMO has been identified as a coherent mode of natural variability occurring in the North Atlantic Ocean with an estimated period of 60–80 years. It is based upon the average anomalies of sea surface temperatures in the North Atlantic basin, typically over 0–80°N. For our analyses ‘cool’ and ‘warm’ phase AMO are used as a categorical variable.

3. Results

3.1. The scavenging amphipod assemblage

From the 19 amphipod trap samples, 106,261 specimens were identified (Table 3a). Sixteen amphipod taxa were recorded, seven of which were found in most of these samples, while the remaining nine taxa were reported in only some of the samples or were rarely collected. The number of specimens collected in each sample was highly variable, from a low of 208 specimens (Sample R, in 2016) to a maximum of 43,240 (Sample M, in 2011). The number of specimens collected was not correlated with soak time (Spearman’s rank, $r_{s[17]} = 0.247$, $p = 0.309$) or with year of collection ($r_{s[17]} = 0.153$, $p = 0.533$), nor did it vary between trap types (Mood’s median test, $\chi^2_{[3]} = 2.60$, $p = 0.458$).

Four taxa, *Abyssorchomene chevreuxi* (Stebbing, 1906), *Paralicella tenuipes* Chevreux, 1908, *P. caperesca* Shulenberger and Barnard, 1976, and *Eurythenes* spp., dominated individual catches across the time series, and were present in all samples considered here. Rank 1 dominance (Berger-Parker index, N_{max}/N; e.g. May, 1975) varied widely, 0.204 to 0.876, but was not correlated with soak time ($r_{s[17]} = -0.067$, $p = 0.786$), year of collection ($r_{s[17]} = 0.255$, $p = 0.291$), or catch size ($r_{s[17]} = 0.365$, $p = 0.124$), nor did it vary between trap types ($\chi^2_{[3]} = 4.60$, $p = 0.203$).

The dominant species varied over the time period studied (Table 3b). *Paralicella tenuipes* was typically dominant (in 8 of 11 samples) in the first half of the time series (1985–1997, comprising between 31 and 77%), having a relative abundance that exhibited a statistically significant negative correlation with year of sampling ($r_{s[17]} = -0.592$, $p = 0.008$). In contrast, its congener, *Paralicella caperesca*, was typically dominant, rank 1 or 2, in the second half of the time series (2011–2016, comprising between 53 and 88%), having a relative abundance that exhibited a statistically significant positive correlation with year of sampling ($r_{s[17]} = 0.687$, $p = 0.001$). Consequently, these two species, *P. tenuipes* and *P. caperesca*, exhibited a statistically significant negative correlation in their relative abundances ($r_{s[17]} = -0.644$, $p = 0.003$), reflecting the switch in dominance from the earlier to later years of the time series.

Other dominant taxa were more variable in their occurrence. *Abyssorchomene chevreuxi* comprised 28% of the sample in 1991, and 57–68% of the samples collected in 2011, and was a co-dominant with *P. tenuipes*, *P. caperesca*, and *Eurythenes* spp. in one of the samples from 1997. The giant amphipod *Eurythenes* spp. contributed substantially to the samples from 1985, 1986, and one of the samples from 1997 (making up 29, 27 and 20% of those catches respectively), and was the rank 1 or 2 taxon in 2016 samples (39–42%). In other years, this genus was relatively less abundant (0.72–12%) with the lowest relative abundances recorded in 1994 and 2012.

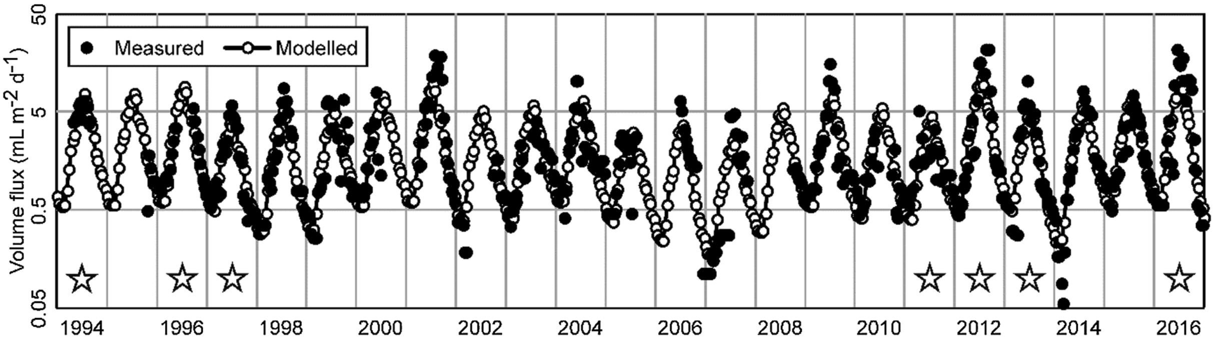

Fig. 3. Estimated volumetric flux of particulate material to moored sediment trap (3000 m water depth) at the Porcupine Abyssal Plain Sustained Observatory site. Measured and modelled values are shown (see text for detail), and years with corresponding amphipod trap catches indicated (star symbol).

Table 2
Environmental factors: North Atlantic Oscillation index (NAO); Atlantic Multi-decadal Oscillation index (AMO); vertical flux of material as measured in a sediment trap moored at 3000 m water depth in the Porcupine Abyssal Plain Sustained Observatory area site, as estimated volumetric flux (EVF), dry weight (DW) and organic carbon flux (CORG).

