

Dead mussels as food-stepping stone habitats for deep-sea hydrothermal fauna.

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Master's Thesis

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Abstract

Hydrothermal vents are patchy ephemeral habitats which are hotspots of productivity in the deep sea. Vent endemic fauna may require intermediate stepping stone habitats to travel from vent to vent with these stepping stones typically comprising of decaying organic matter. Dead *Bathymodiolus* and *Mytilus* mussels were placed in ~2200 meters water depth at approximately 4 km distance from the Rainbow Vent Field for one year in order to measure the propensity for vent fauna to use dead mussels as stepping stone habitats. The vent endemic Dirivultidae copepods, *Bathymodiolus* mussels and generalist Hesionidae and Capillidae polychaetes settled among the mussels. Species richness and evenness was very low among the meiofauna with generalist *Tisbe* copepods accounting for almost all of the copepods. Macrofaunal samples were much richer and more even in comparison. The meat from the vent endemic *Bathymodiolus* mussels was consumed after one year while there was still some meat and a sulphurous smell present in the shallow water *Mytilus* mussels, indicating that decomposition was still taking place. This study indicates that dead mussels could act as a stepping stone habitat for some symbiotic and non-symbiotic vent fauna as such animals were found in the samples. Juvenile *Bathymodiolus* mussels settled among the dead mussels indicating that conditions were suitable for settlement for symbiotic fauna. It is possible that the dead mussels were an effective stepping stone habitat as *Bathymodiolus* mussels can reach sexual maturity in a matter of weeks and months. However, the habitat did not last long enough, nor was it probably productive enough to serve as an effective long-term stepping-stone habitat.

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1. Introduction

The deep sea is the largest habitat on the planet (Ramirez-Llodra et al., 2010). While its benthic component is scattered with interesting bathometric features, it is for the most part, comprised of the rather homogenous landscape that is called the abyssal plain (Ramirez-Llodra et al., 2010). Only 0.5% of the net primary productivity of the euphotic zone reaches past a depth of 2 km and most of the deep-sea benthic environment relies on the downward flux of organic material from surface production (Buesseler et al., 2007; Smith et al., 2008). Leading to the benthic community of the abyssal seafloor having very low faunal biomass and productivity (Rex et al., 2006; Rowe et al., 2008). Along tectonic plate boundaries and back-arc basins however, there are exceptional areas in this landscape where the environment becomes much more extreme. Discovered in 1977, hydrothermal vents are areas where exceptionally hot effluent bubbles up from the earth's crust, carrying with it heat and a cocktail of chemicals that supports a highly productive ecosystem (Corliss et al., 1979).

Hydrothermal vents are habitats characterised by extreme abiotic factors and can be found in both the shallow and deep ocean (Van Dover and Trask, 2000). They are commonly distinguished by high temperature gradients (Johnson et al., 1988), the abundance of reducing chemicals (Johnson et al., 1986) and low oxygen (Hourdez and Lallier, 2006). With deep-sea vents also experiencing high pressure and no light. As well as their extreme abiotic nature, vents are also ephemeral environments lasting from a handful of years to decades to potentially centuries (Van Dover and Trask, 2000; Humphris et al., 2002). Primary production in these habitats is done through chemosynthesis by free-living microbes and by way of symbiotic, chemoautotrophs present in the tissues of characteristic macrofauna (Cavanaugh et al., 2006). *Bathymodiolus* is one such genus of symbiotic vent mussel that is endemic to multiple vent fields along the Mid-Atlantic Ridge (Galkin and Goroslavskaya, 2010). In the aphotic zone, as vent emissions wane their chemoautotrophic based source of primary productivity wanes also, leading to vent senescence and an ultimate permanent change of the habitat (Van Dover, 2000). The succession of vents from active to senescent shifts the fauna present from a vent endemic to a more typical hard substrate benthic community (Van Dover, 2000). While vent fauna at a local level may diminish as their host vent becomes less active, global vent communities continue to proliferate through the systematic colonisation of new vents (Tunnicliffe et al., 1997; Shank et al., 1998).

Despite their temporary nature, hydrothermal vents are areas of high productivity, biomass and are essential habitats for a wide spectrum of deep-sea life. They host complex and often locally unique ecosystems, and although fauna from distant vents can be related, the extent of the connectivity between sites is still not well understood (Breusing et al., 2016). While vents are home to complex ecological networks, a significant proportion of their diversity is found in their meiofaunal communities (Tunnicliffe et al., 1998). Meiofauna refers to animals that pass through a 1 mm sieve and are retained by a 32 µm sieve (Giere, 2008). Whilst permanent meiofauna (such as nematodes and copepods) remain <1 mm when adult, the juvenile macrofauna is <1 mm for a limited amount of time (Giere, 2008). The mega- and macrofauna of hydrothermal vents have been the focus of more studies than vent meiofauna communities. However, 20% of described vent species can be classified into the meiofauna size range (Bright, 2006). In the Atlantic specifically, meiofauna represents at least 50% of the total diversity in vent fauna and within these meiofaunal communities, nematodes and copepods dominate in terms of abundance (Zekely et al., 2006; Sarrazin et al., 2015).

Copepods are a highly diverse and abundant group of meiofauna, with copepods of the order Harpacticoida being the most abundant found in benthic samples (Giere, 2008). As an order, Harpacticoids are very diverse in their environmental preferences and trophic specialisation (Pace and Carman, 1996; De Troch et al., 2003; De Troch et al., 2005). Shallow water species have been the most

comprehensively studied by far with deep-sea species receiving much less attention due to the difficulties associated with deep-sea research. The diversity in the trophic specialisation of harpacticoids has allowed them to coexist with the other most abundant meiofaunal group in the benthos, the nematodes. Harpacticoid copepod species are able to actively swim up into the water column which is called emergence. This, coupled with prolific dispersal methods (Armonies, 1989b; Walters and Bell, 1994; Buffan-Dubau and Castel, 1996), leads them to be highly effective colonisers of new habitats. There has been much study on the modes of harpacticoid distribution, resulting in multiple hypotheses. Such hypotheses include resuspension and marine snow adhesion; in which meiofauna are resuspended into the water column due to disturbances and can be carried along on marine snow (Bell and Sherman, 1980; Shanks and Edmondson, 1990).

