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Deep-Sea Research I

Fishes of the hadal zone including new species, *in situ* observations and depth records of Liparidae

Thomas D. Linley [a], Mackenzie E. Gerringer [b], Paul H. Yancey [c], Jeffrey C. Drazen [b], Chloe L. Weinstock [c], Alan J. Jamieson [a,*]

[a] Oceanlab, Institute of Biological and Environmental Sciences, University of Aberdeen, Main Street, Newburgh, Aberdeenshire AB41 6AA, Scotland, UK
[b] Department of Oceanography, University of Hawai'i at Manoa, Honolulu, HI 96822, United States
[c] Biology Department, Whitman College, Walla Walla, WA 99362, United States

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ABSTRACT

Observations and records for fish exceeding 6000 m deep are few and often spurious. Recent developments in accessing and sampling the hadal zone 6000–11,000 m) have led to an acceleration in new findings in the deep subduction trenches, particularly in the Pacific Ocean. This study describes the discovery of two new species of snailfish (Liparidae) from the Mariana Trench; the 'Mariana snailfish' (6198–8076 m) and the 'Ethereal snailfish' (7939–8145 m). These new findings represent respectively the deepest known specimen caught with corroborating depth data, and the deepest fish seen alive. Further specimens and observations of the Kermadec Trench snailfish, *Notoliparis kermadecensis*, are also presented, as well as the first hadal records of Synaphobranchidae and Zoarcidae (6068 and 6145 m respectively) and a depth extension for the Macrouridae (maximum depth now 7012 m). Details of these new snailfish specimens caught by baited trap and behaviour observations filmed by baited cameras are presented. An updated assessment of fishes from hadal depths is also reported.

1. Introduction

The diversity of fishes in the deep trenches and their bathymetric ranges has, until recently, been unresolved and at best speculative. This is mostly due to a limited number of records, some of which are spurious or erroneous reports (described in Fujii et al., 2010; Jamieson and Yancey, 2012) and generally a low number of *in situ* observations (Jamieson, 2015). Compared with fishes of the bathyal and abyssal zones, records of hadal fishes are considerably less numerous. Often trawl catch or observation records have been reported from single samples, many in extremely poor condition (e.g. Nielsen, 1964; Stein, 2005) or limited in replication (e.g. Fujii et al., 2010).

Many of the known hadal fishes were captured by non-closing trawl in the 1950s and 1960s during the Danish *Galathea* and former-Soviet *Vitjaz* expeditions (Beliaev, 1989). Understanding the occurrence of hadal fishes, and maximum inhabitable depths of major fish groups, has consequently been based upon sparse and inadequate datasets (Fujii et al., 2010). However, recent developments in hadal-rated baited cameras and traps have led to a revival of science beyond abyssal depths. More *in situ* observations

and physical captures have permitted a great deal of progress into the study of hadal fishes in the last 5 years (Jamieson, 2015).

The first hadal fish collected from greater than 6000 m was trawled by the *Princess-Alice* in the east Atlantic Ocean in 1901. This ophidiid (cusk-eel), *Holcomycteronus profundissimus* (Roule, 1913), was considered the 'deepest fish' until the *Galathea* expedition trawled a deeper specimen from 7160 m in the Java Trench. A yet deeper fish was captured by the RV *John Elliott Pillsbury* at 8370 m in the Puerto Rico Trench in 1970. This individual was initially identified as *Holcomycteronus profundissimus* (Staiger, 1972) but later reclassified as a new species, *Abyssobrotula galatheae* (Nielsen, 1977). This specimen is still regarded as the deepest-living fish on record despite popular media disseminating an erroneous account of a 'flatfish' at over 10,900 m in the Mariana Trench (Piccard and Dietz, 1961). This account was refuted even by the scientific experts of the day (Wolff, 1961). Frustratingly, the *Trieste* flatfish is still perpetuated in popular deep-sea folklore despite renewed negation (Jamieson and Yancey, 2012). Although *A. galatheae* is widely accepted as the deepest fish by the scientific community, the record is somewhat questionable given the wide range of the 17 records of this fish available on the fishbase. org database; one bathyal (2330 m; Shcherbachev and Tsinovsky, 1980), 14 abyssal and two hadal (3100–8370 m; Machida, 1989). Further, despite the deeper records being from or in the vicinity of trenches (Puerto Rico, Japan and Izu-Bonin trenches), the

* Corresponding author.
   E-mail address: a.jamieson@abdn.ac.uk (A.J. Jamieson).