Year	NAO index	AMO index	EVF ($mL\ m^{-2}\ d^{-1}$)	DW ($mg\ m^{-2}\ d^{-1}$)	CORG ($mg\ C\ m^{-2}\ d^{-1}$)
1985	−3.09	−0.22	–	–	–
1986	3.14	−0.21	–	–	–
1991	1.14	−0.21	–	–	–
1994	2.86	−0.18	2.73	52.5	–
1996	−1.98	−0.08	3.20	39.8	–
1997	−0.93	−0.04	1.61	55.7	–
2011	2.95	0.14[a]	1.67	44.3	3.14
2012	−0.25	0.14[a]	3.68	72.4	7.50
2013	0.90	0.16[a]	1.79	34.7	2.20
2016	1.70	0.17[a]	3.45	69.1	4.12

[a] 77-month, centred, running mean based on Kaplan sea surface temperature dataset, see text for detail.

Other frequently encountered species included: *Abyssorchomene abyssorum* (Stebbing, 1888) (19/19 samples, maximum relative abundance 18%), *Abyssorchomene gerulicorbis* (14/19, 17%), *Paracallisoma idioxenos* Horton and Thurston, 2015 (18/19, 2%), *Haptocallisoma lemarete* Horton and Thurston, 2015 (11/19, 11%), and *Valettietta gracilis* Lincoln and Thurston, 1983 (10/19, 5%). The less frequently encountered taxa were: *Valettietta lobata* Lincoln and Thurston, 1983 (2/19, 0.2%), *Cyclocaris lowryi* Horton and Thurston, 2014 (6/19, 0.4%), *Paracentromedon* sp. DISCOLL_PAP_52216 (6/19, 2.0%), *Cleonardo* sp. DISCOLL_PAP_13077 (2/19, 0.1%), *Calliopiidae* sp. DISCOLL_PAP_13078 (1/19, 0.2%), *Parandania gigantea* (Stebbing, 1883) (2/19, 0.1%), and *Oedicerina vaderi* Coleman and Thurston, 2014 (1/19, 0.1%). Some of these rarer taxa, including *Paracallisoma idioxenos*, *Haptocallisoma lemarete*, and *Valettietta gracilis* were found in greater numbers in 1997.

Sample compositions in 1991 and 2011 are distinct from other years. In 1991, both *A. chevreuxi* (29%) and *A. abyssorum* (17%) were represented in much greater abundances than in other years. The two traps analysed in 2011 stand out in having the highest overall abundances (43,240 and 32,793 individuals).

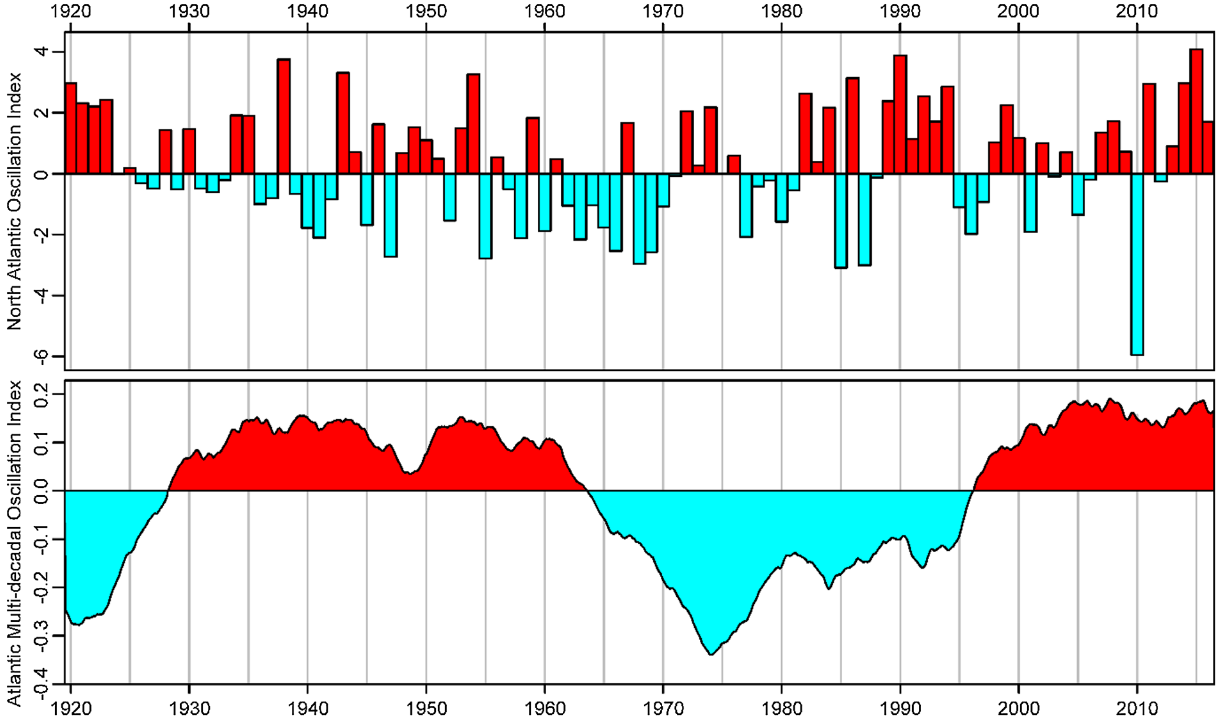

Fig. 4. Long-term variation in Atlantic climatic conditions, illustrated as: (upper panel) winter North Atlantic Oscillation index (station-based); and (lower panel) Atlantic Multi-decadal Oscillation index (77-month, centred, running mean based on Kaplan sea surface temperature dataset, see text for detail).