Vents are irregularly distributed across mid-ocean ridges and back-arc basins. This, coupled with their ephemeral nature, means that the rapid dispersal and colonisation of new vents by fauna is essential for the continuation of species (Tunncliffe et al. 1997; Shank et al. 1998). However, since the majority of the seafloor is not suitable to support the aggregations of life that are found at vents (Smith et al. 2008) and vents can be vast distances apart, vent fauna are faced with the significant problem of reaching new vents. The idea of stepping stone habitats was first suggested by Smith et al. (1989) as a solution to this problem, in which decaying organic matter can act as an intermediary habitat for fauna to colonise as they spread to new locations. Breusing et al. (2016) analysed *Bathymodiolus* mussel populations through genetic pathways and modelling to map related vent mussel populations along the Mid-Atlantic Ridge (MAR). They found that stepping-stone habitats are necessary for colonisation over large distances, as the likelihood of the observed level of connectivity being achieved in a single generation is very small. At stepping-stone habitats, through the microbial degradation of the material, sulphide compounds are produced resulting in the appropriate conditions for sulphide-oxidising bacteria to flourish (Smith et al. 1989). With the presence of these bacteria, this habitat contains enough resemblance to vents that fauna can settle, reproduce and subsequently redistribute larvae back into the water column (Smith et al. 1989). Sources of decaying matter vary from whale falls (Smith et al. 1989) to wood (Turner 1973). When vents no longer produce reducing chemicals for chemosynthesis, they are known as senescent or waning vents. As the source of the primary productivity for the ecosystem disappears, the dead megafauna like mussels or tubeworms degrade but remain for a few years (Gollner et al. 2020). However, the role of decaying megafauna for the dispersal and connectivity of active vent fauna is to date not known.

The aim of this project is to test whether food-enhancement in the form of dead mussels near vents along the mid-ocean ridge can act as stepping stone habitats for vent endemic species. Through this study, the following research questions are asked; What species seem to benefit from food-enhancement? Does food-enhancement in the form of dead mussels act as a stepping-stone for vent fauna? Is abundance and diversity of fauna associated with food-enhancement tied to amount of food and/or type of food (shallow water non-symbiotic *Mytilus* versus deep-sea symbiotic *Bathymodiolus*)?

2. Materials and Methods

2.1. Experimental set-up of Landers

To deploy dead mussels on the sea-floor in 2228 meters depth, landers were used. On the two NIOZ landers used in this study (“Albex 3” and “Trol”), 9 boxes were mounted respectively (Figure 1, 3, 4). Each box was made of a metal frame and a 32 µm net was fitted inside each box. A plastic lid was attached to the boxes to be able to close them upon recovery. The 9 boxes contained dead mussels and empty controls (Figure 1, 5). Different mussels were used on each of the landers. Albex 3 lander contained vent endemic *Bathymodiolus azoricus* mussels. Trol lander contained shallow water *Mytilus edulis* mussels. Different quantities of mussels were used from a wet weight of 667 g to 3070 g (TABLE 1). In the control boxes no mussels were present. Due to the difficulty of sourcing *Bathymodiolus*, fewer *Bathymodiolus* were used in the experiment. All mussels were acquired dead and were thoroughly rinsed with water to remove any associated fauna and were then frozen at -20°C. To avoid any potential introduction of contamination to deep-sea fauna during the deployment, mussels were put on dry ice and sterilised using gamma irradiation at the company Steris, Synergy Health Ede, NL. After sterilisation, mussels were kept at - 20°C until deployment. Mussels were mounted onto the inside of the lid with a net (Figure 5). The lids lay open during the one-year deployment. The landers were deployed through freefall and were recovered using an acoustic release that triggered the closing of the lids and the release of the weights, allowing the landers to float, with closed boxes to the surface. The landers were deployed during leg 12 of the NICO research expedition on the RV Pelagia research vessel on the 18th of July 2018. They were then recovered on the 26th and 27th of June 2019 as a part of the Rainbow 2019 research expedition.

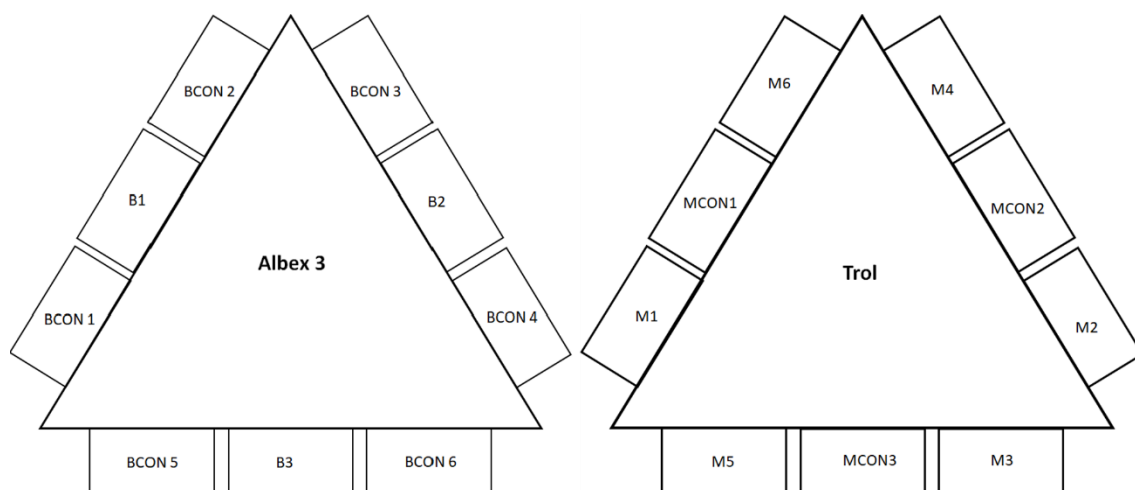


Figure 1 - Lander box positions

2.2 Site description

Landers were deployed at approximately 4 km distance to the Rainbow vent field at a depth of 2228 m (Figure 2). Albex 3 lander was deployed at 36°14,860'N 33°52,607'W, the Trol lander was deployed at 36°14,854'N 33° 52,618'W. The lander deployment location was chosen due to the relatively flat bathymetry of the area to reduce the risk of the lander tipping on uneven substrate.