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specimens appear to have been captured using a non-closing trawl net. The possibility of incidental capture in mid-water was raised by Nielsen (1964), Nielsen and Munk (1964). The true depth range is still not precisely known and until further finds are made this record cannot be proven or refuted.

Other more believable reports of hadal fish began to be made around this time. The French *Archimède* bathyscaphe's pilot saw fish 'similar to liparids' (snailfish) at 7300 m in the Puerto-Rico Trench (Pérês, 1965). With no corroborating images, and the sensationalism of the *Trieste* flatfish story, these records went largely unnoticed. However, with recent more comprehensive appraisals of fish exceeding 6000 m, the Liparidae emerged as being perhaps the most dominant hadal fish (Fujii et al., 2010; Jamieson et al., 2011, 2009). This reappraisal also identified many records as either erroneous or misleading, and in light of new observations an updated version was presented in Jamieson (2015).

The *Galathea* collected five snailfish from 6660 to 6770 m in the Kermadec Trench (*Notoliparis kermadecensis*; Nielsen, 1964; Nielsen, 1964). The *Vityaz* expeditions later captured a single *Pseudoliparis amblystomopsis* (Andriashev, 1955) from 7230 m in the Kuril-Kamchatka Trench and a specimen of the *Careproctus* genus from 7579 m in the Japan Trench (later reclassified as *Pseudoliparis*; Chernova et al., 2004). Two more species, *Notoliparis antonbruuni* Stein, 2005 and *Pseudoliparis belyaevi* Andriyashev and Pitruk, 1993 were described from single specimens from 6150 m in the Peru-Chile Trench and 6380–7587 m in the Japan Trench respectively. The limited number of samples, and in particular, the poor quality of *N. antonbruuni*, unfortunately added little to our understanding of fish populations at these depths. Baited camera deployments in the Peru-Chile Trench in 2010 observed another snailfish relatively frequently at 7050 m (Jamieson, 2015). In the absence of physical samples, and given the poor condition of the deep snailfish previously described from the region (Stein, 2005), it was not possible to determine if this species was *N. antonbruuni*.

In addition to their hadal members, snailfish are also known to inhabit abyssal trenches. For example, *N. macquariensis* Andriashev, 1978; 5400–5419 m, Macquarie-Hjort Trench and *N. kurchatovi* Andriashev, 1975; 5465–5474 m South Orkney Trench. Also, *Careproctus sandwichensis* Andriashev and Stein, 1998 has been reported from 5435 to 5453 m near South Sandwich Trench which is hadal (~8000 m), suggesting this species might inhabit the deeper parts of the trench.

Several other fish species are known from the hadal zone (e. g., Anderson et al., 1985; Chernova et al., 2004; Nielsen et al., 1999; Stein, 2005), but again these were typically single captures and often poor quality specimens.

An analysis of all fish species by Priede et al., (2006) concluded that Chondrichthyes were absent from abyssal depths. Within the same study, analysis of all 9360 fish records in the fishBase. org database (Froese and Pauly, 2016) predicted a linear relationship with depth, culminating in a maximum depth for bony fish to be in the region of 8000–8500 m (Priede et al., 2006). This coincides with the deepest record for *Abyssobrotula galatheae* (Nielsen, 1977). Yancey et al., (2014) showed that it was extremely likely that bony fish cannot inhabit depths greater than ~8200 m, as a result of the osmolyte or so-called 'piezolyte', trimethylamine N-oxide (TMAO) reaching isosmosis with seawater. This molecule, found in all marine fishes, has been shown to protect proteins from inhibitory effects of hydrostatic pressure (reviewed by Yancey et al., 2014). All current evidence suggests that bony fish are indeed limited to approximately 8200 m, which places the 7703 m *in situ* observation of snailfish in the Japan Trench (Fujii et al., 2010) at 500 m shallower than the limit. This species was reported as *Pseudoliparis amblystomopsis,* now thought to be *P. belyaevi* based on morphology of three juveniles caught on the same deployment (pers comm. T. Satoh, NSMT, Tokyo).