Table 3a

Taxon composition of scavenging amphipod samples collected from the Porcupine Abyssal Plain Sustained Observatory area between 1985 and 2016. Samples are coded A-S (na, not applicable; sub., subsample) (see also Table 1 and Fig. 1).

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	Lsub.[a]	M	Msub.[a]	N	O	P	Q	R	S
Abyssorchomene abyssorum (Stebbing, 1888)	175	40	271	8	13	147	11	15	11	16	129	1928	241	3160	395	4	44	20	28	4	6
Abyssorchomene gerulicorbis (Shulenberger and Barnard, 1976)	10	–	7	–	17	6	106	96	15	9	1	32	4	88	11	–	8	54	240	–	–
Abyssorchomene chevreuxi (Stebbing, 1906)	176	5	432	40	211	15	49	50	256	172	203	18,648	2331	29,248	3656	57	1567	32	327	4	5
Paralicella tenuipes Chevreux, 1908	576	321	324	633	922	510	496	42	953	1055	175	2416	302	2176	272	77	756	873	589	44	36
Paralicella caperesca Shulenberger and Barnard, 1976	335	107	375	114	196	212	254	229	244	340	189	8592	1074	6576	822	1218	5588	1565	1924	64	352
Eurythenes spp.	528	179	80	23	10	42	52	24	108	178	202	1161	na	1960	na	31	186	203	440	88	259
Paracallisoma idioxenos Horton and Thurston, 2015	22	1	30	3	5	–	1	1	12	21	13	8	1	32	4	3	5	3	4	4	1
Haptocallisoma lemarete Horton and Thurston, 2015	–	–	1	5	6	3	68	60	111	116	82	8	1	–	–	–	1	–	–	–	–
Valettietta gracilis Lincoln and Thurston, 1983	10	4	7	–	13	2	13	26	2	3	–	–	–	–	–	–	–	–	91	–	–
Valettietta lobata Lincoln and Thurston, 1983	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	2	–	–
Cyclocaris lowryi Horton and Thurston, 2014	2	–	1	–	–	1	2	2	–	–	–	–	–	–	–	–	1	–	–	–	–
Paracentromedon sp. DISCOLL_PAP_52216[b]	1	–	–	–	2	–	7	11	1	–	–	–	–	–	–	–	2	–	–	–	–
Cleonardo sp. DISCOLL_PAP_13077[b]	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Calliopiidae sp. DISCOLL_PAP_13078[b]	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Parandania gigantea (Stebbing, 1883)	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–
Oedicerina vaderi Coleman and Thurston, 2014	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Total number of individuals	1836	657	1528	826	1395	938	1059	558	1714	1911	996	32,793	na	43,240	na	1390	8158	2750	3645	208	659

[a] Samples collected in 2011 were subsampled to 1/8th for enumeration of species other than *Eurythenes* spp.

[b] Discovery Collections species reference numbers.

Table 3b

Relative abundance of scavenging amphipod taxa in samples collected from the Porcupine Abyssal Plain Sustained Observatory area between 1985 and 2016. Samples are coded A-S (see also Table 1 and Fig. 1). The dominant species in each sample is highlighted by bold.