The Rainbow hydrothermal vent field is located about 370 km to the south of the Azores (Figure 2). The field is 100 m long and 200 m wide and sits at approximately 2300 m depth. It was first discovered in 1997 (Fouquet et al. 1997) and is situated close to the vent fields Lucky Strike and Menez Gwen. Although it is geographically close to the other vent fields, it is significantly distinct from all other vent fields along the MAR in key ways. Rainbow releases effluent with the lowest pH, the highest chloride concentration and the highest temperature on the MAR (Douville et al. 2002). As a result, its plume is the most environmentally extreme along the MAR. In 4 km distance, at the Lander site, a plume signal was still detectable. This can be seen in an increased level of turbidity at the lander location (Figure 7).

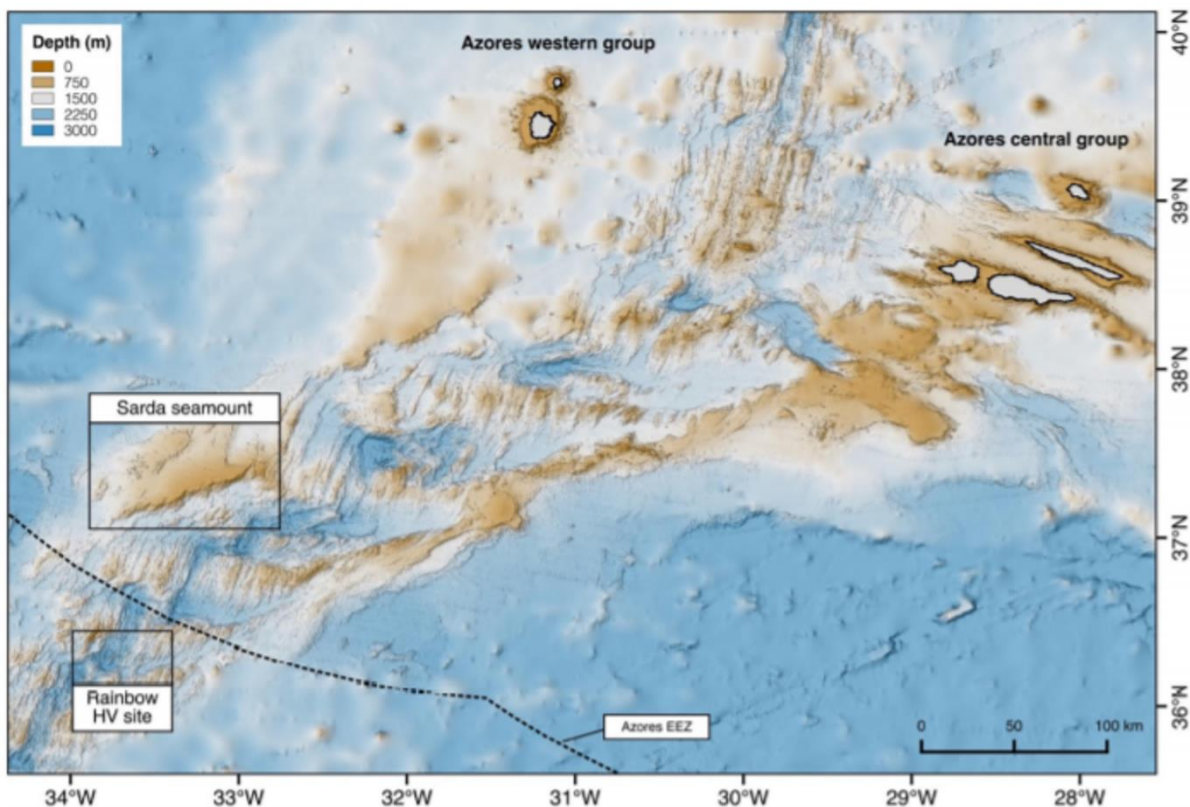


Figure 2 - Rainbow vent site. Map taken from the Rainbow 2019 64PE454 expedition field report

2.3. Sample sorting and analysis

Directly after the lander recovery, the mussels were weighed and the fauna from the nets were sieved through a 1 mm and 32 μ m mesh. The fauna were then fixed in 99% EtOH. Samples were brought to the Royal Netherlands Institute for Sea Research for examination. Samples from each of the lander boxes were sorted and analysed into taxonomic groups using a Leica TL3000 Ergo stereoscopic microscope. A Leica DM1000 light microscope and various taxonomic keys and literature (Lang 1948;

Huys, 1996; Boxshall and Halsey, 2004) were then used to identify the copepods present in the samples. Fauna were identified in both ethanol and glycerine, with the transference of fauna from ethanol to glycerine in gradual changing concentrations as described in Lyke et al. (1989), in which the specimen is suspended in a drop of glycerine on a slide. Wax is used at the slide corners to prevent the specimen from getting crushed.

Polychaetes were identified to a minimum of family level by Dr. Hourdez of the Observatoire océanologique de Banyuls-sur-Mer.

3. Results

3.1 Lander recovery

The landers were collected successfully and worked in principle. However, when the landers were signalled to release their anchors and rise from the seafloor, not all of the boxes closed. On each lander, 3 of the 9 boxes closed successfully. It is speculated that the plastic lids were warped from enduring the pressure for a year and too many mussels were used in the samples, making it more difficult for the boxes to close. While benthic copepods were present in all boxes with mussels that closed, mostly pelagic copepods were present in those that remained open. It is presumed that the benthic copepods were flushed out of the boxes and replaced with pelagic copepods when on transit from the seafloor to the surface. As a result, only the boxes that closed successfully are the focus of the meiofaunal portion study. If this experiment is to be repeated, it is recommended that the lids be made out of a thicker or more durable material.

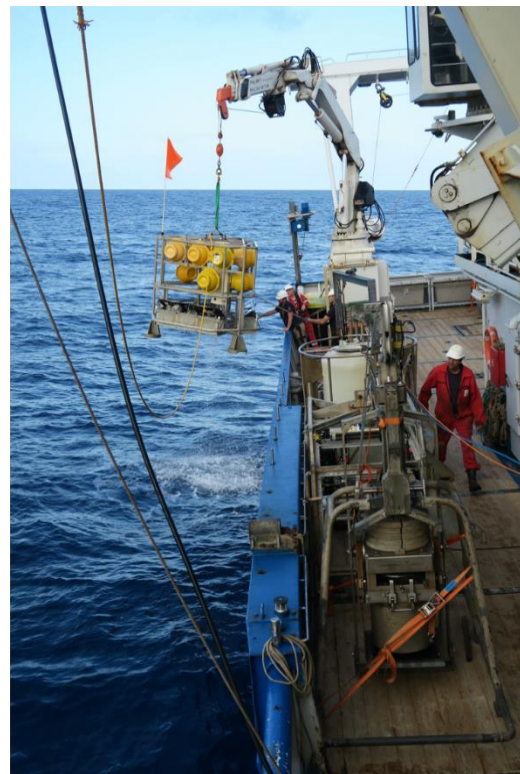


Figure 3 and Figure 4 - Lander recovery. Open boxes can be observed.