In 2014, the international *HADES* project undertook two research campaigns, one to the Kermadec Trench (SW Pacific Ocean, maximum depth 10,200 m) and one to the Mariana Trench (Central Pacific Ocean, maximum depth 10,900 m). Baited landers and traps were deployed in the Kermadec Trench from 1527 to 9005 m (28 imaging lander deployments and 23 trap deployments) and in the Mariana Trench from 4441 to 10,545 m (30 imaging lander deployments and 38 trap deployments). Prior to this, in 2013, the HADEEP project 'Trench Connection' using the same baited landers and traps surveyed the New Hebrides Trench (SW Pacific Ocean, maximum depth = 7156 m) from 2000 to 6896 m (18 imaging lander deployments and 13 trap deployments) and the Kermadec Trench from 997 to 6552 m (13 imaging lander deployments and 8 trap deployments).

Previous expeditions in 2011, 2012 and 2013 had revealed that grenadiers (Macrouridae) and cusk eels (Ophidiidae) are present at depths to around 6945 m (Jamieson et al., 2009) and 6474 m (Jamieson et al., 2013) respectively. These observations represent the deepest limits of these otherwise quintessentially abyssal fishes, which happen to cross the abyssal-hadal boundary. These studies have confirmed that it is in fact the snailfishes (Liparidae) which dominate the hadal fish fauna, with several species known from depths exceeding 6000 m in at least three trenches (Fujii et al., 2010; Jamieson et al., 2013, 2009).

In this study we introduce *in situ* observations of two species of recently discovered snailfishes at 6198 m to 8078 m and 7939 m to 8145 m respectively, with the latter very close to the estimated maximum possible depth of occurrence of 8200 m hypothesised by Yancey et al. (2014). This represents a new record for the deepest fish seen alive with unequivocal proof of depth. We also add new osmotic and TMAO data which support this depth-limit hypothesis. The reappraisal of hadal fish species and bathymetric ranges are updated here in light of these recent expeditions.

2. Materials and methods

2.1. Study sites

The Mariana Trench is located south of the Island of Guam in the Central Pacific. It is the deepest trench in the world, with a maximum depth of ~10,900 m (Gardner et al., 2014). It is 2550 km long with a mean width of 70 km (Angel, 1982). The trench is part of the Izu-Bonin-Mariana subduction system where the western edge of the Pacific Plate is subducted beneath the smaller Mariana Plate to the west. Samples were taken along a transect from Guam down the overriding plate to the second deepest point, *Sirena Deep*, and up the adjacent subducting plate to the South (Fig. 1 Mar).

The Kermadec Trench lies ~120 km off the coast of New Zealand's North Island in the southwest Pacific Ocean and is the 5th deepest trench reaching 10,047 m depth (Angel, 1982). It is approximately 60 km wide and 1500 km long and has the characteristic V-shaped cross section topography, formed by tectonic subduction of the Pacific Plate under the Australian Plate. Samples were taken primarily from down the trench axis (Fig. 1 Kerm).

The New Hebrides Trench is ~1000 km northwest of the Kermadec Trench and partitioned from the Kermadec and Tonga trenches by the Kermadec Fore Arc and the South Fiji Basin. The trench is formed by the Australian plate subducting north-eastward under the overriding Vanuatu archipelago. The trench is ~200 km long and reaches a maximum depth of 7156 m. Samples were taken primarily down the overriding plate from west to east. During transit samples were also taken at the South Fiji Basin (Fig. 1 NHeb and SFB).

