



Bait attending fishes of the abyssal zone and hadal boundary: Community structure, functional groups and species distribution in the Kermadec, New Hebrides and Mariana trenches

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ARTICLE INFO

Keywords:

Deep-sea fish

Deep sea

Zonation

Kermadec Trench

New Hebrides Trench

South Fiji Basin

Mariana Trench

Pacific Ocean

Abyssal hadal transition zone

AHTZ

ABSTRACT

Baited landers were deployed at 83 stations at four locations in the west Pacific Ocean from bathyal to hadal depths: The Kermadec Trench, the New Hebrides Trench, the adjoining South Fiji Basin and the Mariana Trench. Forty-seven putative fish species were observed. Distinct fish faunal groups were identified based on maximum numbers and percentage of observations. Both analyses broadly agreed on the community structure: A bathyal group at < 3000 m in the New Hebrides and Kermadec trenches, an abyssal group (3039–4692 m) in the Kermadec Trench, an abyssal-hadal transition zone (AHTZ) group (Kermadec: 4707–6068 m, Mariana: 4506–6198 m, New Hebrides: 2578–6898 m, South Fiji Basin: 4074–4101 m), and a hadal group of endemic snailfish in the Kermadec and Mariana trenches (6750–7669 m and 6831–8143 m respectively). The abyssal and hadal groups were absent from the New Hebrides Trench. Depth was the single factor that best explained the biological variation between samples (16%), the addition of temperature and average surface primary production for the previous year increased this to 36% of variation.

The absence of the abyssal group from the New Hebrides Trench and South Fiji Basin was due to the absence of macrourids (*Coryphaenoides* spp.), which defined the group. The macrourids may be energetically limited in these areas. In their absence the species of the AHTZ group appear released of competition with the macrourids and are found far shallower at these sites.

The fish groups had distinct feeding strategies while attending the bait: The bathyal and abyssal groups were almost exclusively necrophagous, the AHTZ group comprised predatory and generalist feeders, while the hadal snailfishes were exclusively predators. With increasing depth, predation was found to increase while scavenging decreased. The data suggest scavenging fish fauna do not extend deeper than the hadal boundary.

1. Introduction

The abyssal zone (3000–6000 m) accounts for the majority of the world's surface (Vinogradova, 1997) with the average global ocean depth of ~4200 m (Danovaro et al., 2014; Thurber et al., 2014). With the exception of some small, isolated basins (e.g. in the Mediterranean sea, parts of the Indo-West Pacific and the Guatemalan Basin), deep water corridors are found between the majority of the world's abyssal basins (Briones et al., 2009). It is assumed that abyssal fish species possess large geographical ranges unimpeded by depth barriers (Vinogradova, 1997).

Despite assumed wide distribution, the bathymetric and geographic extent of abyssal fish species is only known at the resolution of which sampling has occurred (Carney, 2005). The abyssal, and in particular the lower-abyssal to abyssal-hadal transition zone (AHTZ; Jamieson et al., 2011), are seldom studied due to the technical challenges of sampling at increasing distance from the vessel, and hydrostatic pressures. Furthermore, the geographic extent of the abyssal zone is such that even geographically wide studies are performed in relatively small areas and there are few that unequivocally define geographic boundaries. This is especially the case in the

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Pacific Ocean due to its immense size (165.2 million km², mean depth = 4280 m). The expense of sea-time has led to a tendency for research to be carried out in relatively close proximity to land masses (Kintisch, 2013), specifically around nations actively involved in deep-sea research (e.g. Japan, New Zealand, USA). Studies seldom addressed the distribution of fishes on greater geographic scales and across areas of contrasting environmental conditions. Fish beyond the abyssal-hadal transition zone have rarely been studied (Fujii et al., 2010; Jamieson et al., 2010; Nielsen, 1964) although the bathymetric range of fishes is known to exceed 8000 m (Linley et al., 2016; Yancey et al., 2014).

In addition to the geographic and bathymetric expanse, the deep Pacific Ocean seafloor underlies highly variable surface productivity, with two very large oligotrophic gyres in the northern and southern hemispheres. The distribution and community structure of deep fishes is often observed to change in response to variation in overlying surface productivity resulting in a non-homogeneous distribution. This effect is usually explored through comparison of a high and low productivity location (e.g. Cousins et al., 2013a; Priede et al., 2003; Sulak, 1982). Determining the drivers of community structure and thereby disentangling the effects of depth, location, food supply and other environmental parameters requires standardised data over large areas and greater depth ranges.

Conventional sampling of abyssal fish using trawls is problematic. It is very time consuming and requires specialised and expensive vessels and equipment, which reduces opportunity and restricts access (Kintisch, 2013). These challenges have prompted extensive use of free-fall baited landers as an alternative to trawls, which offer increased opportunity for access from vessels of a wide range of size and capabilities, relatively unrestricted by depth. With baited landers, the results are limited to scavenging species and species that prey upon scavengers (necrophagivores), collectively referred to as 'bait-attending'.

The baited lander methodology emulates a natural process. Large food falls, often in the form of the carcasses of shallower living fauna but also including wood and macroalgae, represent a local and highly concentrated organic input to the deep sea. The scale of such food falls can range from fishes and birds (mesocarrion ~1 kg), to seals and dolphins (macro carrion ~100 kg) and the largest cetaceans (megacarrion > 100 000 kg) (Bailey et al., 2007; Britton and Morton, 1994; Higgs et al., 2014; Kemp et al., 2006; Smith et al., 2015; Stockton and DeLaca, 1982). Particulate material from surface productivity decreases rapidly with depth (Lutz et al., 2007) whereas carrion-falls should in theory occur irrespective of depth. It is hypothesised that direct scavenging (or indirect predation through 'bait-attending') may have an increasingly important role in maintaining deep-water fish communities with increasing depth (Yeh and Drazen, 2011).

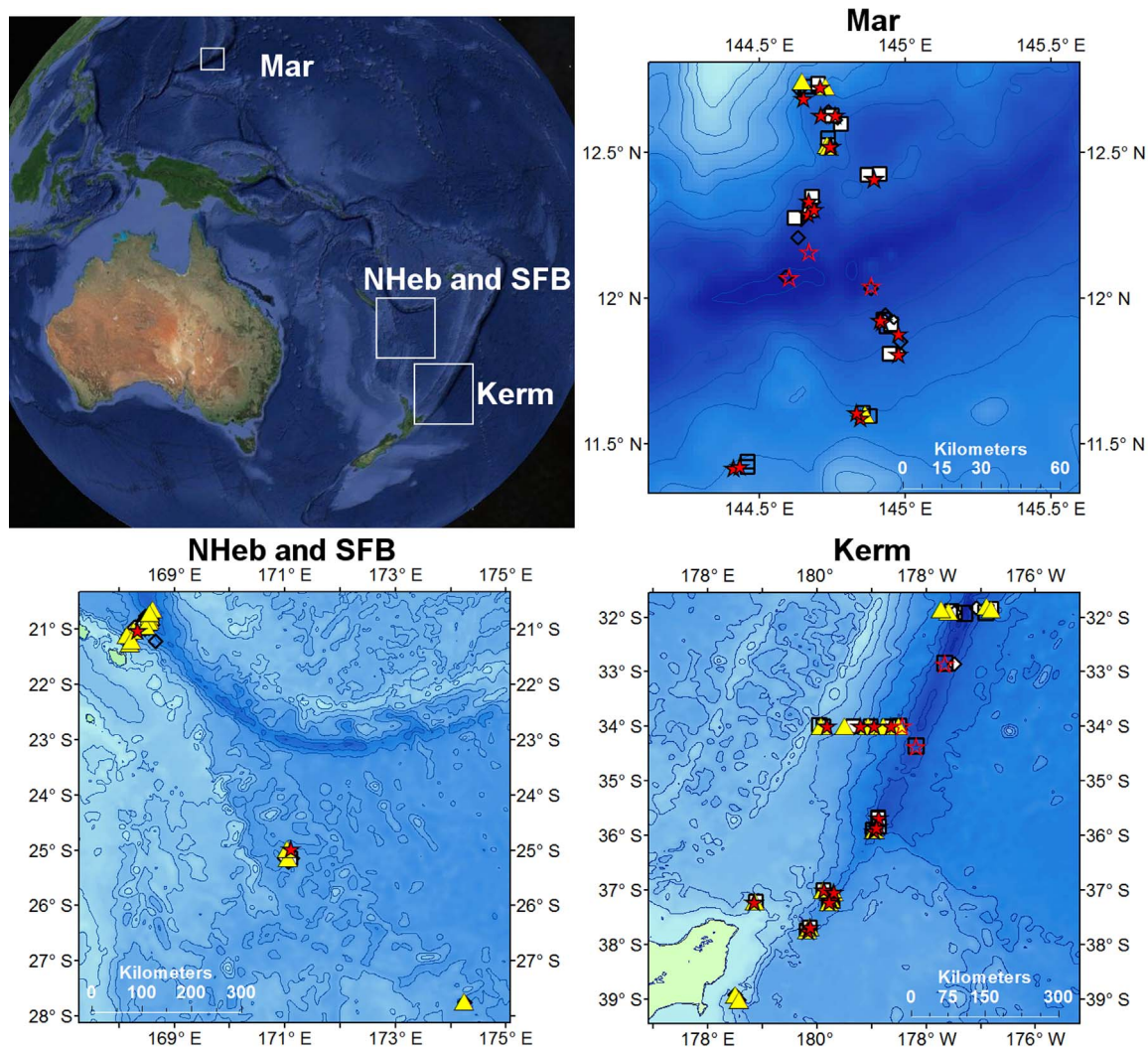


Fig. 1. Sampling locations. Triangles represent *Abyssal-lander* deployments, stars the *Hadal-lander* deployments, squares the *Large Fish Trap* and diamonds the *Small Fish Trap*. Deployments that did not record fish are hollow outlines. Isobaths have been added at 1000 m intervals. Global overview is adapted from Google Earth (Google, 2016), the location maps are produced from GEBCO bathymetry data (GEBCO, 2015).

The current study examined trends in the species composition and function (whether scavenging or predatory) of bait-attending fish communities in three hadal trench systems in order to explore:

1. The occurrence of distinct fish communities from bathyal to hadal depths.
2. If the same pattern is common to all trenches.
3. Drivers of community change, bathymetrically and/or geographically.