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
Abyssorchomene abyssorum (Stebbing, 1888)	9.53	6.09	17.74	0.97	0.93	15.67	1.04	2.69	0.64	0.84	12.95	5.88	7.31	0.29	0.54	0.73	0.77	0.91	1.92
Abyssorchomene gerulicorbis (Shulenberger and Barnard, 1976)	0.54	–	0.46	–	1.22	0.64	10.01	17.20	0.88	0.47	0.10	0.10	0.20	–	0.10	1.96	6.58	–	–
Abyssorchomene chevreuxi (Stebbing, 1906)	9.59	0.76	**28.27**	4.84	15.13	1.60	4.63	8.96	14.94	9.00	**20.38**	**56.87**	**67.64**	4.10	19.21	1.16	8.97	0.76	1.92
Paralicella tenuipes Chevreux, 1908	**31.37**	**48.86**	21.20	**76.63**	**66.09**	**54.37**	**46.84**	7.53	**55.60**	**55.21**	17.57	7.37	5.03	5.54	9.27	31.75	16.16	5.46	21.15
Paralicella caperesca Shulenberger and Barnard, 1976	18.25	16.29	24.54	13.80	14.05	22.60	23.98	**41.04**	14.24	17.79	18.98	26.20	15.21	**87.63**	**68.50**	**56.91**	**52.78**	**53.41**	30.77
Eurythenes spp.	28.76	27.25	5.24	2.78	0.72	4.48	4.91	4.30	6.30	9.31	20.28	3.54	4.53	2.23	2.28	7.38	12.07	39.30	**42.31**
Paracallisoma idioxenos Horton and Thurston, 2015	1.20	0.15	1.96	0.36	0.36	–	0.09	0.18	0.70	1.10	1.31	0.02	0.07	0.22	0.06	0.11	0.11	0.15	1.92
Haptocallisoma lemarete Horton and Thurston, 2015	–	–	0.07	0.61	0.43	0.32	6.42	10.75	6.48	6.07	8.23	0.02	–	–	0.01	–	–	–	–
Valettietta gracilis Lincoln and Thurston, 1983	0.54	0.61	0.46	–	0.93	0.21	1.23	4.66	0.12	0.16	–	–	–	–	–	–	2.50	–	–
Valettietta lobata Lincoln and Thurston, 1983	–	–	–	–	–	–	–	0.18	–	–	–	–	–	–	–	–	0.05	–	–
Cyclocaris lowryi Horton and Thurston, 2014	0.11	–	0.07	–	–	0.11	0.19	0.36	–	–	–	–	–	–	0.01	–	–	–	–
Paracentromedon sp. DISCOLL_PAP_52216[a]	0.05	–	–	–	0.14	–	0.66	1.97	0.06	–	–	–	–	–	0.02	–	–	–	–
Cleonardo sp. DISCOLL_PAP_13077[a]	0.05	–	–	–	–	–	–	–	0.06	–	–	–	–	–	–	–	–	–	–
Calliopiidae sp. DISCOLL_PAP_13078[a]	–	–	–	–	–	–	–	0.18	–	–	–	–	–	–	–	–	–	–	–
Parandania gigantea (Stebbing, 1883)	–	–	–	–	–	–	–	–	–	0.05	0.10	–	–	–	–	–	–	–	–
Oedicerina vaderi Coleman and Thurston, 2014	–	–	–	–	–	–	–	–	–	–	0.10	–	–	–	–	–	–	–	–

[a] Discovery Collections species reference numbers.

Table 4
Diversity of amphipod taxa in samples collected from the Porcupine Abyssal Plain Sustained Observatory area between 1985 and 2016. Samples are coded A-S (see also Table 1 and Fig. 1). N, number of specimens recovered[a]; S, number of species recovered[a]; diversity indices: Sest, estimated species richness; Exp(H′), exponential form of the Shannon index; 1/λ, inverse form of Simpson's index, are provided as rarified/extrapolated to 500 or 1000 individuals on a per sample (s) or per year (y) basis (see also Supplementary Table 1).

Sample	Year	N	S	Sest s500	Exp(H') s500	1/λ s500	Sest s1000	Exp(H') s1000	1/λ s1000	Sest y1000	Exp(H') y1000	1/λ y1000
A	1985	1836	11	8.9	4.9	4.3	9.9	5.0	4.3	9.9	5.0	4.3
B	1986	657	7	6.8	3.5	2.9	7.0	3.5	2.9	7.0	3.5	2.9
C	1991	1284	10	8.5	5.1	4.5	9.3	5.1	4.5	9.3	5.1	4.5
D	1994	826	7	6.9	2.3	1.6	7.0	2.3	1.6	9.7	2.8	2.0
E	1994	1395	10	9.4	2.9	2.1	9.9	2.9	2.1			
F	1996	938	9	8.2	3.4	2.7	9.1	3.4	2.7	9.1	3.4	2.7
G	1997	1059	11	10.2	4.7	3.4	10.9	4.7	3.4	11.4	5.3	3.8
H	1997	558	13	12.7	6.2	4.4	14.8	6.3	4.4			
I	1997	1714	11	9.0	3.9	2.8	10.0	3.9	2.8			
J	1997	1911	10	8.8	3.9	2.8	9.4	3.9	2.8			
K	1997	996	10	8.5	6.1	5.7	10.0	6.2	5.8			
L[a]	2011	32,793	8	5.7	3.2	2.5	6.2	3.2	2.5	6.3	3.0	2.2
M[a]	2011	43,238	7	6.0	2.8	2.0	6.5	2.9	2.0			
N	2012	1390	6	5.6	1.7	1.3	6.0	1.7	1.3	6.6	2.4	1.8
O	2012	8158	10	5.8	2.5	1.9	6.6	2.5	1.9			
P	2013	2750	7	6.4	2.8	2.3	6.7	2.9	2.3	8.0	3.7	2.7
Q	2013	3645	9	7.7	4.1	3.0	8.2	4.1	3.0			
R	2016	208	6	6.0	3.6	3.1	6.0	3.7	3.2	6.0	2.9	2.5
S	2016	659	6	5.8	2.6	2.3	6.0	2.6	2.3			

[a] Note samples collected in 2011 were subsampled to 1/8th for enumeration of species other than *Eurythenes* spp., N and S values are full sample approximations.

3.2. *Temporal variation in amphipod species diversity*

Diversity measures (Sest, Exp[H′], 1/λ; Table 4; Supplementary Table 1) exhibited no significant correlation (Spearman's rank, $p > 0.5$) with soak time. Soak time was not correlated with catch size (Spearman's rank correlation, 0.252, $p = 0.291$), nor was there a significant difference in catch size between trap designs (catch size transformed $y = \log10[x]$; Welch's Test, $F_{[2,\ 2.98]} = 1.88$, $p = 0.296$). Catch size, diversity measures (S total, and ${}^{0}D$, ${}^{1}D$, and ${}^{2}D$ for 500 and 1000 individuals), and MDSx as a summary of species composition exhibited no statistically significant differences ($p > 0.05$) between phytodetritus seasons.