An overview map indicating the three sampling areas is also
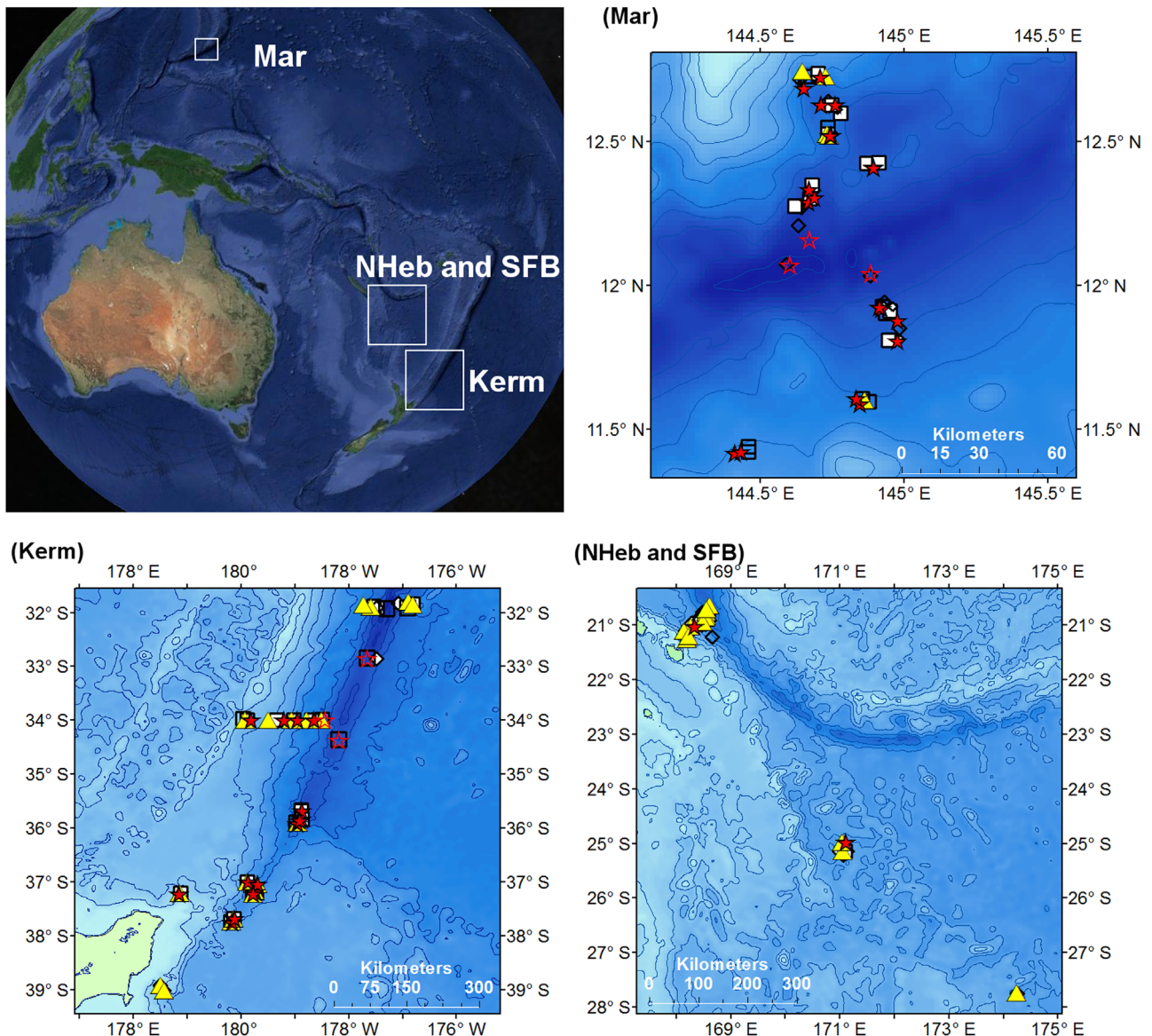
Fig. 1. Sampling locations in the three trench regions (Mar) Mariana, (Kerm) Kermadec and (NHeb and SFB) New Hebrides Trench and South Fiji Basin. Triangles represent *Abyssal-lander* deployments, stars the *Hadal-lander*, squares the *large fish trap* and diamonds the *wee-trap*. Deployments that did not record fish are hollow outlines. Isobaths represent 1000 m intervals. Global overview is adapted from Google Earth (Google, 2016) and the location maps are produced from GEBCO (2015) bathymetry data.

shown in Fig. 1.