2. Materials and methods

2.1. Study sites

The four study locations (Fig. 1) in the west Pacific can be characterised as follows:

1. The Kermadec Trench (Kerm) is a deep (10,047 m), cold trench which underlies the most productive surface waters within this study. The trench is formed by the subduction of the Pacific Plate under the Australian Plate resulting in a trench 1500 km long and on average 60 km wide (Angel, 1982).
2. The New Hebrides Trench (NHeb) is 1000 km to the northwest of the Kermadec Trench. It is a shallower trench of ~7156 m. Relative to the other trenches in this study it is the warmest, and underlies intermediate productivity. The trench is formed by the Australian plate subducting north-eastwards under the overriding Vanuatu archipelago resulting in a trench ~ 1200 km long.
3. The South Fiji Basin (SFB) partitions the Kermadec and New Hebrides trenches. The basin is a uniform abyssal plain (~4100 m) with similar water temperature and average surface productivity as the New Hebrides Trench.
4. The Mariana Trench (Mar) is located southeast of the island of Guam in the Central Pacific. It is of intermediate bottom temperature. It underlies the lowest surface productivity of the areas studied. It is the deepest trench in the world, with a maximum depth of ~11,000 m (Gardner et al., 2014) and is 2550 km long with a mean width of 70 km (Angel, 1982). The trench is formed as the Pacific Plate subducts beneath the Mariana Plate to the west.

When discussed in the text the names of the trenches refer to an area wider than just the trench and include the surrounding bathyal and abyssal depths.

2.2. Equipment

Data were collected by the 6000 m rated *Abyssal-lander*, and the full-ocean depth *Hadal-lander*, part of the Oceanlab fleet of autonomous landers at the University of Aberdeen. The systems are negatively buoyant on release from the vessel and free-fall to the seafloor. Upon acoustic command from the surface, ballast is jettisoned via dual acoustic releases, and the systems return to the surface by virtue of a positively buoyant moored glass sphere (Nautilus, Germany) floatation array above the landers.

The *Abyssal-lander* is described in Linley et al. (2015). The *Abyssal-lander's* 5 megapixel digital still camera is suspended 2 m above the seabed and is optimised to this focal length. The camera faces vertically downwards to a steel ballast clump, a scale cruciform (50 cm axis length, 10 cm markers) and 500 g of bait, resting on the seafloor. All systems were baited with a locally sourced ungutted oily fish; mackerel (*Scomber* spp.) or jack mackerel (*Trachurus* spp.). The area of seabed recorded by the *Abyssal-lander* was 2×1.5 m, and an image was taken every 60 s throughout the deployment.

The *Abyssal-lander* also included a Seaguard recording platform (Aanderaa, Norway) equipped with a Doppler current meter (RDCM) and conductivity, temperature and pressure (CTD) probes recording at 30 s intervals, ~2.5 m above the seabed.

The *Hadal-lander* (described in Jamieson (2015)) lands directly onto the seabed, resting on the frame feet and records video in a near-horizontal orientation. A 120 cm long tubular arm secured the bait within view of the camera and included a horizontal scale bar at the point of bait attachment. The field of view was approximately 40° giving ~75 cm scene width at 120 cm in front of the camera. The basic delivery system was the same as the *Abyssal-lander*, but rated to 11,000 m operational depth. The scientific payload comprised a 3CCD Hitachi colour video camera (800 TV lines), controlled and logged autonomously by a custom built control system (NETmc Marine, UK). Illumination was provided by two LED lamps within glass vacuum spheres. The camera was pre-programmed to take 1 min of video in every 5 min, and was powered by a 12V lead acid battery (SeaBattery; DSP & L, US). An SBE-39 pressure and temperature sensor (Sea-Bird Electronics, US) logged at 30 s intervals throughout.

Trapping systems were deployed alongside the imaging landers to collect voucher specimens to verify the image identifications. Two traps were used, both were deployed and recovered using the same method as the imaging landers. The *Small Fish Trap*; was described in Jamieson et al. (2013). The *Large Fish Trap* was a 1×1×2 m netting covered frame. Two entrance configurations were used: four tapering 20 cm² funnel entrances or two wide openings 70×15 cm close to the seabed and four 15×30 cm on the alternate sides. Mesh size was 1.5 cm at widest point in all systems.

2.3. Data processing

Each *Abyssal-lander* image and *Hadal-lander* video was analysed manually and all observed fish were identified to the lowest possible taxonomic level. Anderson et al. (1998) provided a general overview of bathyal species known in the New Zealand Exclusive Economic Zone (EEZ) which helped in identifications. Specific taxonomic texts were consulted for each of the major groups. The macrourids were identified following Cohen et al. (1990), with Jamieson et al. (2012) allowing distinction between *Coryphaenoides armatus* and *C. yaquinae* from *in situ* images. The ophiidiids were identified following Nielsen et al. (1999) and Nielsen and Merrett (2000). Additional sources consulted included: Anderson (1994), Castle (1968), Froese and Pauly (2016), Gon and Heemstra (1990), Iwamoto and Sazonov (1988), Karmovskaya and Merrett (1998), Sulak and Shcherbachev (1997).

The *Hadal-lander's* horizontally oriented camera imaged fish in a lateral view that provided more taxonomic detail. Deinterlaced stills were taken from the video using VLC media player (VideoLAN, 2013) when the target animal was best positioned. The open-source image analysis software package 'Fiji' (Schindelin et al., 2012) was used to measure relative body proportions of distinct individuals (identified through differences in colouration, size or scarring). If the animal was parallel to the scale bar and at the same distance from the camera as the scale bar, length estimation was also possible. The cell counter plugin (De Vos and Rueden, 2015) was used to count fin rays and scale rows.

The video recorded by the *Hadal-lander* allowed for the observation of feeding behaviour. A feeding event was defined as either suction feeding directed at, or a fish's jaw closing on, the bait (necrophagy) or another animal (predation). No distinction was made between successful and unsuccessful strikes, as this could not often be determined. Multiple feeding events by the same animal were all counted. Fish suction feeding at the surface of the bait would often take bait into their mouth also. These feeding events were considered necrophagous. When being compared, the feeding events were standardised to events per fish (of that species) per minute.

In addition to the environmental data from the Seaguard platform, the biological pump model outlined in Lutz et al. (2007) provided an estimate of particulate organic carbon (POC) transport to the seabed at the sampling locations. The Ocean Productivity Datasets (Behrenfeld and Falkowski, 1997) were used to estimate surface primary produc-

tion at each location during the month of the deployment and an average value for the previous year. The time of day that the lander arrived at the seabed, expressed as ‘quarter of day’ (6 h blocks from midnight) was included to detect any diurnal variation. In the absence of samples the seabed sediments were interpreted from lander images using a modified classification based on Wentworth (1922) and Folk (1954). Six categories were identified: bedrock, cobbles and pebbles, muddy gravel, gravelly fine-grained sediment, slightly gravelly fine-grained sediment, and fine grained-sediment. It was not possible to categorise the 5254 m site within the Kermadec Trench as the seabed was not clearly visible in the image.

2.4. Analysis

All non-permutation based statistical analysis was produced using R (R Development Core Team, 2005), figures were produced using ggplot2 (Wickham and Chang, 2007). Relationships between feeding type and location and depth were explored through fitting of generalised linear models (GLM) using the Gaussian family. The significance of explanatory variables, residual plots and Akaike Information Criterion (AIC) values were referenced to adjust the models to best fit the data. The resulting models were assessed through Analysis of Variance (ANOVA) F-tests using type-II sum of squares.

The two landers are not directly comparable due to their different fields of view and sampling frequencies. Data collected by the *Abyssal-lander* lends itself better to statistical analysis due to its fixed field of

view, discrete sampling method and larger suit of environmental sensors. Two metrics are commonly extracted from lander data (Farnsworth et al., 2007; Fleury and Drazen, 2013): (1) The time of first arrival (T_{arr}) is the time from the arrival of the lander at the seabed until the first arrival of each species; and (2) The maximum number (MaxN) of individuals of each species observed simultaneously. T_{arr} can be difficult to work with due to its high variability and inverse relationship with fish abundance (Farnsworth et al., 2007; Friede et al., 1990). MaxN is a more reliable proxy of local fish density than T_{arr} (Stoner et al., 2008; Willis and Babcock, 2000; Yeh and Drazen, 2011). The MaxN data from the *Abyssal-lander* formed the initial basis of the quantitative multivariate analysis. A second “percent of observations” (%Ob) dataset included both the *Abyssal-lander* and *Hadal-lander* data: Each image or video sequence was considered a single observation and fish species were characterised by what proportion of observations they were present in, for each camera deployment. In order to validate combining the data in this way, a one-way analysis of similarities (ANOSIM) for location and lander with up to 999 permutations was performed on the %Ob dataset for the depth range sampled by both landers.

Community structure analysis was performed in Primer 6.1.14 (Clarke and Gorley, 2006). A square root transformation was applied to the MaxN *Abyssal-lander* data and the %Ob data from both lander systems. Before proceeding a RELATE test using Spearman rank correlation on 999 permutations was used to evaluate if the duration of the deployments had a significant effect on the biological data.