Estimated species richness of the scavenging amphipod assemblage by individual sample (rarefied and extrapolated to 500 individuals) and by samples aggregated to years (rarefied and extrapolated to 1000 individuals) was generally higher in the early part of the time series (1986–1997; Sest 500 = 6.8–12.7, Fig. 5a, Sest 1000 = 7.0–11.4, Fig. 5b) than the recent sampling (2011–2016; Sest 500 = 5.6–7.7, Fig. 5a, Sest 1000 = 6.0–8.2, Fig. 5b). Estimated species richness aggregated to year (Sest 1000) exhibited a significant negative correlation with the AMO index (Spearman's rank, $r_{s[17]} = 0.593$, $p = 0.007$), other diversity measures (Exp[H́], 1/λ) did not ($p > 0.08$; Supplementary Fig. 7).

When 'cool' and 'warm' phase AMO were used as a categorical variable, amphipod species richness varied significantly between phases (Mood's median test, $\chi^2_{[3]} = 12.44$, $p < 0.001$). Estimated cool phase richness for 1000 individuals is 9.7 (8.4–10.9, 95.5% Wilcoxon signed rank confidence interval), for warm phase, 6.4 (6.0–7.1, 94.1% confidence interval).

Species composition was assessed via non-metric multidimensional scaling ordination of Bray-Curtis dissimilarity based on sample-standardised data (i.e. percentage composition). When 'cool' and 'warm' phase AMO were used as a categorical variable, amphipod species composition varied significantly between phases (ANOSIM, $R = 0.539$, $p < 0.001$). No significant variation was apparent when positive and negative values of the NAO were used as a categorical variable.

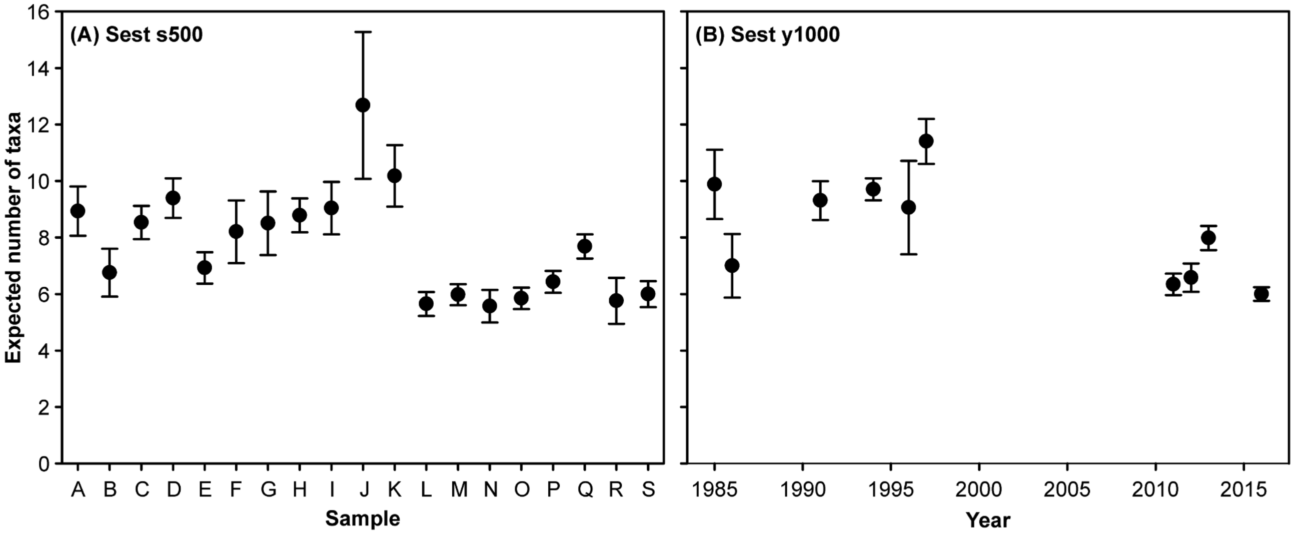

Fig. 5. Scavenging amphipod species richness at PAP-SO as rarified/extrapolated to 500 or 1000 individuals. Sest, estimated species richness by (A) individual samples (s) and (B) samples aggregated to years (y).