2.2. Sampling equipment

Two baited imaging systems were used in this study, an 11,000 m rated video lander (*Hadal-lander*; Fig. 2(a)) and a 6000 m rated stills camera lander (*Abyssal-lander*; Fig. 2(b)). The *Hadal-lander* basic delivery system comprises a lander frame with an 80 m mooring line supporting ten Vitrovex 17″ spheres rated for 11,000 m. The lander descends by virtue of a steel ballast weight and has a negative buoyancy of ~100 kg. The lander frame settles directly on the seabed and records video in a near horizontal orientation. At the end of the deployment the ballast weights are jettisoned by acoustic command from the surface via a tandem set of acoustic releases (Oceano 2500 ti-Deep, IXSEA, France). The scientific payload comprises a bespoke 3CCD Hitachi color video camera (800 TV lines), controlled and logged autonomously by a custom built control system (NETmc Marine, UK). Illumination is provided by two LED lamps. The camera is pre-programmed to

take 1 min of video every 5 min throughout and is powered by a 12V lead acid battery (SeaBattery; DSP&L, US). An SBE-39 sensor (Seabird Electronics Ltd., USA) logged pressure and temperature every 30 s throughout the dive.

The *Abyssal-lander* is described in Linley et al., (2015). The mooring is composed of 6000 m rated Vitrovex 17″ spheres for floatation. The lander descends by being negatively buoyant by a ballast weight, consisting of 12 mild steel plates weighing ~92 kg in total and which are attached at the end of a 2 m wire strop. The ballast weights are jettisoned in the same way as the *Hadal-lander* but with 6000 m rated acoustic releases (IXSEA, Oceano 2500 Universal). The scientific payload comprises a downward facing 5 megapixel stills camera and flash (Kongsberg Maritime, UK) capturing ~2×1.5 m^2 of seabed. The camera was pre-programmed to take 1 image every 60 s and is powered by a 24 V lead acid battery (SeaBattery; DSP&L, US). The lander also had a Seaguard recording platform with CTD probe and Doppler current meter (DCM, Aanderaa, Norway) that recorded every 30 s throughout.
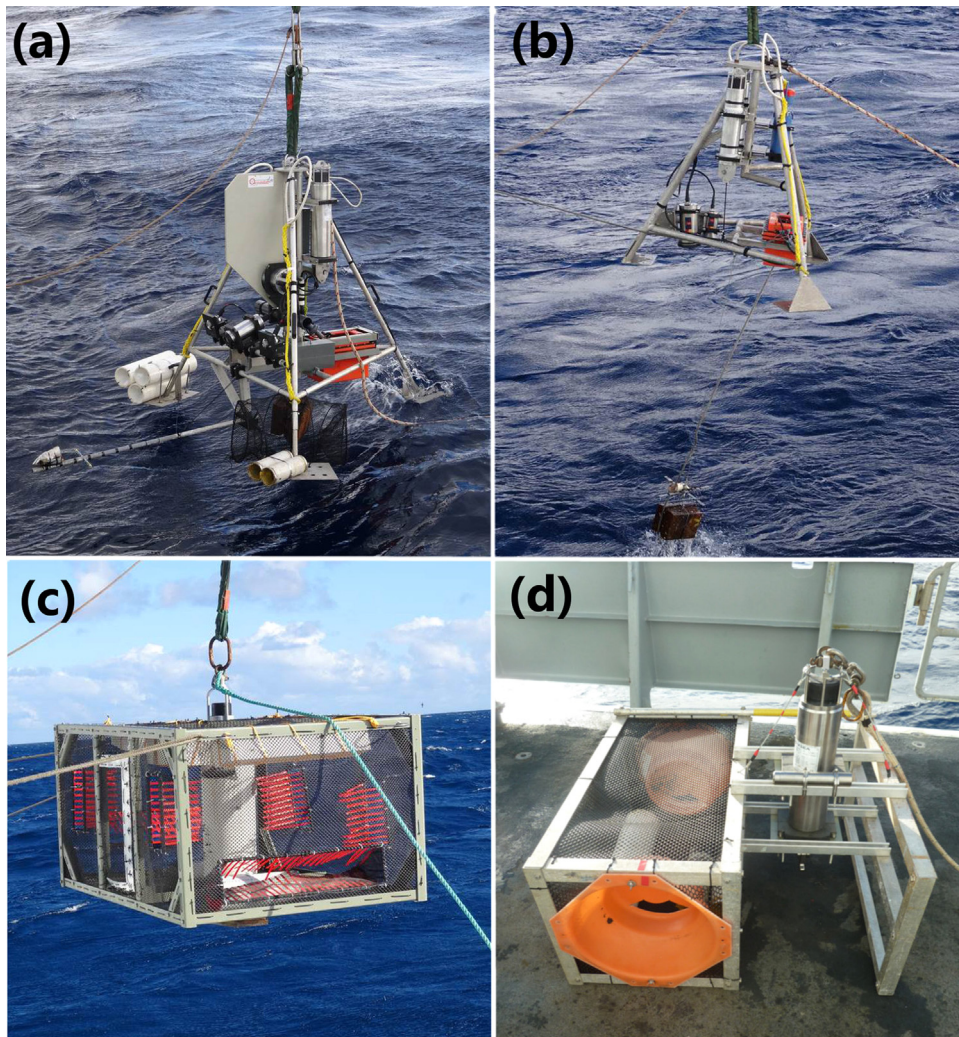
Fig. 2. Sampling equipment, where (a) *Hadal-Lander*, (b) *Abyssal-Lander*, (c) large fish trap and (d) the smaller 'wee trap'.