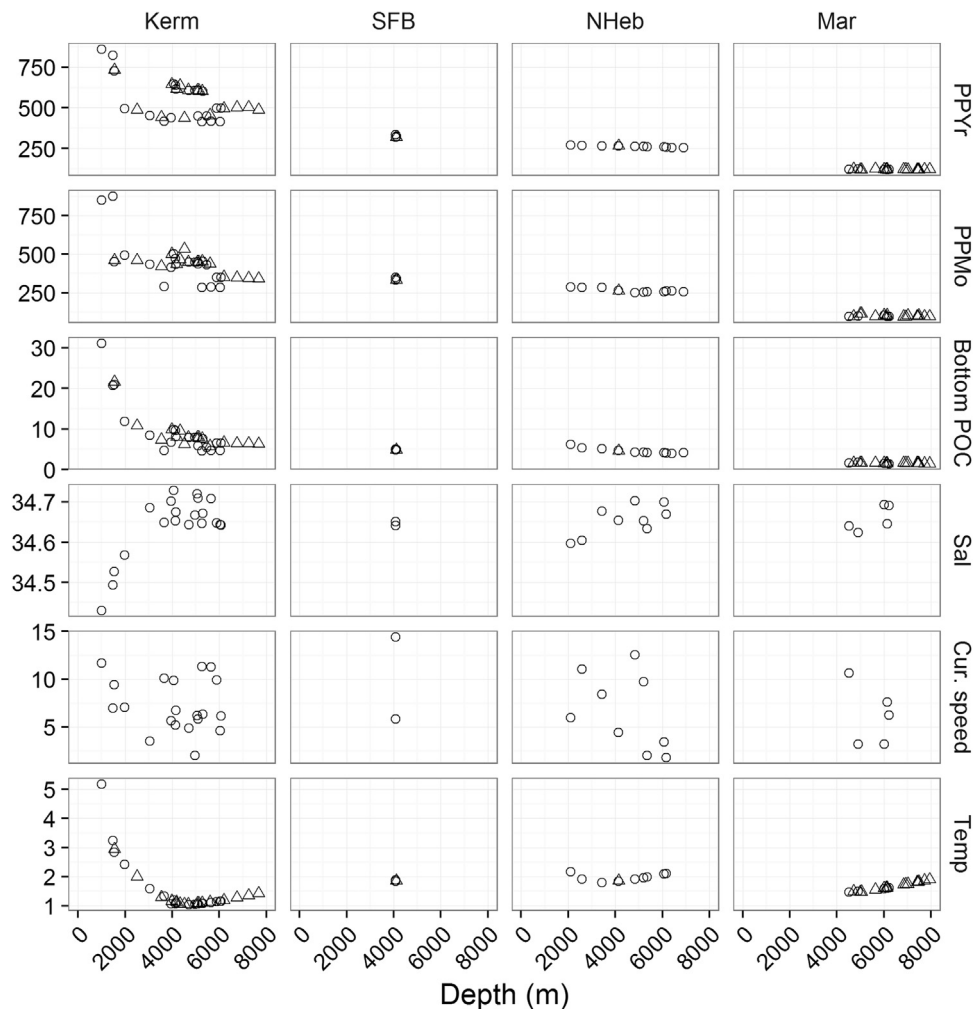


Fig. 2. Estimated surface primary production for the previous year (PPYr), the month of the deployment (PPMo) and flux to the seabed (Bottom POC) in $\text{mg C/m}^2/\text{day}$, Salinity (Sal) in PSU, Current speed (Cur. Speed; cm/s) and temperature (Temp) in $^{\circ}\text{C}$ measured by the Abyssal-lander (circles) and Hadal-lander (triangles) in the Kermadec Trench (Kerm), South Fiji Basin (SFB), New Hebrides (NHeb) and Mariana (Mar) trenches.

Bray-Curtis similarity was applied pairwise to all deployments to produce a resemblance matrix of fish community distance between deployments. CLUSTER (hierarchical agglomerative/bottom-up clustering) group average analysis was then performed. The structure formed through clustering was assessed with a similarity profile analysis (SIMPROF) test of 999 permutations at the 5% significance level. This was used to group deployments into statistically distinct groups based on their community structure which were then displayed using non-metric multidimensional scaling (MDS). Similarity percentages analysis (SIMPER) was performed to quantify the similarity/dissimilarity among the identified groups, and to identify those species

most responsible (up to 90% cumulative within-group similarity) for defining those groups.

Environmental predictors were pairwise plotted against each other (Draftsman plots), to identify any skew or inter-correlation. A heavy right-skew to temperature was corrected through natural log transformation. All environmental data were then normalised to make the different measurement scales comparable.

Distance-based linear models (DISTILM) as part of the PERMANOVA (Gorley and Clarke, 2008) expansion to PRIMER 6 were used to explore the relationship between fish community structure and the potential environmental predictors. BEST procedure (all

Table 1

Fish categories and the depth range (m) observed in each study area. Data from imaging landers and traps. * denotes extreme of range from trap, † denotes voucher specimen captured.

Family	Species	Study Site			
		Kerm	SFB	NHeb	Mar
Myxinidae	<i>Neomyxine caesiovitita</i> Stewart & Zintzen, 2015, in Zintzen et al. (2015)	997	– 1013†		
Chimaeridae	<i>Hydrolagus</i> cf. <i>affinis</i> (de Brito Capello, 1868)	1527	– 2503	2087	– 2578
Somniosidae	<i>Centroscymnus</i> cf. <i>coelolepis</i> Barbosa du Bocage & de Brito Capello, 1864	997	– 1971		
	<i>Centroscymnus oustonii</i> Garman 1906	1527	– 1980		
Etmopteridae	<i>Etmopterus baxteri</i> Garrick, 1957	1473	– 1554		
Rajidae	<i>Amblyraja hyperborea</i> (Collett, 1879)	1527	– 1554		
Arhynchobatidae	cf. <i>Bathyraja richardsoni</i> (Garrick, 1961)	1971	– 2503	2087	– 2578
Halosauridae	<i>Aldrovandia affinis</i> (Günther, 1877)		4078	– 4078	
	<i>Halosaurusopsis macrochir</i> (Günther, 1877)	1473	– 1473		
Congridae	<i>Bassanago bulbiceps</i> Whitley, 1948	997	– 1527		
Synphobranchidae	<i>Diastobranchus capensis</i> , Barnard, 1923	997	– 1971†		
	<i>Ilyophis robbinsae</i> / Large Synphobranchidae Sulak and Shcherbachev, 1997	3039	– 6068	4074	– 4100
	<i>Simenchelys parasitica</i> Gill, 1879	997	– 2503†		
	<i>Synphobranchus brevidorsalis</i> Günther, 1887			2087	– 2087
Alepocephalidae	<i>Alepocephalid</i> spp.	1554	– 1554	2578	– 2578
Macrouridae	<i>Bathygadus</i> sp.	1473	– 1554		
	<i>Coelorinchus</i> sp.	997	– 997		
	<i>Coryphaenoides armatus</i> (Hector, 1875)	3039	– 4692†		
	<i>Coryphaenoides ferrieri</i> (Regan, 1913)	1527	– 3975		
	<i>Coryphaenoides</i> cf. <i>filicauda</i> Günther, 1878	4194	– 4194		
	<i>Coryphaenoides leointei</i> (Dollo, 1900)	4953	– 4953		
	<i>Coryphaenoides leptolepis</i> Günther, 1877	3655	– 4138		
	<i>Coryphaenoides longifilis</i> Günther, 1877	1971	– 1971	2087	– 2087
	<i>Coryphaenoides rudis</i> Günther, 1878	1971	– 1971	2087	– 2087
	<i>Coryphaenoides yaquinae</i> Iwamoto & Stein, 1974	3655*†	– 5879		4441*†
	<i>Trachyrincus longirostris</i> (Günther, 1878)	997	– 997		– 7012
	Macrourid 1	1527	– 1971		
	Macrourid 2	4138	– 4138		
	Macrourid 3	1527	– 1527		
	Macrourid 4	5281	– 5281		
	Macrourid 5	4158	– 4953		
Moridae	<i>Antimora rostrata</i> (Günther, 1878)	1473	– 2503	2087	– 2578
	<i>Lepidion microcephalus</i> Cowper, 1956	997	– 997		
	<i>Mora moro</i> (Risso, 1810)	997	– 997		
Carapidae	<i>Echiodon cryomargarites</i> Markle et al., 1983	1473	– 1473		
Ophidiidae	<i>Barathrites iris</i> Zugmayer, 1911	5254	– 5254	4074	– 4100†
	cf. <i>Bassogigas</i> sp.		4100†	4700	– 5300*†
	<i>Bassozetes</i> spp.	4519	– 6750	4074	– 4100
	cf. <i>Bassozetes glutinosus</i> (Alcock, 1890)			2087	– 6898
	<i>Bassozetes</i> cf. <i>compressus</i> (Günther, 1878)			2578	– 2578
	<i>Bathyonus caudalis</i> (Garman, 1899)	3039	– 3039		4506
	<i>Spectrunculus grandis</i> (Günther, 1877)	1980*†	– 4332	2578	– 2578
Psychrolutidae	<i>Psychrolutes microporos</i> (Nelson, 1995)	1473	– 1527		
Liparidae	<i>Notoliparis kermadecensis</i> (Nielsen, 1964)	5879	– 7669†		
	Mariana snailfish			6198	– 8078†
	Ethereal snailfish			8007	– 8143
Zoarcidae	Gen et spp.	3039	– 4989*†	4074	– 4100*†
				3424	– 6162†
				5044	– 6142

possible combinations of predictors) was performed with Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) selection criteria. The two measures differ in their ‘penalty’ towards the addition of predictors; AIC has a lower penalty and is therefore more generous in the addition of predictors than BIC (Gorley and Clarke, 2008). Marginal tests were used to remove predictors not significantly ($\alpha=0.05$) correlated with the biological data. Heavily inter-correlated and therefore interchangeable predictors were explored. Variables were selected over their correlates if they had more significant p-values and explained more of the biological variation when combined with other variables. The models were then visualised using Distance Based Redundancy Analysis (dbRDA).

Across all study locations, 83 lander and 84 trap deployments were achieved (Fig. 1). Full deployment details are included in Supplementary material (lander deployments: Table S1, trap deployments: Table S2). When specific deployments are referred to it will be by their region and depth as defined in the Supplementary material.

3. Results

3.1. Environmental characteristics

The depth related trends of the recorded or estimated environmental variables at each of the study locations are illustrated in Fig. 2.

3.2. Species diversity

Of the 83 Abyssal-lander and Hadal-lander deployments 77 included fish observations (Supplement Table S1). A total of 47 fish Operational Taxonomic Units (OTUs) were identified. Nine categories could only be resolved to family level, five were resolved to genus level and the remaining categories (33) could be given a likely species identification. Twelve species were confirmed through the capture of voucher specimens from the trap systems (Supplement Table S2). A full species list is presented in Table 1 with example images in Figs. 3–6.

There are two known species of the genus *Spectrunculus* which are not possible to differentiate visually. *Spectrunculus crassus* have not been recorded from the Central or South Pacific. The otolith morphology, and the ratios of dorsal fin rays to vertebrae of captured specimens appear to conform to *S. grandis* (see Uiblein et al. (2008)). The observed species are thereby designated *S. grandis*.

The zoarcid OTU is known to contain *Pachycara moelleri* (Shinohara, 2012) as specimens were captured in the South Fiji Basin and New Hebrides Trench at 4100 m depth. Specimens from the Kermadec Trench are currently under assessment and include one specimen of *Pyrolycus* cf. *moelleri* (Anderson, 2006). Visually distinct zoarcids in the lander images support that there are multiple species which cannot be resolved from images (Fig. 3).

Identifying eels in the Family Synphobranchidae can be extremely difficult as they are very similar (Sulak and Shcherbachev, 1997). No more than two species of this family are known to co-occur within a single bathymetric or geographical zone (Sulak and Shcherbachev, 1997). *Ilyophis robbinsae* was captured in the New Hebrides Trench at 5180 m depth. However, it is very possible that other species are present. In the southern Kermadec Trench region, *Histiobranchus australis* and *H. bruuni* have been recorded, the latter from 3000 to 4974 m depth (Roberts et al., 2015). The OTU “Large Synphobranchidae” will be used to differentiate the large deeper-occurring eels (Fig. 4) from the visually distinct *Diastobranchus capensis*, *Simenchelys parasitica* and *Synphobranchus brevidorsalis* (Fig. 6).