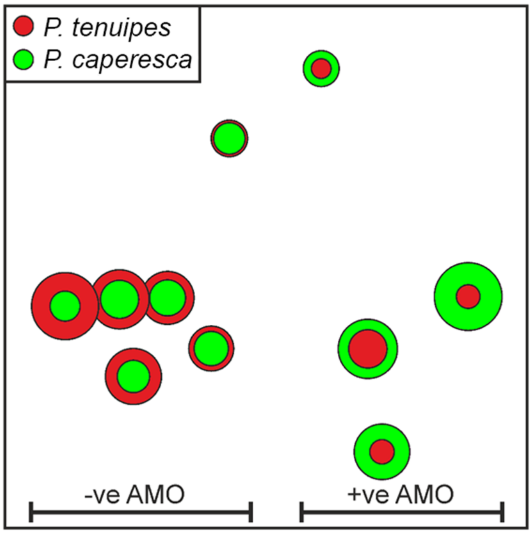

Fig. 6. Non-metric multidimensional scaling ordination of PAP-SO scavenging amphipod assemblage composition by year of observation. Symbols are scaled to the relative abundance of two key species, *Paralicella tenuipes* (red) and *P. caperesca* (green). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Paralicella tenuipes is identified as the key characterising species of the cool phase, and *P. caperesca* as the key characterising species of the warm phase (SIMPER). Amphipod faunal composition (as summarised by the MDSx variable) exhibited a significant correlation with the AMO index (Spearman's rank, $r_{s[17]} = -0.754$, $p < 0.001$). The relative abundance of *P. tenuipes* exhibited a significant negative correlation with the AMO index (Spearman's rank, $r_{s[17]} = -0.583$, $p = 0.009$), and the relative abundance of *P. caperesca* exhibited a significant positive correlation with the AMO index (Spearman's rank, $r_{s[17]} = 0.759$, $p < 0.001$). Fig. 6 illustrates this in a single plot of the non-metric multidimensional scaling ordination showing the scavenging amphipod assemblage composition by year of observation. The bubble plot symbols are scaled to the relative abundance of the two key species *Paralicella tenuipes* and *P. caperesca* and Years appear to group (on the x-axis) to periods of positive (warm) and negative (cool) phases of the AMO.

For the years where matching data were available, there is a negative trend between annual flux at 3000 m and amphipod diversity. All diversity parameters ($n = 500$ and $n = 1000$ ^0D, ^1D, and ^2D) were negatively correlated with all flux measures (EVF, DW, and CORG), however, these correlations were only statistically significant in the case of EVF values ($r_{s[17]} = \geq -0.655$, p-adjusted ≤ 0.018), i.e. amphipod diversity was lower in high EVF years.

4. Discussion

Our results indicate that the dominant species of scavenging amphipod attracted to baited traps at the Porcupine Abyssal Plain Sustained Observatory changed over time. This can be summarised by variations in dominance between the species *Paralicella caperesca*, *Paralicella tenuipes*, and *Abyssorchomene chevreuxi* from samples collected over > 30 years, with some years having notably higher or lower percentage abundances of the giant amphipod genus *Eurythenes*.

There is a marked change in amphipod community composition in the year 2011, when the total number of amphipods caught in the traps was also much higher than any other year (32,793 and 43,240). The use of a splitter to analyse samples is methodologically sound (Dahiya, 1980; Griffiths et al., 1984; Horton et al., 2013), however, it may have resulted in some rarer species being unrecorded in these samples. This may, in part, explain the lower number of species found in these traps. There are no obvious explanations to account for these very high numbers, but in addition to having the highest overall abundances, this year also recorded a change in the dominant species from *Paralicella* spp. to *A. chevreuxi*. Community compositions in 2011 and 1991 have low similarities to other years but have a high resemblance to one another, potentially indicating that similar environmental factors may have been acting in those years. While we cannot be certain what caused the changes in this case, drastic changes in community composition have been reported previously, resulting from catastrophic events. Frutos and Sorbe (2017) recorded a temporal dominance of the amphipod scavenger *Tmetonyx similis* (Sars, 1891) in the Capbreton Canyon, likely related to increased amounts of local dead fauna caused by a turbidity event. The greatly increased abundances seen in 2011 could be a result of catastrophic disturbances, as major slope failures do occur at PAP-SO from the abyssal hills (Ruhl, 2013) and such events would potentially cause extinctions of local invertebrate fauna. While it is well-known that fisheries discards have impacts on local scavenging faunas (Depestele et al., 2019) there are no commercial demersal fishing activities in the vicinity of PAP-SO, the nearest being on the Porcupine Bank around 2000 m (Priede et al., 2011).

Our results indicate the existence of a possible ‘regime shift’ in scavenging amphipod communities following a ‘regime shift’ in surface ocean biological communities (the amphipod food source), which is driven by a phase shift in Atlantic climate (from cool to warm AMO). Changes in the carbon flux from the upper oceans have both direct and indirect influences on the scavenging community (Duffy et al., 2012). Direct impacts may be through changes in food supply (abundance and/or quality), as not all scavenging amphipods are obligate necrophages and may use phytodetritus or macrophytes as a food source (Lawson et al., 1993; Dauby et al., 2001; Blankenship and Levin, 2007). Indirect impacts include changes in the upper ocean pelagic community composition resulting in altered quantities and qualities of large food-falls. It is possible that other benthos at the PAP-SO have followed the same pattern and this warrants further investigation. Similar effects have been noted more widely in both pelagic and benthic systems (Edwards et al., 2013; Alheit et al., 2014; Harris et al., 2014; Smith et al., 2016). In the North Sea, long-term climate cycles, e.g. North Atlantic Oscillation and Atlantic Multi-decadal Oscillation have been shown to affect the benthos (Dippner et al., 2014; Birchenough et al., 2015), pelagic systems and fish stocks (Gröger et al., 2010; Auber et al., 2015).