Figure 5 - Mussel recovery

3.2. Decomposition of dead mussels

While fauna of the open boxes must be discounted as pelagic animals were captured as well, the mussels of the opened boxes still contained the consumed mussels as these were mounted with a net into the box. The wet weight of the mussels was recorded before and after deployment to measure how much the mussels had degraded, and if there was a difference between the deep-sea vent endemic symbiotic species and the non-symbiotic shallow species.

The *Bathymodiolus* samples were completely stripped of all meat with only the shells remaining. While the *Mytilus* samples still had some meat remaining and had a strong smell of sulphide on them, indicating that they were still being decomposed/consumed. The shells of both *Bathymodiolus* and *Mytilus* were all intact upon recovery.

Table 1 - Dead mussel conditions before and after deployment.

Sample		No. of Mussels	WW Before (g)	WW After (g)	% Remaining	% Degraded	Sulphide Smell
Albex 3	B1	11	670	221	32.99	67.01	No
	B2	11	690	252	36.52	63.48	No
	B3	12	683	250	36.60	63.40	No
Trol	M1	52	667	288	43.18	56.82	Yes
	M2	53	666	257	38.59	61.41	Yes
	M3	49	670	246	36.72	63.28	Yes
	M4	252	3057	1280	41.87	58.13	Yes
	M5	251	3055	1284	42.03	57.97	Yes
	M6	258	3070	1355	44.14	55.86	Yes

3.3. Macrofauna colonisers

In terms of macrofauna, vent animals colonised the dead mussels. The bivalves found were 3 vent-endemic *Bathymodiolus* juveniles (Figure 6). 31 polychaete individuals were encountered, including members of the Hesionidae family and the *Ophryotrocha* genus, both common at hydrothermal vents (see 3.4 Macrofauna polychaete samples). Other polychaete families included Capotellidae, Eunicidae and Terebelidae. The polychaetes were present in almost all of the mussel boxes (Table 2). 338 amphipods were found in the samples, although it is unknown whether they are vent or background species as they were not identified in the framework of this master thesis. No live gastropods were found in the samples and all gastropods found consisted of empty and broken shells. There appears to be no difference in the identified vent taxa preference between the *Bathymodiolus* and *Mytilus* mussels (Table 3, 4).

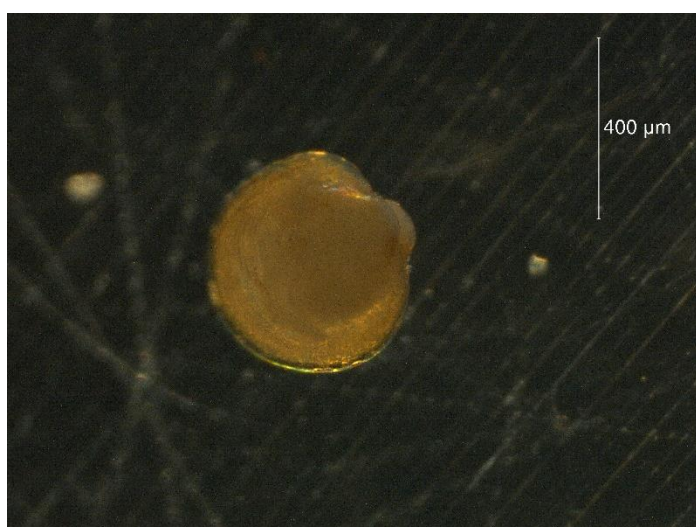


Figure 6 - *Bathymodiolus* juvenile from B2

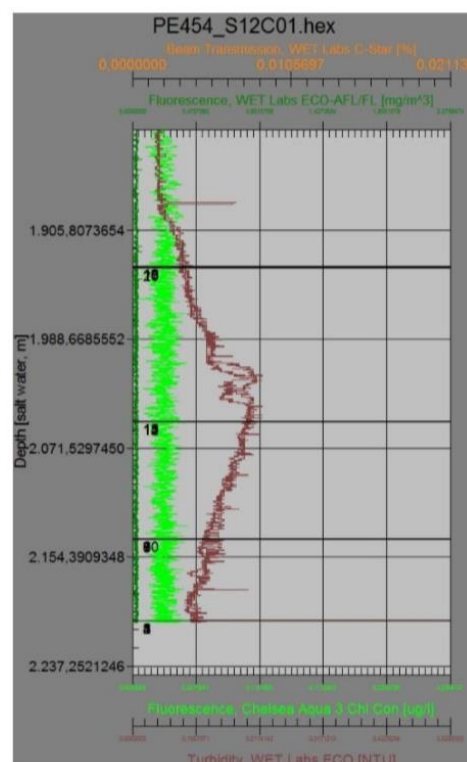


Figure 7 - CTD taken at the lander site indicating that the plume reached the landers. This graph is from the Rainbow 2019 cruise report.