A large cusk-eel featured prominently in the observed fish fauna. Discussion with J.G. Nielsen indicated that the fish was a member of the genus *Bassozetus*. These were never caught in the fish traps, which precluded species identification. When viewed laterally meristic and morphometric measurements suggested *Bassozetus robustus* and *B.*

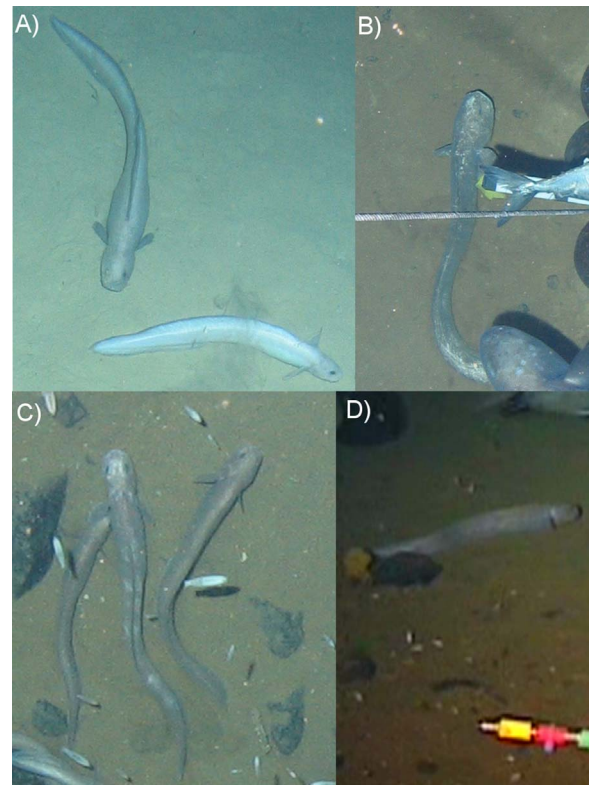


Fig. 3. Examples of the Zoarcidae recorded at (A) the Kermadec Trench at 3940 m, (B) The South Fiji Basin at 4074 m, (C) the New Hebrides Trench at 6056 m and (D) the Mariana Trench at 6142 m.

levistomatus (Fig. 5) however it was not possible to distinguish between these tentative identifications in most images. Hence, they were categorised as *Bassozetus* spp.

The number of fish species declined significantly with increasing depth in the Kermadec ($R^2=0.732$, $F_{1,30}=81.755$, $p<0.001$) and Mariana ($R^2=0.391$, $F_{1,23}=14.771$, $p<0.001$) trenches. The New Hebrides Trench approached significance ($R^2=0.541$, $F_{1,5}=5.88$, $p=0.059$) but was potentially restricted by smaller sample size (Fig. 7).

3.3. Community structure

Prior to analysis, potential influences from the experimental design were explored. A RELATE test indicated that the duration of the deployment did not have a significant effect on the MaxN ($p=0.048$, $p=0.232$) or %Ob ($p=0.008$, $p=0.388$) datasets. ANOSIM did not detect a significant effect of lander type in the %Ob dataset ($R=0.006$, $p=0.365$).

Significantly distinct fish community groups are presented in greater detail in Supplementary Table S3. In the Kermadec Trench three significant fish community groups in the MaxN dataset (Fig. 8a) and five in the %Ob dataset Fig. 8b were detected. Within the MaxN dataset a bathyal fish community from 997 to 1971 m depth was detected. Over 70% of the bathyal group's within group similarity was due to the Synphobranchid eels *Diastobranchus capensis* and *Simenchelys parasitica*. There was an abyssal fish community from 3039 to 4185 m where *Coryphaenoides armatus*, *C. yaquinae*, *Spectrunculus grandis* and the Large Synphobranchid accounted for more than 90% of the within group similarity. Thirdly, an Abyssal Hadal Transition Zone (AHTZ) fish community occurred from 4707 to 6068 m where *Bassozetus* spp., *C. yaquinae* and Large Synphobranchid accounted for over 98% of the within group similarity. The %Ob dataset generally agreed in these groups, differing in one deployment at 5295 m. The same species accounted for the majority of

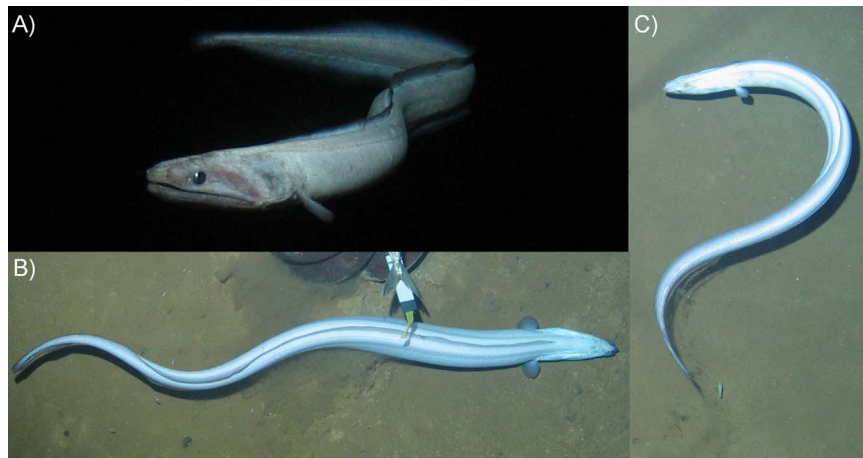


Fig. 4. Large Synphobranchid (A) 5254 m Kermadec Trench, (B) 4100 m South Fiji Basin, (C) 4123 m New Hebrides Trench.

the within group similarity with the exception of the Large Synphobranchid. These eels have short staying times at the bait and as such are likely to be underrepresented in both datasets, but more so in the %Ob dataset. A greater depth resolution in the %Ob dataset improved the community boundaries; bathyal 997–2503 m, abyssal 3039–4692, AHTZ 4707–6068 m. In addition, the %Ob dataset included data from the deeper-capable *Hadal-lander* and so included two deeper groups: (1) A shallower hadal community (including 5295 m deployment that fell within the AHTZ community in the MaxN dataset) from 5295 to 6191 m with *Bassozetus* spp. accounting for 100% of the within group similarity; (2) A deeper hadal group 6750–7669 m with the endemic snailfish *Notoliparis kermadecensis* accounting for 100% of the within group similarity.

The South Fiji Basin possessed no detectable community structure in either dataset. *Bassozetus* spp., Zoarcidae Gen et spp. and *Barathrites iris* were responsible for more than 85% of the similarity between deployments in both datasets. The MaxN dataset also detected the Large Synphobranchid eel as contributing 15% to similarity between deployments.

The New Hebrides Trench possessed no detectable community structure. Both datasets suggested that the shallowest deployment at 2087 m had greater dissimilarity from the other deployments (mean dissimilarity of 2078 m from other deployments in the New Hebrides Trench: 72%, mean between all other deployments 43% in the MaxN dataset) but this was not significant. This deployment is distinct as it contains the macrourids *Coryphaenoides rudis* and *C. longifilis*, which were the only macrourids detected in the New Hebrides Trench. Both datasets identified *Bassozetus* spp. as the OTU responsible for over 75% of the similarity between deployments in the New Hebrides Trench and was observed in every deployment. The MaxN dataset additionally identified the Large Synphobranchid (17% similarity)

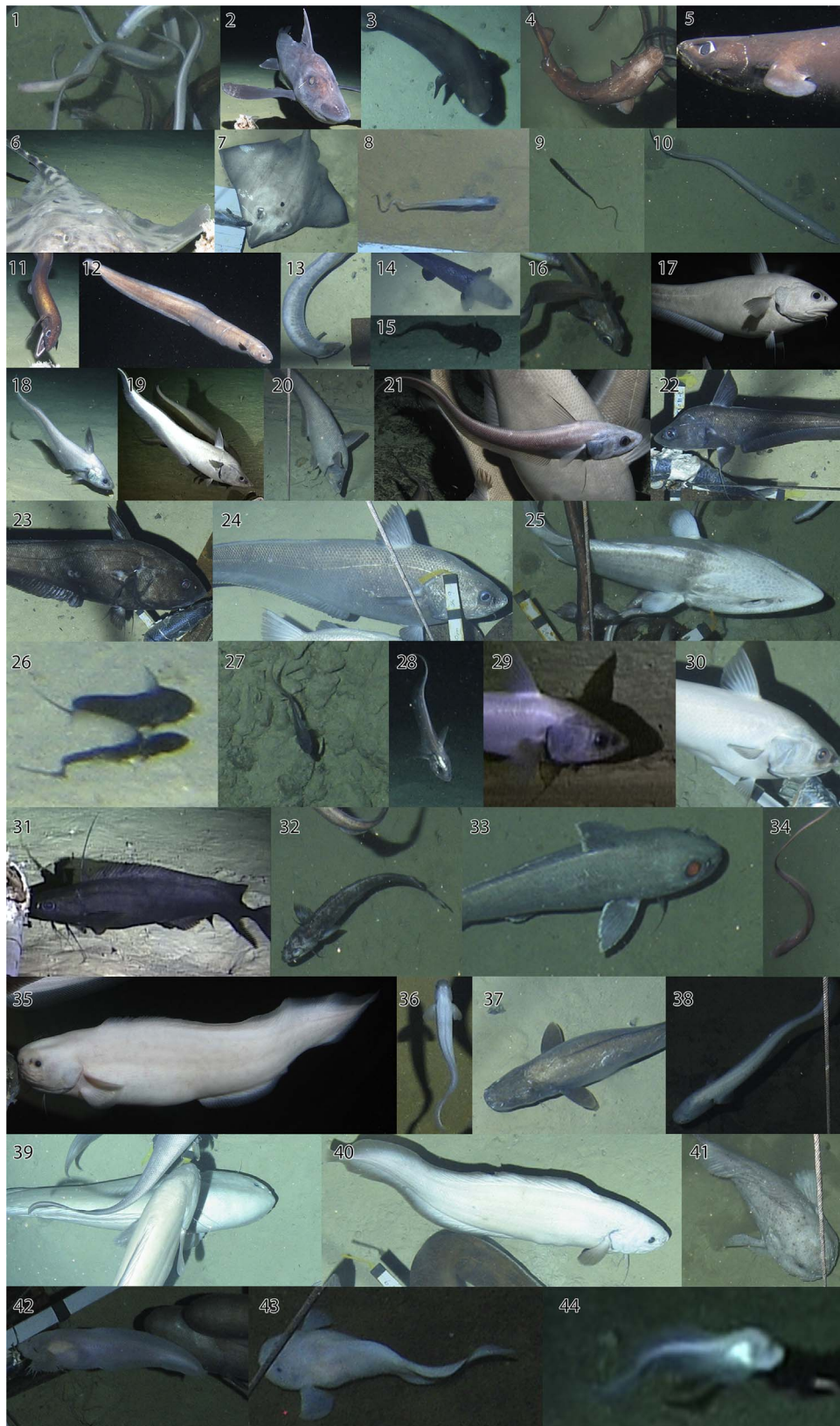
while the %Ob dataset identified Zoarcidae Gen et spp. (9% similarity).