Five replicate traps from 1997, revealed differences in the species compositions and warrant some discussion here. In three of the five 1997 samples, *P. tenuipes* was the dominant species. In one sample (Sample H, Station 13077#35), the dominant species was *P. caperesca* with *P. tenuipes* representing a much smaller proportion of the sample (Table 3b). Additionally, in this trap, *A. gerulicorbis* is the dominant species of *Abyssorchomene,* whereas in other samples this species contributes much smaller proportions. There is also a greater representation of the rarer species in this trap, including *Haptocallisoma lemarete, Valettietta gracilis, Valettietta lobata, Cyclocaris lowryi,* Calliopiidae sp. DISCOLL_PAP_13077 and *Paracentromedon* sp. DISCOLL_PAP_52216. Sample G (Station 13077#4, collected in 1997) has a similar composition as sample H but the dominant species is *P. tenuipes*. Both of these samples differ from others in the dataset as they were simple pipe traps set at three different heights above the seabed (450, 1050 and 2100 mm), rather than being comprised of a benthic and suprabenthic trap. These two samples also had the longest soak times of the whole dataset (84 and 104 h). An additional sample with a long soak time also had a higher proportion of *A. gerulicorbis* (Sample Q, 62 h). It is likely that these factors have resulted in the markedly different species compositions recorded. Sample K (13078#22, collected in 1997) also differs in some respects in having a more even species composition, with the four important species (*P. tenuipes*, *P. caperesca*, *A. chevreuxi*, and *Eurythenes* spp.) each contributing about 20% to the catch. This trap had the shortest soak time of the whole dataset with just six hours on the seabed. In such a short time span, the trap will not have experienced a full tidal cycle and the odour plume is unlikely to have travelled as far as for other traps, limiting the number of amphipods of different species attracted to the trap. The different species attracted are likely to have different swimming speeds and chemosensory abilities and thus distances of attraction to the bait.

Paralicella spp. have been identified as specialist scavengers which often monopolise bathyal and abyssal food-falls (Duffy et al., 2012, 2016). Their life cycle is closely linked to an input of food, allowing them to reproduce quickly in the presence of increased nutrients and therefore dominate scavenging amphipod assemblages at large food-falls (Duffy et al., 2016). It is possible that in the years when *Paralicella* spp. are not dominating the assemblage, other species with increased plasticity in their diet, such as *Eurythenes* spp. (Janßen et al., 2000; Blankenship and Levin, 2007) and *Abyssorchomene* spp. (Dauby et al., 2001) have increased success. The proportion of a population drawn to bait may correspond with that species' dependence on food-falls and the availability of other food sources (Janßen et al., 2000), providing a possible reason for the increased prevalence of *Abyssorchomene* spp. in years with increased organic matter. In 1991 and 2011, there were significant community shifts that resulted in *Abyssorchomene* spp. becoming the dominant species in these samples. Frigstad et al. (2015) report short bursts of unusually high sediment flux during summers of 2004, 2009 and 2012. It is possible that the influx of carbon in 2009, led to increased food availability for abyssal scavengers and potentially increased success for *Abyssorchomene* spp. compared with *Paralicella* spp. owing not only to the ability of *Abyssorchomene* to include organic matter in their diet (Dauby et al., 2001), but also to have multiple broods in a lifetime, an iteroparous reproductive strategy that takes advantage of increased nutrient input (Duffy et al., 2013).

There was a significant decline in sample species diversity with increasing organic matter input (as measured by EVF). Obligate necrophages may have less success in these years compared with facultative necrophages with more diverse diets (Janßen et al., 2000). Samples from 1991 and 2011 are dominated by *Abyssorchomene* spp. which have the ability to utilise organic matter as a source of nutrients (Dauby et al., 2001), and are also able to respond by reproducing quickly and at earlier instars than the slower growing, semelparous obligate necrophages (Duffy et al., 2016). It should also be noted that a similar trend is seen in years of low organic input to the benthos when the samples are less diverse, likely as a result of the dominance of obligate necrophages, which have experienced no disruption to their stable food source.

The first changes associated with the *Amperima* event were recorded in 1996 (Billett et al., 2001; Billett et al., 2010). The mean annual volumetric flux recorded in 1994 was the third highest, which may have resulted in the rapid changes in the benthic environment associated with the *Amperima* event. Studies at Station M in the Pacific Ocean have also observed changes in megafaunal community composition between the years 2006–2012 (Kuhnz et al., 2014). It was noted that at the start of that study, the diversity (as measured using Simpsons Diversity Index) was high, although the density of organisms was low. Over an 18-month period starting in 2011, there was an order of magnitude increase in mobile organisms, and in 2012 four holothurian species recorded the highest densities since the start of investigations in 1989. These changes were correlated with a variation in organic flux levels and are remarkably similar to those observed during the *Amperima* event in the North Atlantic (Billett et al., 2001; Billett et al., 2010).

There is evidence that carbon flux to the deep seafloor acts as both a food store and carbon sink hence the effect of increased influx may manifest years later (Jones et al., 1998; Alve, 2010). It is likely that the community changes caused by an input of organic matter will persist for some time after an influx due to the slow response of deep-sea organisms to environmental change (Seibel and Walsh, 2003) and the persistence of organic matter in deep sediments (Jones et al., 1998; Alve, 2010). It is possible that any changes to the scavenging amphipod community resulting from this input may not be apparent immediately, as the deep sea is often slow to react to changes as a result of low temperatures and limited food supply impacting the metabolism of deep-sea organisms (Janßen et al., 2000; Hoegh-Guldberg and Bruno, 2010). Ruhl (2007) and Ruhl and Smith (2004), reported that the changes in larger epifaunal megafauna populations at Station M in the Pacific, lag the particulate flux by 11–22 months, while Drazen et al. (2012) noted that scavenging grenadier populations at the same site lagged by about 6 months relative to the pelagic nekton populations, indicating that scavengers respond more quickly to trophically more important carrion (albeit likely through migration, rather than population growth in this case). The possible links (and time-lags) between changes in scavenging amphipod populations at the PAP-SO and pelagic nekton populations have not been investigated here, but should be investigated in future studies.