Table 2 - Trol lander fauane

Box	Amphipods	Copepods	Polychaetes	Gastropods	Bivalves	Status
M1	20	261	14	0	0	Open
M2	34	390	0	0	0	Closed
M3	32	241	6	1	0	Open
M4	8	963	1	5	0	Closed
M5	2	870	1	0	0	Open
M6	137	832	7	0	1	Open
MCON1	1	76	0	0	0	Open
MCON2	1	3	0	1	0	Closed
MCON3	0	13	0	0	0	Open
Total	235	3649	29	7	1	

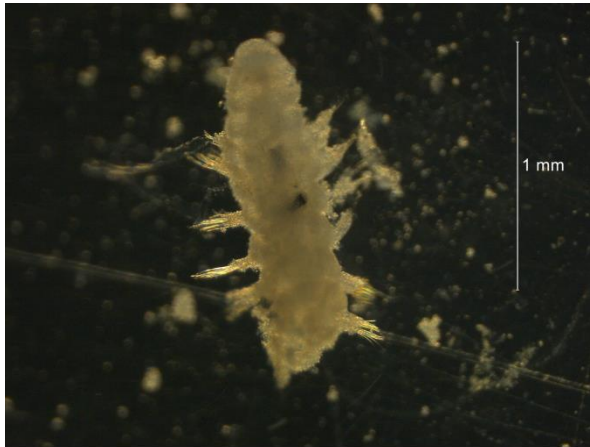
Table 3 - Albex 3 lander fauna

Box	Amphipods	Copepods	Polychaetes	Gastropods	Bivalves	Status
B1	3	302	1	2	1	Open
B2	53	112	5	0	1	Closed
B3	40	209	2	0	0	Open
BCON1	1	351	0	3	0	Open
BCON2	0	288	2	0	0	Open
BCON3	2	6	0	0	0	Closed
BCON4	0	0	0	0	0	Closed
BCON5	2	155	0	4	0	Open
BCON6	2	77	0	1	0	Open
Total	103	1500	10	10	2	

Table 4 - Identified macrofauna

Class	Order	Family	Genus	No. Found	Box Status	Box Name
Polychaete	Eunicida	Dorvilleidae	<i>Ophryotrocha</i>	3	Closed	B2
		Eunicidae		1	Open	M6
	Canalipalpata	Terebellidae		1	Open	M1
	Aciculata	Hesionidae		11	Open	B3, BCON2, M1, M3, M4, M5, M6
		Capitellidae		12	Open	M1, M6
	Unknown Polychaete			3	Open	M1, M6
Bivalve	Mytilida	Mytilidae	<i>Bathymodiolus</i>	3	Open & Closed	B1, B2, M6
Unknown				1	Open	M1