The Mariana Trench shows no community structure in the MaxN dataset. However, the larger and bathymetrically broader %Ob dataset detected two significant fish communities (Fig. 9): An AHTZ community from 4506 to 6189 m with *Bassozetus* spp. and *Coryphaenoides yaquinae* accounting for more than 99% of the similarity between deployments; and a deeper hadal community from 6831 to 8143 m with the undescribed ‘Mariana snailfish’ accounting for 98.93% of the similarity between deployments. The deepest deployment contains only the OTU designated ‘ethereal snailfish’ (see Linley et al. (2016)) which was also detected at 8007 m alongside the Mariana snailfish. The deepest deployment therefore possesses greater dissimilarity yet is statistically part of the hadal group.

Despite the wide geographic range there are similarities evident in the fish communities. Cluster analyses on all deployments detected similar groups and revealed structure in the New Hebrides Trench and South Fiji Basin (Fig. 10). Four significant fish community groups were detected in the MaxN and five in the %Ob dataset. The MaxN dataset contained two significant bathyal groups; a shallower (997–1527 m) cluster of deployments in the Kermadec Trench region (the only location to include such shallow deployments) with *Diastobranchius capensis* and *Simechelys parasitica* accounting for 82% of the within group similarity; and a deeper (1971–2087 m) bathyal group of Kermadec and New Hebrides Trench deployments containing only the macrourids *Coryphaenoides rudis* and *C. longifilis* and the elasmobranchs *Amblyraja hyperborea*, *Bathyraja* cf. *richardsoni* and *Hydrolagus* cf. *affinis*. Other clusters were an abyssal group found only in the Kermadec Trench (3039–4158 m) with 96% of the within group similarity due to *Coryphaenoides armatus*, *C. yaquinae*, *Spectrunculus grandis* and Large Synphobranchid; an AHTZ group containing deployments from all locations, covering a wide bathymetric



Fig. 5. Variation within the *Bassozetus* observed. *Bassozetus* cf. *robustus* (A–B), *Bassozetus* cf. *levistomatus* (C–D). All images were taken at 5254 m depth in the Kermadec Trench.



range (2578–6898 m), as it contained all New Hebrides Trench deployments but the shallowest. *Bassozetus* spp., Large Synaphobranchid and *Coryphaenoides yaquinae* accounted for 96% of the AHTZ within group similarity.

The %Ob dataset combined the MaxN shallow and deep bathyal deployments as a single bathyal group (997–2503 m) with

Diastobranchius capensis, *Simenchelys parasitica* and *Antimora ros-trata* accounting for 77% of the within group similarity. Both datasets agreed on a Kermadec Trench abyssal group (3039–4692 m) with 96% of the within group similarity due to *Coryphaenoides armatus*, *C. yaquinae*, and *Spectrunculus grandis*. As observed previously Large Synaphobranchid was not detected in this dataset. Both datasets also

Fig. 6. Fish species recorded attending the *Abyssal-lander* and *Hadal-lander* in the Kermadec (Kerm), South Fiji Basin (SFB), New Hebrides Trench (NHeb) and Mariana Trench (MAR); 1) *Neomyxine caesiiovitta* (Kerm, 997 m), 2) *Hydrolagus cf. affinis* (Kerm, 1527 m), 3) *Centroscymnus cf. coelolepis* (Kerm, 1971 m), 4) *Etmopterus cf. baxteri* (Kerm, 1473 m), 5) *Centroscymnus owstonii* (Kerm, 1527 m), 6) *Amblyraja hyperborea* (Kerm, 1527 m), 7) *Bathyrhaja cf. richardsoni* (NHeb, 2578 m), 8) *Aldrovandia affinis* (SFB, 4078 m), 9) *Halosaurus macrochir* (Kerm, 1473 m), 10) *Bassanago bulbiceps* (Kerm, 997 m), 11) *Diastobranchus capensis* (Kerm, 1527 m), 12) *Simenchelys parasitica* (Kerm, 1527 m), 13) *Synaphobranchus brevidorsalis* (NHeb, 2078 m), 14) *Alepocephalid* spp. (NHeb, 2578 m), 15) *Bathygadus* sp. (Kerm, 1554 m), 16) *Coelorinchus* sp. (Kerm, 997 m), 17) *Coryphaenoides armatus* (Kerm, 3655 m), 18) *Coryphaenoides ferrieri* (Kerm, 1527 m), 19) *Coryphaenoides cf. filicauda* (Kerm, 4194 m), 20) *Coryphaenoides lecointei* (Kerm, 4953 m), 21) *Coryphaenoides leptolepis* (Kerm, 3665 m), 22) *Coryphaenoides longifilis* (NHeb, 2087 m), 23) *Coryphaenoides rudis* (NHeb, 2087 m), 24) *Coryphaenoides yaquinae* (Kerm, 3940 m), 25) *Trachyrincus longirostris* (Kerm, 997 m), 26) Macrourid 1 (Kerm, 1527 m), 27) Macrourid 2 (Kerm, 4138 m), 28) Macrourid 3 (Kerm, 1527 m), 29) Macrourid 4 (Kerm, 5281 m), 30) Macrourid 5 (Kerm, 4953 m), 31) *Antimora rostrata* (Kerm, 1554 m), 32) *Lepidion microcephalus* (Kerm, 997 m), 33) *Mora moro* (Kerm, 997 m), 34) *Echiodon cryomargarites* (Kerm, 1473 m), 35) *Barathrites iris* (Kerm, 5254 m), 36) cf. *Bassogigas* sp. (SFB, 4100 m), 37) *Bassozetes cf. glutinosus* (NHeb, 2578 m), 38) *Bassozetes cf. compressus* (Mar, 4506 m), 39) *Bathyonus caudalis* (Kerm, 3039 m), 40) *Spectrunculus grandis* (Kerm, 3039 m), 41) *Psychrolutes microporos* (Kerm, 1527 m), 42) *Notoliparis kermadecensis* (Kerm, 5879 m), 43) Mariana snailfish (Mar, 6198 m), 44) Ethereal snailfish (Mar, 8078 m).

agreed on the AHTZ group. The deeper range of the %Ob dataset identified two groups of endemic hadal snailfish; one in the Kermadec Trench (6750–7669 m) containing only *Notoliparis kermadecensis*; and a second in the Mariana Trench (6831–8143 m) with the 'Mariana snailfish' accounting for 99% of the within group similarity.

The prominent abyssal macrourids *Coryphaenoides armatus* and *C. yaquinae* were not observed in either the New Hebrides Trench or South Fiji Basin. This resulted in the abyssal group, detected in the adjoining Kermadec Trench, being absent from these locations. In the absence of this group, the AHTZ group appeared to occupy a wider bathymetric range, extending shallower (Fig. 11). An endemic hadal snailfish is also notably lacking from the New Hebrides Trench.

3.4. Environmental drivers

DistLM was used to explore the potential environmental drivers of community structure. All environmental data are available in Table S4. The hadal snailfish OTU were combined for this analysis as their endemism is likely due to their isolation as stenobathic hadal fish, and they are functionally very similar (see Linley et al. (2016)). Marginal tests of the MaxN dataset indicated that neither current speed (Pseudo- $F_{28}=0.849$, $p=0.488$) or salinity (Pseudo- $F_{28}=1.162$, $p=0.319$) had a significant effect on community structure at the observed levels. The analysis could therefore be performed on the larger %Ob dataset which lacked these data. Marginal tests detected significant relationships between community structure and depth (Pseudo- $F_{64}=12.579$, $p=0.001$), temperature (Pseudo- $F_{64}=7.635$, $p=0.001$), bottom POC

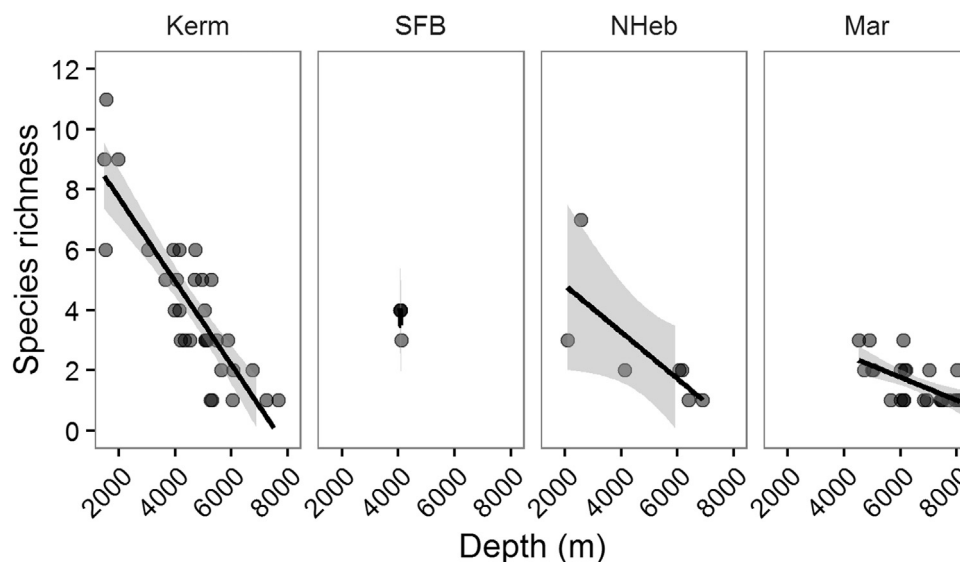


Fig. 7. The number of fish species observed by the *Abyssal-lander* and *Hadal-lander* systems at different depths in each of the study areas. A linear model with 95% confidence interval has been fitted.