Soak time was evaluated as part of our study owing to evidence of a temporal succession of scavenging amphipods on carcasses (Thurston, 1990; Jones et al., 1998), although we have found no statistically significant impact of soak time on the scavenging community composition. Increased soak time may result in the arrival of facultative or more specialist necrophages. These less common species (e.g. *Valettietta* spp.) may not possess the same well-developed sensory organs as found in the obligate necrophage species or may be reacting to a different spectrum of chemical cues that are dependent on 'ageing' of the food fall, and therefore arrive at the bait later (Thurston, 1990). Traps that are left on the seabed for longer are therefore more likely to attract these species, and there is evidence of this in our dataset, with the traps having the longest soak times (G, H, and Q) also attracting the largest numbers of specimens of *Valettietta gracilis* (13, 26, and 91 respectively). These same three traps also attract the largest numbers of *A. gerulicorbis*, possibly indicating that this species is also a facultative scavenger.

The season when sampling took place is linked to the organic matter input due to the seasonal cycle of phytoplankton blooms in the upper ocean (Frigstad et al., 2015). Similarly, it has been shown that there is a seasonal influence on catch size in arctic regions (Nygard et al., 2012). It was therefore important that this factor is excluded as having a significant impact on the community studied here. Our analyses revealed no significant influence of season on community composition. Both benthic and suprabenthic traps were used in this study, but the results were reported as combined specimen numbers for each station. The numbers of individuals in the suprabenthic traps were much lower than in the benthic traps, and rarer species were absent. An in-depth analysis of the species found in the suprabenthic versus benthic traps was not possible as detailed data were only available for certain years.

5. Future work

It would be interesting to investigate further what differentiates *P. tenuipes* and *P. caperesca*. They are very similar morphologically but do have eyes that are strikingly different in size and shape, and can be easily separated both morphologically (Shulenberger and Barnard, 1976) and molecularly (Ritchie et al., 2017). *P. caperesca* populations in the North Atlantic have been studied in detail (Duffy et al., 2016), but its congener, *P. tenuipes*, has not. Gut content analyses, stable isotope analyses and detailed biochemical composition could help determine differences in diet and variations in natural history and ecology of these two species. The genus *Eurythenes* present at the PAP is now known to comprise four species, one of which is new to science (Horton et al., 2020a), and the species composition will need to be reassessed to be included in any future analysis of this time series. This will require the re-identification of the 5754 specimens reported in this study which until now were recorded as *Eurythenes gryllus*, a species that is confirmed only from Arctic and Antarctic waters but is not found at the PAP (d'Udekem d'Acoz and Havermans, 2015; Horton et al., 2020a).

It will also be useful to include biomass as an additional measure in any future studies of scavenging amphipods since there are marked differences in the body sizes of the species attending baited traps. Hatchlings of the *Eurythenes* specimen (body length 120 mm, attributed to *E. gryllus* by Thurston and Bett (1995) but not belonging to that species), had a mean length of about 11 mm. The maximum body length reported for *Abyssorchomene abyssorum* is less than 17 mm (Duffy et al., 2013), for *Abyssorchomene distinctus* (Birstein and Vinogradov, 1960), 19 mm (Duffy et al., 2016) and it is unlikely that species of *Paralicella* would exceed 20 mm (Thurston, 1979). The respective contributions of these different species to the amount of carbon consumed could be analysed by making simple measurements of volumetric contribution of each species to the whole sample.

While this study has provided a first look at the variations of an abyssal scavenging amphipod community over time, it will be critical to continue observing these populations for the next decade to see if the AMO switches back to 'cool' phase and whether the amphipod species composition changes as a consequence. A fundamental question that then arises, but still remains elusive, is when will the current warm phase of the AMO begin to decline (~2025 based on a 60-year cycle) and will it be significant enough to trigger habitat switching in the North Atlantic and associated shelf seas, or will external climate warming override this natural signal? The continued collection and maintenance of long-term time series at PAP-SO and other abyssal sites are important to enable the monitoring needed to detect predicted changes in benthic biomass related to climate change (Jones et al., 2014).

6. Conclusions

Our analyses have revealed shifts in scavenging amphipod communities in relation to changing levels of organic matter deposited in the abyss. This shift manifests itself in a remarkable change to the dominant species, from obligate necrophages such as *Paralicella* spp., with semelparous reproduction to *Abyssorchomene* spp. with a more varied diet and iteroparous reproduction and therefore perhaps more able to take advantage of increased food availability from organic flux input. Samples are less diverse in those years with significantly increased organic matter due to a single species dominating the sample. Trap type, season, and soak time have no significant impact on the diversity, number of species or community composition at the PAP, although detailed examination of the composition shows some interesting patterns that may become clearer with further samples and a longer time series.

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.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2020.102318.

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