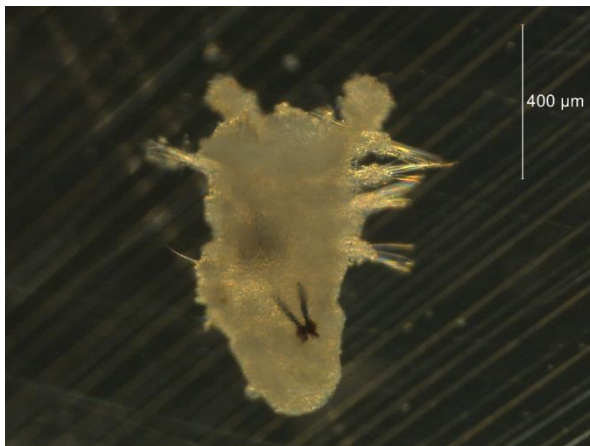
Macrofauna polychaete samples



Ophryotrocha sp. – B2



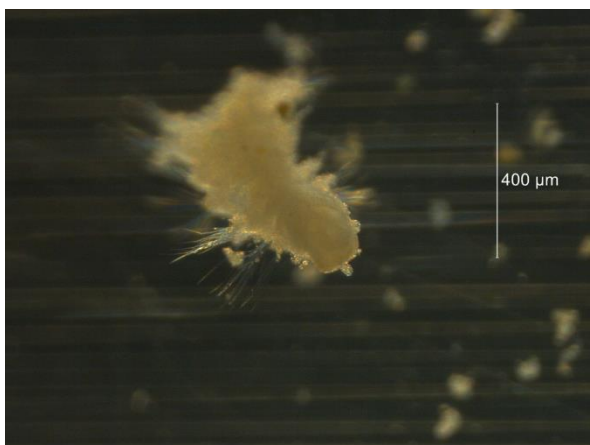
Ophryotrocha sp. – B2



Ophryotrocha sp. – B2



Hesionidae sp. – B3



Hesionidae sp. – B3



Hesionidae sp. – BCON2



Hesionidae sp. – BCON2



Hesionidae sp. – BCON2



Hesionidae sp. – M1



Capitellidae sp. – M1



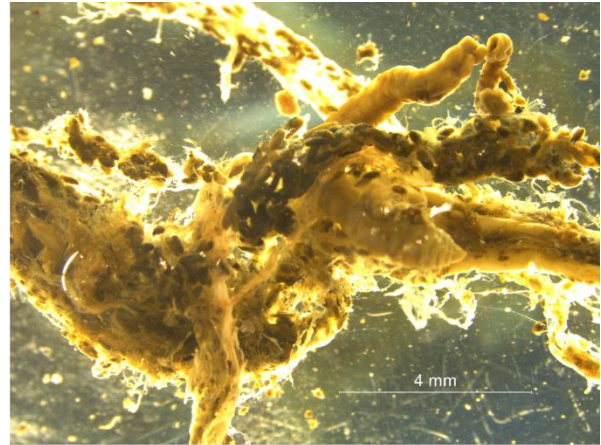
Capitellidae sp. – M1



Capitellidae sp. – M1



Terebellidae sp. – M1



Capitellidae sp. – M1



Hesionidae sp. – M1



Hesionidae sp. – M3



Hesionidae sp. – M4



Hesionidae sp. – M5



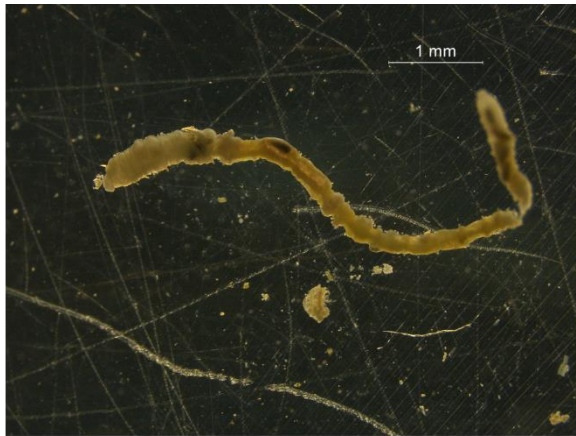
Hesionidae sp. – M6



Capitellidae sp. – M6



Eunicidae sp. – M6



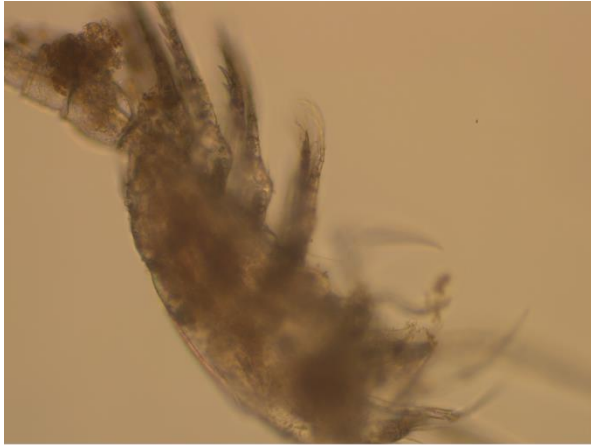
Capitellidae sp. – M6

3.4. Meiofauna colonisers

The only meiofauna present in the samples were copepods. No nematodes or ostracods were present. In total, 1,474 benthic copepods were inspected from both landers. Almost all of the examined copepods were *Tisbe* sp. with only 3 exceptions that were of the vent endemic family *Dirivultidae* which were present in both the dead *Bathymodiolus* and *Mytilus* mussels. Identification of many of the *Tisbe* (3.6 Meiofauna copepod samples) may not be possible as a variety of copepodite life stages were observed in the samples, including some nauplii. Two of the *Dirivulidae* (see 3.6 Meiofauna copepod samples) present were adults and one was a copepodite.

Meiofauna copepod samples

It should be noted that no scale bars are present in the copepod pictures. Due to the COVID-19 virus outbreak, it was not permitted to return to the lab and take pictures to the best possible standards. Each copepod was approximately 1 mm in length.



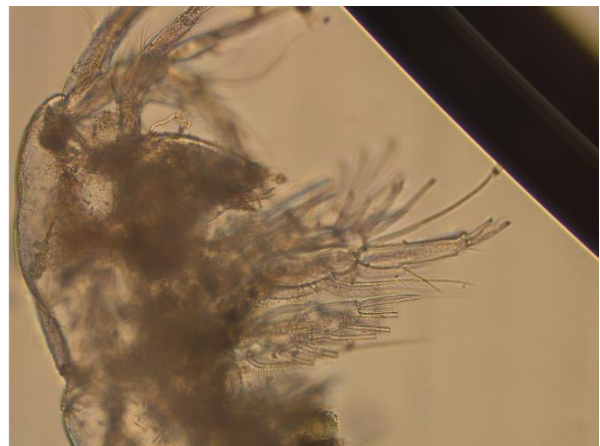
Dirivultidae sp – M4



Dirivultidae sp – M4



Tisbe sp – M4



Tisbe sp – M4



Tisbe sp – M4



Tisbe sp – M4

4. Discussion

The principle objective of this thesis was to test whether food enhancement in the form of dead mussels along mid-ocean ridges could act as a stepping stone for vent fauna. Both macrofauna and meiofauna endemic to vent habitats settled amongst the dead mussels. The identified vent endemic fauna were *Bathymodiolus* mussels and *Dirivultidae* copepods. Fauna that are not necessarily vent endemic, but have been found at active vent sites were polychaetes of the families Hesionidae, Capitellidae and Dorvilleidae, as well as *Tisbe* copepods.

4.1. Which species benefit from food-enhancement?

Whale falls and wood falls are comparative situations to the input of mussels into the deep-sea environment. Much like the results seen in this present study, organisms associated with hydrothermal vents have been found on the carcasses of whales, with similar small portions of vent taxa present and species richness being the result of mostly background taxa (Bennett et al. 1994; Smith et al. 2002; Baco and Smith, 2003; Smith and Baco, 2003; Lundsten et al., 2010). Although there also is evidence of no settlement of vent organisms on whale falls, despite the whale fall being located close to vents (Fujiwara et al. 2007).

While there are animals that are considered vent obligate species, there is not necessarily a clear distinction. The similar conditions between reducing habitats (whale falls, wood falls, hydrothermal vents, cold seeps) are often suitable for taxa that were once thought to be exclusive to a particular habitat. Sibuet and Olu (1998) estimated that 6% of taxa were shared between cold seeps and hydrothermal vents. And Smith and Baco (1998) found that 3.6% of taxa were shared between cold seeps and whale falls. Many of the taxa found in the samples of this study were comprised of background taxa. *Tisbe* and Capitellidae are known generalists and are not endemic to vent environments.

4.2. Background fauna encountered amongst the dead mussels

The copepod genus that was the most abundant in the decomposing mussels was of the genus *Tisbe*, indicating that they benefit the most. They made up almost the entirety of the meiofauna present in the samples to the exclusion of almost all other meiofauna. Tisbidae are typical epibenthic harpacticoids with a cosmopolitan distribution that are mostly associated with hard substrate. They are considered generalist opportunists (Plum et al., 2017) and have been found in both *B. azoricus* assemblages (Ivanenko et al., 2011) and are known to be colonisers of decaying organic matter near to vents (a few 100 m) (Cuvelier et al., 2014; Plum et al., 2017). While they are not endemic to vent habitats, they are tolerant of the abiotic conditions present around hydrothermal vents to an extent (Ivanenko et al., 2011; Plum et al. 2017). In their colonisations study of the Lucky Strike vent field, Plum et al. (2017) counted *Tisbe* as one of the most dominant copepod groups present, settling on wood, bare basalt and bone. In this present study, adult and juvenile *Tisbe* spp. were present in high abundance in the decaying mussels in 4 km distance to the vent, indicating that *Tisbe* is able to very successfully colonise food rich environments. It is unknown yet, if *Tisbe* needs food-stepping stones to successfully colonise vents, or if *Tisbe* is common on hard-substrate along the mid-ocean ridges.

Polychaetes of the family Capitellidae were the most abundant macrofauna in the samples and are often associated with deep-sea high productivity habitats. These organisms were previously found among mussel beds and hydrothermal vents at the MAR, although not previously at Rainbow (Gebruk

et al. 2000; Galkin and Goroslavskaya, 2010; Goroslavskaya and Galkin, 2011, Fabri et al. 2011). Capitellidae can be found in a diverse range of environments and habitats, from the intertidal zone to the deep-sea. Most live in tubes or burrows that they create out of mucous (Blake 2000) (see Macrofauna polychaete samples). In the Atlantic, they have been found in benthic trawls of ridges with low levels of productivity (Kongsrud et al. 2013), and at highly productive whale falls (Silva et al. 2016). Members of this family are described as opportunistic (Blake et al. 2009), as a result, it is no surprise that members of the Capitellidae family are present among the dead mussels. Of the other polychaetes represented in the samples, members of the Eunicidae and Terebellidae families were present. Members of these families have been found in benthic trawls of the MAR along with Capitellids (Kongsrud et al. 2013). Further identification of polychaetes (to species level) is necessary to be able to conclude whether the polychaetes encountered in the experiment are typical vent species. Further, studies in the vent-surrounding are needed to clarify whether vent polychaetes are strictly vent endemic.