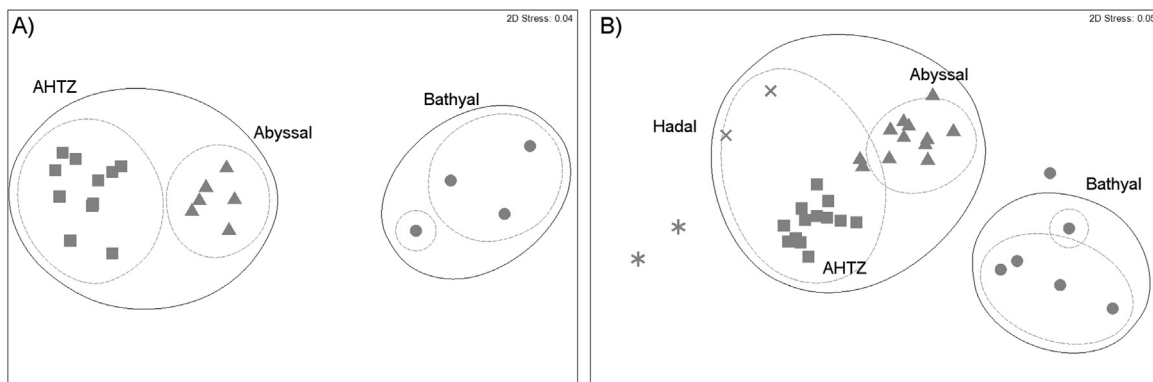


Fig. 8. MDS plot of the Kermadec Trench deployments in the a) MaxN and b) %Ob datasets. Resemblance has been overlaid at 20% (solid line) and 40% (dashed line). Significant groups (SIMPROF, $p < 0.05$) are Bathyal (circle), Abyssal (triangle), AHTZ (square), shallow hadal (cross) and deep hadal (asterisk).

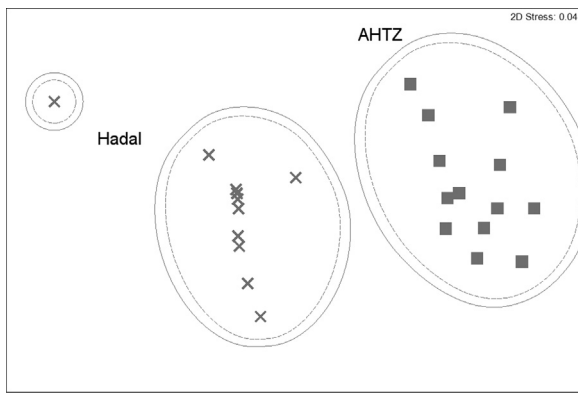


Fig. 9. MDS plot of the Mariana Trench deployments in the %Ob dataset. Resemblance has been overlaid at 20% (solid line) and 40% (dashed line). Significant groups are AHTZ (square) and Hadal (cross).

(Pseudo- $F_{64}=7.327$, $p=0.001$), PPYr (Pseudo- $F_{64}=5.205$, $p=0.001$), PPMo (Pseudo- $F_{64}=5.949$, $p=0.001$), but not 'quarter of day' (Pseudo- $F_{64}=1.123$, $p=0.347$) or the sediment classification (Pseudo- $F_{64}=0.868$, $p=0.508$). Both AIC and BIC based model selection measures agreed

that the best environmental predictors for the observed biological pattern were depth, temperature and PPYr (Fig. 12). These predictors could explain 36% of the biological variability.

3.5. Feeding observations

The *Hadal-lander* video recorded fish behaviour at the bait. Some species were observed to feed exclusively on the bait (number of observed feeding events in brackets): *Simenchelys parasitica* (135), *Antimora rostrata* (10), *Coryphaenoides armatus* (454), *Barathrites iris* (16), *Spectrunculus grandis* (8), *Centroscymnus cf. coelolepis* (9), *Etmopterus cf. baxteri* (3) and the Large Synphobranchid (2). However, some bait-attending species were also observed preying on scavenging invertebrates (mainly amphipods and on occasion, decapods). Species observed to most often feed on the bait but occasionally prey upon other scavengers were: *Coryphaenoides yaquinae* (89% necrophagy, $n=369$) and *D. capensis* (97% necrophagy, $n=145$). Species that were observed to prey almost exclusively on other scavengers: *Bassozetus* spp. (98% predation, $n=290$), which were observed specifically targeting large amphipods and decapods (Supplementary video 1), and Zoarcid Gen et spp. (97.2% predation, $n=106$). All of the hadal snailfish were seen to target amphipods

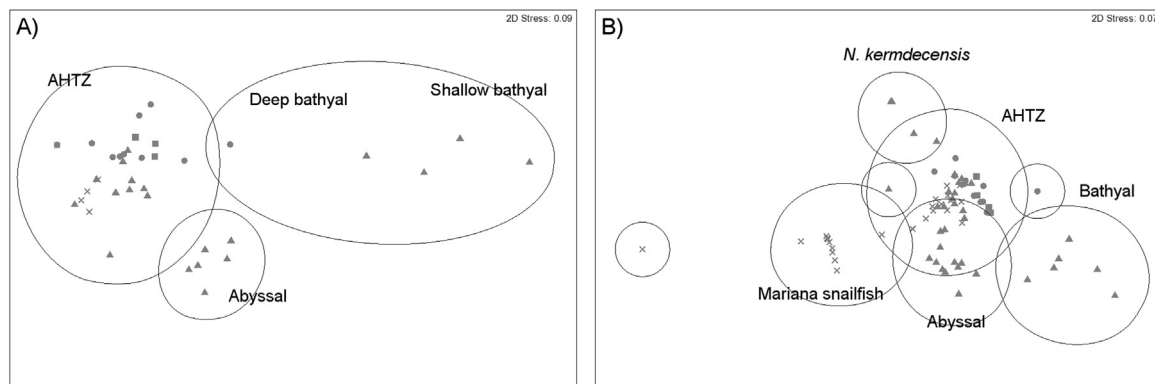


Fig. 10. MDS plot of all study deployments in the (A) MaxN and (B) %Ob datasets. Deployments are labelled with their depth. Similarity boundaries have been overlaid at 20% and annotated. Study locations are Kermadec Trench (triangle), South Fiji Basin (square), Hew Hebrides Trench (circle) and Mariana Trench (cross).

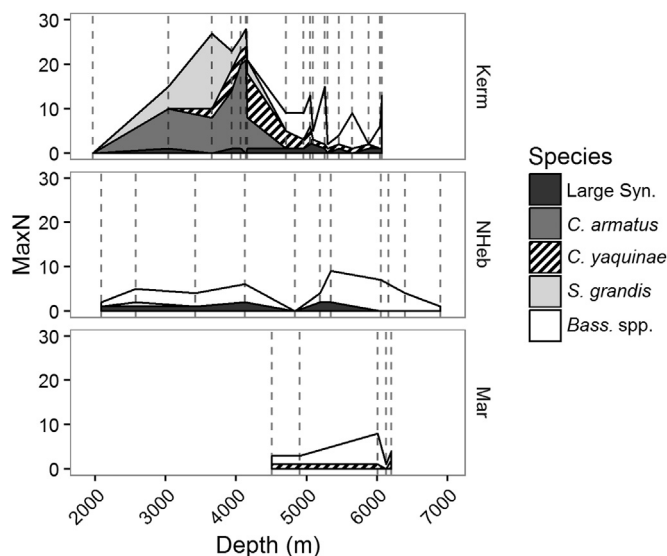


Fig. 11. Stacked plots of Abyssal-lander MaxN of the fish species that defined the abyssal and AHTZ groups; Large Synphobranchid (Large Syn.), *Coryphaenoides armatus* (*C. armatus*), *Coryphaenoides yaquinae* (*C. yaquinae*), *Spectrunculus grandis* (*S. grandis*) and *Bassozetus* spp. (*Bass. spp.*). Dashed lines indicate deployment depths.

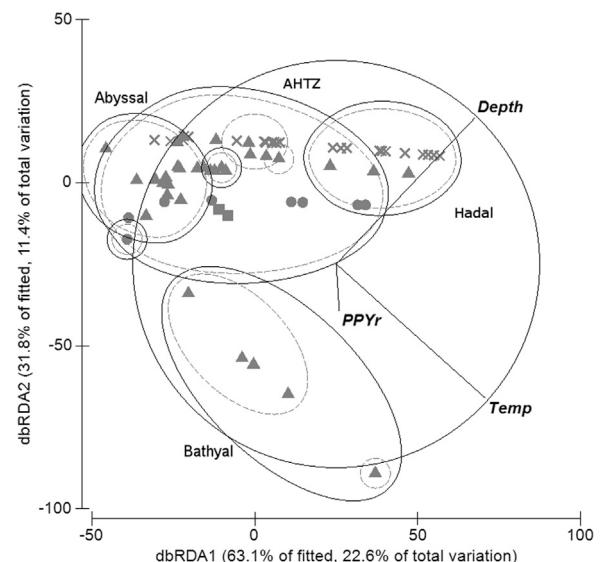


Fig. 12. dbRDA of the final DistLM model. Vectors have been added for the explanatory environmental variables. Points represent individual deployments; Kermadec Trench (triangle), South Fiji Basin (square), Hew Hebrides Trench (circle) and Mariana Trench (cross). Similarity boundaries have been overlaid at 20% (solid line) and 40% (dashed line) and annotated with the groups they represent. How well each axis represents the model (fitted) and the actual biological data (total) are displayed on the axis.

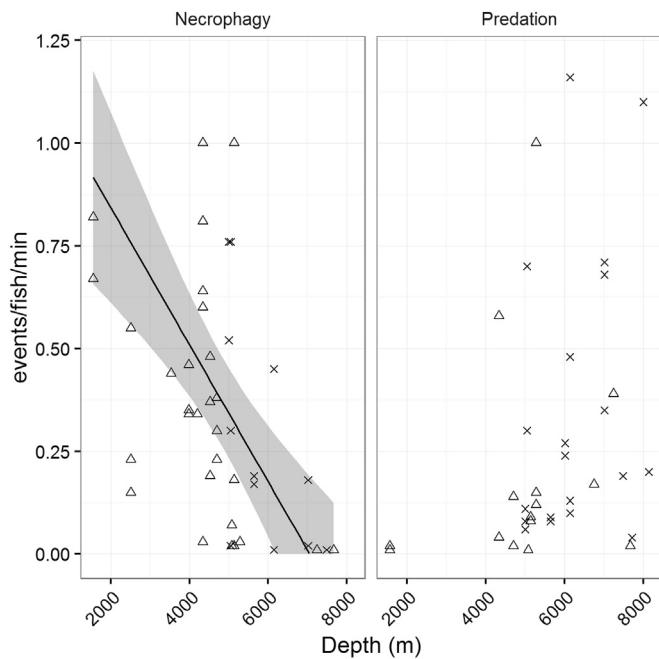


Fig. 13. Feeding events (necrophagy or predation) per fish per minute in relation to depth in the Kermadec (triangle) and Mariana (cross) trenches. The significant relationship between necrophagy and depth is plotted with 95% confidence intervals.

feeding at the bait: *Notoliparis kermadecensis* (96% predation, $n=531$), the Mariana snailfish (98%, $n=753$) and the ethereal snailfish (100% predation, $n=8$). Ingesting bait while suction feeding amphipods appeared to be accidental in the snailfish and bait material was often ejected from the mouth following what would have been counted as a necrophagy feeding event.

Supplementary material related to this article can be found online at doi:10.1016/j.dsr.2016.12.009.

The species that defined the fish community groups had distinct feeding strategies: the bathyal group and the Kermadec abyssal group were almost exclusively necrophagous, the AHTZ group comprised predatory and more generalist feeders, while the hadal snailfishes were predators.

While abyssal macrourids were absent from the New Hebrides Trench and South Fiji Basin, necrophagy was still observed by the cusk-eels *Barathrites iris* and *Spectrunculus grandis* respectively. The most prominent scavenger in the New Hebrides Trench and South Fiji Basin however was the shrimp *Cerataspis monstrosus* (Grey, 1828) (previously recorded as *Plesiopenaeus armatus* (Spence Bate, 1881); see Bracken-Grissom et al. (2012)). While only one or two simultaneous individuals had been observed in the other trenches up to nine occurred in the New Hebrides Trench.

Feeding events at the bait (corrected for the number of fish present and duration observed) suggested that with increasing depth the frequency of predatory feeding events increased while the frequency of scavenging events was reduced (Fig. 13). A significant inverse relationship occurred between depth and the frequency of scavenging events ($F_{1,47}=19.303$, $p<0.001$) with no detectable difference between the Kermadec and Mariana trenches ($F_{1,47}=0.442$, $p=0.503$). No relationship was detected between predatory feeding events with depth ($F_{1,42}=1.034$, $p=0.315$) or trench ($F_{1,42}=0.224$, $p=0.137$).

3.6. Summary

The observed trends between the identified environmental predictors and the feeding character of each significant fish group is summarised in Fig. 14.

4. Discussion

Generally, there was agreement between the MaxN and %Ob datasets. Both datasets agreed upon the major fish community groups across all deployments: (1) a varied group of bathyal species < 3000 m depth, (2) a macrourid dominated abyssal group of predominantly scavenging fish, (3) a *Bassozetis* spp. dominated AHTZ group of predatory and generalist feeders, particularly, in %Ob data, (4) a hadal group comprising of endemic snailfish.

4.1. Macrourid or ophidiid dominated communities

Abyssal macrourids were prominent components of Kermadec and Mariana Trench fish fauna but were absent from the New Hebrides Trench and South Fiji Basin. Macrourids are well represented at bathyal depths around New Caledonia (Clark and Roberts, 2008; Zintzen et al., 2011) adjacent the New Hebrides Trench and were observed at bathyal deployments (Table 1). The macrourids *Coryphaenoides armatus* and *C. yaquinae* readily gather at baited landers (Armstrong et al., 1991; Collins et al., 1999; Cousins et al., 2013b; Henriques et al., 2002; Isaacs and Schwartzlose, 1975; King et al., 2006; Priede and Bagley, 2001). It is highly unlikely that *Coryphaenoides armatus* and *C. yaquinae* were present in the New Hebrides Trench and South Fiji Basin and failed to be detected using baited landers. In their absence an ophidiid-based community appears to dominate. Examples from the literature exist of such communities. For example, Anderson et al. (1985) reported an ophidiid dominated community (mainly unidentified *Bassozetis* spp.) in the Caribbean Sea. The only reported macrourid was restricted to ~3500 m depth. A similar community was reported in the basins east of the Bahamas (Sulak, 1982). Baited lander deployments by Fleury and Drzen (2013) in the Sargasso Sea observed *Coryphaenoides armatus*, but it was rare and one of the last fish species to arrive. Their deployments were also dominated by a *Bassozetis* spp., closely resembling those discussed herein, that was never observed to feed on the bait. Janßen et al. (2000) observed similar bait attending behaviour in the ophidiid *Holcomycteronus aequatorius*. Yeh and Drzen (2009) found a dominance of ophidiids in the low productivity North Pacific subtropical gyre. Janßen et al. (2000) and Christiansen and Martin (2000) reported a surprising lack of macrourid fishes (a single individual was photographed) and an ophidiid based community in the Arabian Sea. Macrourids are only found at bathyal depths in the Arabian Sea (Christiansen and Martin, 2000; Janßen et al., 2000; Shcherbachev and Iwamoto, 1995; Witte, 1999). In the Northern Atlantic Merrett (1992) observed a shift from macrourid to ophidiid community from north to south along the productivity gradient. The majority of the authors cited above suggested surface productivity was the driver of these observed differences in the benthic community.

The Hadal-lander video data indicated that *Bassozetis* spp. were discouraged from bait-attending by the voracious feeding of the scavenging macrourids *Coryphaenoides armatus* and *C. yaquinae*, which dispersed the scavenging amphipods on which *Bassozetis* spp. were feeding. Competition may be more direct when these macrourids act as predators. Sulak (1982) suggested that low-energy ophidiid based communities occurred when competition from more energetically expensive macrourids was eased. In the Kermadec Trench this boundary is bathymetric and the *Bassozetis* spp. occurs deeper than the macrourids. In the New Hebrides Trench and South Fiji Basin, more energetically-expensive macrourids are excluded, allowing the low-energy ophidiid to dominate and extend shallower than in the other trenches studied. This is in keeping with the Species Interactions-Abiotic Stress Hypothesis (SIASH; see Louthan et al. (2015)); the deeper limits of these species are probably set by their physiological depth-tolerances (Yancey et al., 2014), of which *Bassozetis* spp. is greater, whereas the shallower limit of *Bassozetis* spp. is set by its competitive exclusion by the macrourids and is seen to relax in their absence.

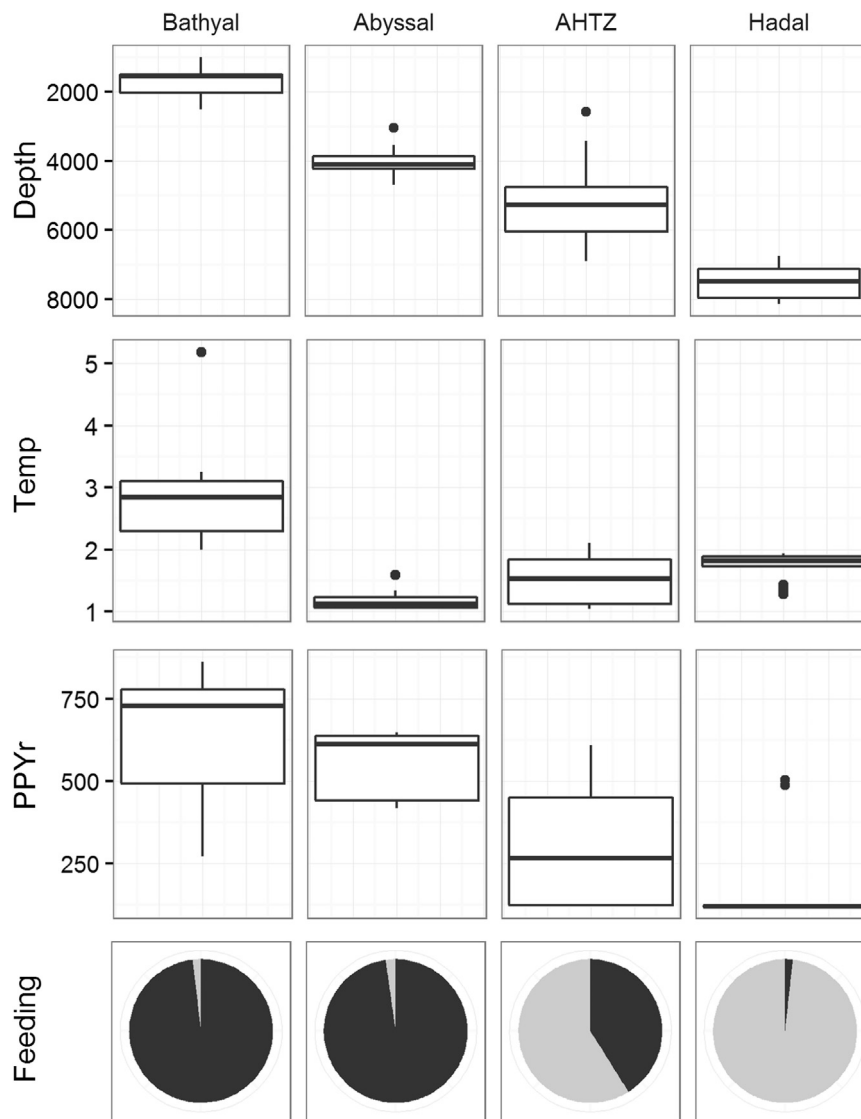


Fig. 14. Summary of the environmental conditions influencing fish community structure within the significant fish groups. Depth (m), temperature (°C), estimated surface primary production for the previous year (PPYr; mg C/m²/day), and the proportion of necrophagous (black) and predatory (grey) feeding events observed within those groups.

The macrourid based scavenging community is often thought of as representative of the world's abyssal plains (Christiansen and Martin, 2000; Janßen et al., 2000; Jamieson et al., 2011). Examples of deviations from this appear in the literature in a range of areas associated with lower surface productivity and warmer latitudes. Sampling of the deep sea has not been uniform, the cost of vessel time has resulted in sampling biased towards areas close to land masses (Ebbe et al., 2010; Jamieson, 2015), enriched through upwelling and terrestrial runoff and subsequent downslope transport (Gove et al., 2016; Henriques et al., 2002; Merrett, 1992; Müller and Suess, 1979) where localised, macrourid based, scavenging communities can occur (Henriques et al., 2002; Sulak, 1982). As a result, our idea of the ubiquitous scavenging abyssal fish communities may be greatly skewed and an ophiidiid dominated predatory community may be more common globally.

4.2. Feeding

Bait-attending species that are observed for long periods but never seen to feed on the bait can be said with some confidence to not rely upon necrophagy as part of their natural feeding strategy. The inverse cannot be confidently said and it is likely that the species that were seen

to only feed on the bait also feed on other food sources. Community zonation by trophic guilds is potentially an important factor in the deep sea (Cartes and Carrassón, 2004). In the northern Pacific Ocean scavenging fish species, as a proportion of total fish diversity, have been found to increase from 100 to 3000 m (Yeh and Drazen, 2011, 2009). Despite a generally decreasing trend being observed in the current study, the peak in necrophagous feeding at abyssal depths does not contradict the result of Yeh and Drazen (2011). The reduction in scavenging feeding events with depth found in the Kermadec and Mariana trenches predicted a loss of necrophagy in fish within the AHTZ. This hypothesis is supported by stomach contents and stable isotope analyses performed on collected trap specimens (Gerringer et al., 2016).