Polychaetes of the family Hesionidae were the second most abundant macrofauna present in the samples. These are probably vent species, although there is somewhat of a blurry line as to what is exactly vent endemic in the deep sea. Most deep-sea hesionids have been found in energy rich locations (Summers et al. 2015) including hydrothermal vents and hydrothermal vents along the MAR (Blake 1985; Gebruk et al. 2000, Galkin and Goroslavskaya, 2010; Fabri et al. 2011), cold seeps (Desbruyères and Toulmond, 1998) and whale falls (Pleijel et al. 2008). Due to their almost common nature at sites that have been enriched with organic matter, it is of no surprise that they are present in the dead mussel samples.

The other vent polychaetes represented in the samples were three members of the genus *Ophryotrocha*. The polychaete *Ophryotrocha* is a genus that has been found at both the direct vent environment and at distances of 1 km away from other vent colonisation studies in shallow environments (Tarasov et al. 2005). It has also been found on whale falls (Smith et al. 2002). Further identification of polychaetes (to species level) is necessary to be able to conclude whether the polychaetes encountered in the experiment are typical vent species. Further, studies in the vent-surrounding are needed to clarify whether vent polychaetes are strictly vent endemic.

4.3 Vent fauna encountered amongst dead mussels

Although present, Dirivultid copepods were not present in the abundances that would be expected considering their typical dominance at vent habitats (Gollner et al., 2010). Dirivultid copepods are an epibenthic taxon endemic to hydrothermal vents (Humes and Segonzac, 1998). They are considered hard-substrate species and are known to live where macrofauna like bivalves and tubeworms aggregate (Gollner et al. 2010). Dirivultids are considered habitat generalists within chemosynthetic ecosystems as they are tolerant of different vent flux regimes and temperature gradients (Gollner et al., 2010, Gollner et al., 2011).

In terms of symbiotic macrofauna found in the samples, 3 *Bathymodiolus* juveniles settled in both the *Bathymodiolus* and *Mytilus* landers. *Bathymodiolus* mussels are vent endemic and are only found at hydrothermal vents. The genus is closely related to mussels that specialise in the colonisation of bone or wood (Distel et al., 2000). These communities are based on the microbial decomposition of organic material and the resulting production of hydrogen sulphide (Distel et al., 2000). Genetic analysis has revealed that that vent mytilids evolved from shallow water and cold seep species (Hecker, 1985; McLean, 1985; Newman, 1985), a slow invasion from shallow water into the deep sea is the most likely the origin of vent mytilids and potentially vent fauna in general (Newman, 1985; Caddock et al., 1995). Distel et al., (2000) suggest from their analysis of rRNA sequences, that *Bathymodiolus* and their

relatives first evolved to colonise habitats that would be considered stepping stones, before they evolved to survive the extreme environments of hydrothermal vents.

4.4 Vent meiofauna not encountered amongst dead mussels

No nematodes were present in the samples. This result is surprising as nematodes are usually the most abundant animals found at stepping stone habitats like whale falls (Soltwedel et al., 2018). They have also been found to be the most abundant meiofauna on live *Bathymodiolus* mussel beds (Zekely et al., 2006; Copley et al., 2007) and are the second most abundant taxa found at Rainbow *B. azoricus* mussel assemblages (Galkin and Goroslavskaya, 2010; Goroslavskaya and Glakin, 2011). They were also abundant at senescent vents (Gollner et al. 2020). While their lack of presence in the samples may be influenced by their poor dispersal capabilities (Higgins and Thiel, 1988), they may not be present due to the nature of the lander itself. Nematodes require sediment to burrow through, while benthic copepods can swim. The lander was raised approximately 1 m above the sediment, it is probable that the nematodes simply had no sediment to live in and would potentially be present in the samples if the mussels were closer to, or on the sediment. Future lander experiments could consider the possibility that nematodes could be at significantly higher abundances underneath the lander, as a result of falling decaying mussel material enriching the sediment below and producing a nutrient shadow. While it may be difficult to undertake, taking a boxcore of the lander site directly after its recovery may yield interesting results.

4.5 Can food-enhancement in the form of dead mussels act as a stepping-stone habitat for vent fauna?

While it can be seen from this study that decaying mussels can be a habitat suitable for settlement and colonisation, it is unsure if the dead mussels used in the study would have lasted long enough for the reproduction of symbiotic vent fauna, as the mussel meat was consumed in a year. Three *Bathymodiolus* juveniles were found in this study, indicating that conditions were potentially suitable for settlement of larvae. As adult, *Bathymodiolus*' primary sources of energy are through its resident symbiotic bacteria which oxidize reduced sulphur and methane into organic compounds (Fiala-Médioni and Felbeck, 1990). As well as their obtained energy from their symbionts, *Bathymodiolus* mussels can also filter feed (Page et al., 1991), allowing them to be potentially very successful colonisers. Due to the relatively small amount of hydrogen sulphide present at the site, it is rather unlikely that the juveniles would have enough energy available to them to be able to reproduce. However, there are members of the Bathymodiolinae subfamily who are sexually mature in an incredibly short amount of time, when they are at very small sizes (Laming et al., 2014). *B. azoricus* reaches 1st maturity at a length of ≥ 30 mm (Colaço et al., 2006). *B. azoricus* specimens that have been collected from Menez Gwen reveal a seasonal spawning pattern, with spawning occurring potentially from December to January (Dixon et al., 2006). If this pattern is also representative of Rainbow then the lander juveniles may have only settled approximately halfway through the lander experiment. Accounting for the time it would take to travel from the vent to the landers it is possible that the settling mussels had enough time to reach sexual maturity. If it is the case that these *Bathymodiolus* juveniles in the lander samples had reached sexual maturity, despite their small sizes then the dead mussels would be able to act as an effective stepping stone within one year. However, it is to date unknown how long entire hydrothermal vent mussel beds take to decompose after vent fluid emissions have ebbed.