Drazen et al. (2008) hypothesised that *Coryphaenoides armatus* and *C. yaquinae* bypass the benthic food web, gaining most of their energetic input from nekton carcasses. *Coryphaenoides armatus* and *C. yaquinae* are very similar and commonly confused species (Iwamoto and Stein, 1974): *C. armatus* is the more specialised scavenger while *C. yaquinae* feeds more on infauna and epifauna (Drazen, 2007; Drazen et al., 2008), agreeing with the feeding observations in the current study. *Coryphaenoides yaquinae* was seen to span the abyssal and AHTZ groups while *C. armatus* was found only in the abyssal group,

illustrating the proposed shift from scavengers to a more generalist feeding character in these community groups.

Scavenging behaviour was still observed in the New Hebrides Trench and South Fiji Basin by ophiidid rather than macrourid scavengers. *Barathrites iris* has been observed feeding at mackerel baits in previous studies (Fleury and Drazen, 2013; Henriques et al., 2002; Janßen et al., 2000) as has *Spectrunculus grandis* (Cousins et al., 2013b; Henriques et al., 2002; Janßen et al., 2000). These two species were present in the South Fiji Basin and New Hebrides Trench respectively and may represent lower energy/opportunistic scavengers. Janßen et al. (2000) suggested flexibility in *Barathrites iris* and *Pachycara* spp. (Zoarcidae), as they were observed at baited lander deployments in fewer images at more productive sites where alternative food sources are presumed to reduce the need to scavenge. Facultative scavengers may be a feature of intermediately productive areas or areas with high seasonality such as the Arabian Sea (Janßen et al., 2000). Zoarcids were observed in large numbers (up to 23 individuals) in the New Hebrides Trench while maximum numbers were much lower in the Kermadec and Mariana Trenches (5 and 1 respectively). *Pachycara* species have been observed to take up long-term residence around large carcasses, often beyond its potential as a food source (Henriques et al., 2002; Jones et al., 1998).

The loss of scavenging fishes at the boundary of the hadal zone emphasises the zone's distinct faunal community (Wolff, 1970) and coincides with ecological boundaries in other faunal groups (Jamieson, 2011; Lacey et al., 2016). Scavenging at hadal depths appears dominated by the amphipods of the Superfamily Lysianassoidea (Blankenship-Williams and Levin, 2009; Lacey et al., 2016). *Bassozetus* spp. appeared to target large amphipods and decapods when it was observed feeding, and the hadal snailfishes also appear to bait-attend to prey on the gathered invertebrate scavengers (necrophagivorey). Unlike fish, scavenging amphipods can be detritivores (Blankenship and Levin, 2007). It would appear that *Bassozetus* spp. and the other members of the AHTZ and hadal predatory groups rely on the benthic food-web to consolidate surface-derived material through detritivorous and necrophagous invertebrates.

4.3. Environmental drivers

Depth, surface productivity and temperature were identified as environmental predictors that best explained the fish community structure.

Depth is unsurprisingly revealed as the strongest factor affecting fish community composition in trench systems and the surrounding abyssal plains. In addition to depth there appears to be a subtle interaction between surface productivity and temperature that determines whether the abyssal scavenging macrourids are present. A linkage of surface productivity with numbers of animals attracted to baited landers has been observed since Isaacs and Schwartzlose (1975), early pioneers of the method. However, proxies for nutrient input such as particle flux and surface productivity may not represent the resources available to a specific species or benthic fauna as a whole (Carney, 2005). Also, the identified environmental factors may not be the environmental force driving the biological pattern but correlated to it. With this caveat in mind, two hypotheses, based on the available data, are proposed below related to fish energy budget and different water masses within the study areas.

4.4. Energy budget

Depth and temperature affect a wide range of physiological processes, and are thought to be important to deep-sea organism distribution, with surface productivity acting as a proxy for food availability (Watling et al., 2013). Differences between adjacent areas are more likely to be influenced by energetic input than temperature (Carney, 2005; Watling et al., 2013). The Mariana Trench is the least

productive area in this study but it is also colder than the New Hebrides Trench. *Coryphaenoides yaquinae* were present in the Mariana Trench and it is anticipated that future shallower studies around the Mariana Trench will likely reveal that *C. armatus* are also present. This species is known from 4100 to 4220 m in the Japan Trench (Endo and Okamura, 1992). The Peru-Chile Trench is relatively warm (1.8–2.25 °C; Fujii et al., 2013) and highly eutrophic due to upwelling, the Humbolt current system, and its proximity to land mass (Daneri et al., 2000). Baited lander deployments in the Peru-Chile Trench (Jamieson et al., 2012) observed both *Coryphaenoides yaquinae* and *C. armatus*, supporting the idea an interplay between temperature and surface productivity that may explain the absence of these species in the New Hebrides and South Fiji Basin.

Low surface productivity (leading to fewer food falls) coupled with higher temperatures (accelerating metabolism) may be prohibitive to scavengers; especially those that expend energy searching for odour plumes such as *Coryphaenoides armatus* (Armstrong et al., 1991; Drazen, 2008, 2002; Priede et al., 1990). High temperature but high productivity (e.g. Peru-Chile Trench), and low temperature and low productivity (e.g. Mariana Trench) still allow this lifestyle.

4.5. Water mass

An alternative hypothesis is that the differences between the Kermadec Trench and the South Fiji Basin and New Hebrides Trench are due to different water masses. Boundaries between water masses are often suggested as a driver of zonation but the precise mechanism is not fully understood (Carney, 2005). The most recent biogeographical assessment of the study areas by Watling et al. (2013) considers the trenches beyond 6500 m distinct, but their surrounding abyssal depths a single province agreeing with previous outlines from Beliaev (1989) and Vinogradova (1997). Despite the difference in environmental conditions between the Kermadec and New Hebrides trenches being relatively slight, a faunal divide in this region has been detected in the bathyal ophiuroid (O'Hara et al., 2011) and fish communities (Clark et al., 2003; Zintzen et al., 2011). This ecotone appears to take place at the Tasman Front that marks the path of the East Australian Current (Ridgway and Dunn, 2003). Temperature may have appeared to be a strong environmental driver only because it differentiated the sides of this boundary. Differences in productivity, standing crop and phytoplankton size distribution across a front will have effects up the food chain (Baird et al., 2008). On the Kermadec Trench side of the front more nitrogen crosses the thermocline and is available to phytoplankton (Ellwood et al., 2013), a longer residence time also allows phytoplankton growth to deplete nutrients and develop not only a higher and distinct phytoplankton standing stock, but also larger zooplankton size classes (Baird et al., 2008; Ellwood et al., 2013) and distinct pelagic fish and crustacean fauna (Griffiths and Wadley, 1986). Griffiths and Wadley (1986) found that pelagic fishes from the New Hebrides Trench (northern) side of the front were able to enter the Kermadec (southern) side but the front appeared to act as a barrier to northward movement, as appears the case in the current study. The front is unlikely to directly restrict fishes at abyssal depths and deeper but the link, particularly in scavengers, to the shallower food-webs may drive the mirroring of this pattern at greater depths.

While the differences between the Kermadec and Mariana Trenches are less pronounced than the differences between them and the New Hebrides Trench, there is still variation. The Mariana Trench was unusual in lacking a large synphobranchid eel at the depths sampled. *Coryphaenoides yaquinae* is also more prominent in the Mariana Trench community than it was in the Kermadec Trench.

4.6. Limitations

It is disappointing that the *Bassozetus* species that features so prominently in this study could not be positively identified. The

revision of this genus by Nielsen and Merrett (2000), was based on preserved specimens. These fish have loose, fluid filled, skin around the head and snout (Machida and Tachibana, 1986; Nielsen et al., 1999; Nielsen and Merrett, 2000) which becomes ‘deflated’ during capture and preservation. This can make correlation between vouchers and *in situ* images challenging. Fresh or *in situ* individuals often have longer snout measurements and a differing head profile than that of preserved specimens (Berbel-Filho et al., 2013; Machida and Tachibana, 1986).

The inclusion of temperature as an environmental predictor sits well with the proposed energy budget hypothesis and records from other locations, but it is also linked closely to depth (although the relationship is complex due to adiabatic heating). The very strong match of depth as a predictor could explain the weaker explanatory power provided by temperature. However, it is not possible now to resolve if the role of temperature is its direct physiological effect on fish distribution or if it is an indirect proxy for other effects of water masses.

The current hypothesis is based on the relative oligotrophic designation of the Mariana Trench as interpreted from surface primary production. However, trenches may accumulate organic matter through downslope funnelling of detritus (George and Higgins, 1979; Ichino et al., 2015; Itou et al., 2000) or chemosynthetic communities (Fujikura et al., 1999). Sediment respirometry in the trench shows high metabolic rates (Glud et al., 2013).

Acknowledgments

This work was funded by the TOTAL Foundation (France) through the projects ‘Multi-disciplinary investigations of the deepest scavengers on Earth’ (2010–2012) and ‘Trench Connection’ (2013–2015) awarded to A.J.J. The 2014 field work was funded by the HADES-K and HADES-M projects supported by the National Science Foundation (NSF) and the Schmidt Ocean Institute (SOI) respectively. We thank the crew and company of the RV *Kaharoa* (KAH1109, KAH1202, KAH1301 and KAH1310), and NIWA Vessels Management, New Zealand. We also thank the crew and company of the RV *Thomas G. Thompson* (TN309; HADES-K) and the RV *Falkor* (FK141109; HADES-M). T.D.L. and A.J.J. are supported by the Marine Alliance for Science and Technology for Scotland (MASTS) pooling initiative, whose support is gratefully acknowledged. P.J.M. and M.R.C. participated in the study through the New Zealand Foundation for Research, Science and Technology (now Ministry for Business, Innovation and Education) funded project ‘Impact of Resource Use on Vulnerable Deep-Sea Communities’ (CO1X0906). J.C.D. and M.E.G. were supported by NSF (OCE-1130712) and M.E.G. was also funded by the NSF Graduate Research Fellowships Program, both of whose support is gratefully acknowledged. ALS contribution was supported (in part) by the NZ Ministry of Research and Innovation through Te Papa subcontract within NIWA’s Biodiversity and Biosecurity Science Programme (previously NIWA’s ForST contract CO1X0502). Thanks are extended to Dr Kenneth J. Sulak of the U.S. Geological Survey and Dr Jørgen Nielsen of the Natural History Museum of Denmark for discussion on the identification of the synbranchid eels and *Bassozetus* spp. respectively. Thanks also to Matteo Ichino of the National Oceanographic Centre who assisted with the benthic POC estimates and Heather Stewart of the British Geological Survey who categorised the sediment types seen in the lander images.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2016.12.009.

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