With regards to non-symbiotic vent fauna, the stepping stone was in principle suitable for the settlement and reproduction for the vent endemic Dirivultidae copepods, since adult and juvenile specimens were detected. Dirivultids can swim (Heptner and Ivanenko, 2002), however their principle opportunity for dispersal comes before they reach adulthood as many of their copepodite stages have been found in water column samples taken above vents (Ivanenko, 1998; Gollner et al., 2015). Analysis of their COI gene suggests that dirivultids have a high dispersal capability along ocean ridges (Gollner et al., 2011). The CTD measurements taken during the Rainbow 2019 cruise (Figure 7), showed that the vent plume was still detectable at the lander site, indicating that the vent plume reached the landers and revealed the vent copepods likely route to settle at the mussels. Gollner et al., (2015) demonstrated that despite their key differences in life traits, vent animals do not necessarily need a vent habitat to settle, although there will be differences in abundance and survival rates. However, while initial conditions may have been suitable for settlement of the juveniles, productivity appears to be the limiting factor in the distribution of vent fauna (Mullineaux et al. 2009). Dirivultid copepods typically reach sexual maturity already on the scale of weeks (Gollner et al., 2010), which is well within the timescale of the complete *B. azoricus* degradation. Therefore the dead mussels of this study could be an effective stepping stone habitat for the vent-endemic Dirivultid copepods, with adults and juveniles present.

4.6. Potential explanations for the low diversity encountered in the experiment

Diversity cannot be statistically quantified due to two main reasons; not all of the box lids closed upon recovery leaving a sample size which is too small, and the animals found in the samples were not identified to species level. Despite this, low richness and evenness can still be observed in the copepod results. This result is unexpected as copepod diversity has been typically much higher at similar wood deposits, whalefalls and food-enrichment studies (Amon et al., 2017; Plum et al., 2017). While it is mostly speculative, reflecting on possible explanations can be useful for formulating new hypotheses for future studies.

In the deep-sea environment, the most influential variable on the diversity and abundance of species in a habitat are the abiotic environmental conditions (Mullineaux et al., 2003; Gollner et al., 2010b, 2015; Ivanenko et al., 2011; Plum et al., 2017). Hydrogen sulphide, the principle source of energy in these habitats, is a toxic chemical that may cause less diverse communities (Sarrazin and Juniper, 1999; Van Dover, 2002; Gollner et al., 2010; Gollner et al., 2020). In environments where it is present, only the tolerant or the specialists are able to endure its effects and so diversity is reduced as a result (Gollner et al., 2010). However, while the presence of H₂S in the landers may have deterred more sensitive species, it is unlikely that the relatively low concentrations that would have been present would have resulted in the low diversity that has been observed. Particularly since analogous whale and wood fall habitats typically do not have similarly low levels of diversity (Smith and Baco, 2003).

Alternatively, it could be the case that the low diversity present at the landers are a reflection of the Rainbow vent field itself. Rainbow is known for its extreme and intense effluent (Douville et al., 2002). And it is well understood that fewer species are able to survive in more extreme conditions, leading to less diverse communities (Galkin and Goroslavskaya, 2010; Ivanenko et al., 2011; Gollner et al., 2010, 2015). When comparing Rainbow communities to the Lucky Strike and Menez Gwen fields, Rainbow has lower levels of diversity (Galkin and Goroslavskaya, 2010). While there have been general diversity studies done at Rainbow, no studies focussing on meiofauna have been done to date. It is possible that the lack of diversity in the meiofaunal lander samples mirror the levels of copepods diversity at Rainbow.

4.7. Association between diversity and type of food (shallow water non-symbiotic *Mytilus* versus deep-sea symbiotic *Bathymodiolus*)?

Due to the fact that the lids on the boxes did not close for all of the boxes, the sample sizes between the two landers are too small to be able to undertake robust statistical analysis. As it stands between the two landers, there was no difference in meiofaunal diversity between the two landers. The identified vent macrofauna appeared to have no preference between the *Bathymodiolus* and *Mytilus* mussels as the *Bathymodiolus* juveniles and the Hesionid polychaetes were found in both landers.

The key difference to note between the *Mytilus* and the *Bathymodiolus* mussels was the rate of decomposition over the course of the year. There are many possible factors that contribute to this outcome. Some such explanations could be the morphological differences influencing the feeding of scavengers. Another could be the deep-sea microbes responsible for the mussel degradation would be better adapted to decompose deep sea mussels instead of shallow mussels.

4.8. Lander comments

The landers don't collect any information from sediment colonisers which explains why there are no nematodes in the samples. This is leaving out a significant portion of the meiofaunal community and it is possible that vent species were not collected due to this.

Another limitation would be the length of deployment time. With an experiment of this size, there wasn't enough food to provide an insight into further stages of succession. Having a larger experiment with more food would possibly allow for succession of animals after the pioneer *Tisbe*. The *Bathymodiolus* mussels were completely stripped of all meat after one year so there may be a much larger quantity of mussels required to keep the experiment running longer, and it may quickly reach a point of diminishing returns. Further experimentation with dead mussels could consider the role that depth plays in terms of both species' richness and the rapidity at which the carcasses degrade.

One potential problem was the level of taxonomic resolution performed on the samples. Copepods were identified to the genus level and macrofauna were predominantly identified to the family level. As a result, it can be expected that the level of richness in the samples could be higher than what is recorded here.

5. Conclusion

Dead mussels act as a stepping stone for vent endemic dirivultid copepods, with juvenile and adult specimens living amongst the dead mussels. Juvenile vent-endemic *Bathymodiolus* mussels could settle amongst the food provided and may reach sexual maturity quickly, but it is not known if this habitat provides enough energy for its reproduction. In addition, numerous adult and juvenile *Tisbe* copepods were encountered, a genus that is an abundant pioneer at vents but not restricted to vents. Similarly, polychaetes of the families Hesionidae, Capitellidae and Dorvilleidae are not necessarily vent endemic, but have been found at active vent sites. Dead mussels can act as stepping stones for at least some vents species. Future studies may include analyses of biodiversity in the vent-surrounding to better understand endemism at vents.

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