Two traps were used in this study: a large fish trap (Fig. 2(c)), and 'wee-trap' (Fig. 2(d); a smaller fish and invertebrate trap).

The wee-trap was an 11,000 m rated baited fish trap. The trap was deployed and recovered using the same method as the landers but with a single acoustic release, 92 kg of ballast and five 17″ glass floats. The trap was 45 cm × 45 cm × 1000 cm and wrapped with plastic mesh of approximately 1 cm gauge. Two 17″ glass sphere hard hats were inverted and used as funnel entrances with the openings close to the seafloor (< 20 cm). An SBE-39 pressure and temperature sensor (Seabird Electronics Ltd., USA) was logging at 30 seconds interval throughout.

The large trap, also rated to 11,000 m, comprised an approximately 1 × 1 × 2 m³ fibreglass frame, with 1 cm thick plastic netting. The trap mooring supported seven 17″ glass floats. Approximately 120 kg of steel ballast weight was ejected at the end of each deployment using an acoustic release (Teledyne Benthos, USA). Due to the fragile nature of hadal snailfish, nylon mesh was added to line the inside of the trap and minimize damage.

Both landers and both traps were baited using locally sourced Blue Mackerel, *Scomber australasicus*.

2.3. Data analysis

Stills collected by the *Abyssal-lander* were analysed manually. For each image collected, all visible fish were identified to the lowest possible taxonomic level. Identification was supported by lateral images captured by the *Hadal-lander* and by trapped voucher specimens. Video from the *Hadal-lander* was analysed in the same way as the *Abyssal-lander*. The maximum number of each fish species seen within one video frame of each 1 min video was used as the MaxN count for the 5 min interval.

From both the visual lander systems, the time that each species was first observed (T_{arr}) and the maximum number of individuals observed simultaneously (MaxN) were extracted for each deployment. When direct comparisons are being made between deployments of differing durations the MaxN value is within the first 10 h of the deployment.

Statistical analysis was performed with the software package R 3.3.2 (R Development Core Team, 2005). All plots were also produced in R unless otherwise specified. Where models are fitted, selection is based on the observed data distribution. Factors that have a significant effect on the response are identified through ANOVA using type-III sum of squares.

Upon capture, fish were photographed, weighed, and measured. Sex was determined visually. Some individuals were preserved whole for taxonomy. Fin clips or tissue were preserved in ethanol for genetic analysis. Tissues were collected and frozen for a number of other studies including TMAO contents. In some cases, dissected muscle samples, and blood or pericardial fluid extracted by syringe, were used immediately on the ship for osmolality measurements.
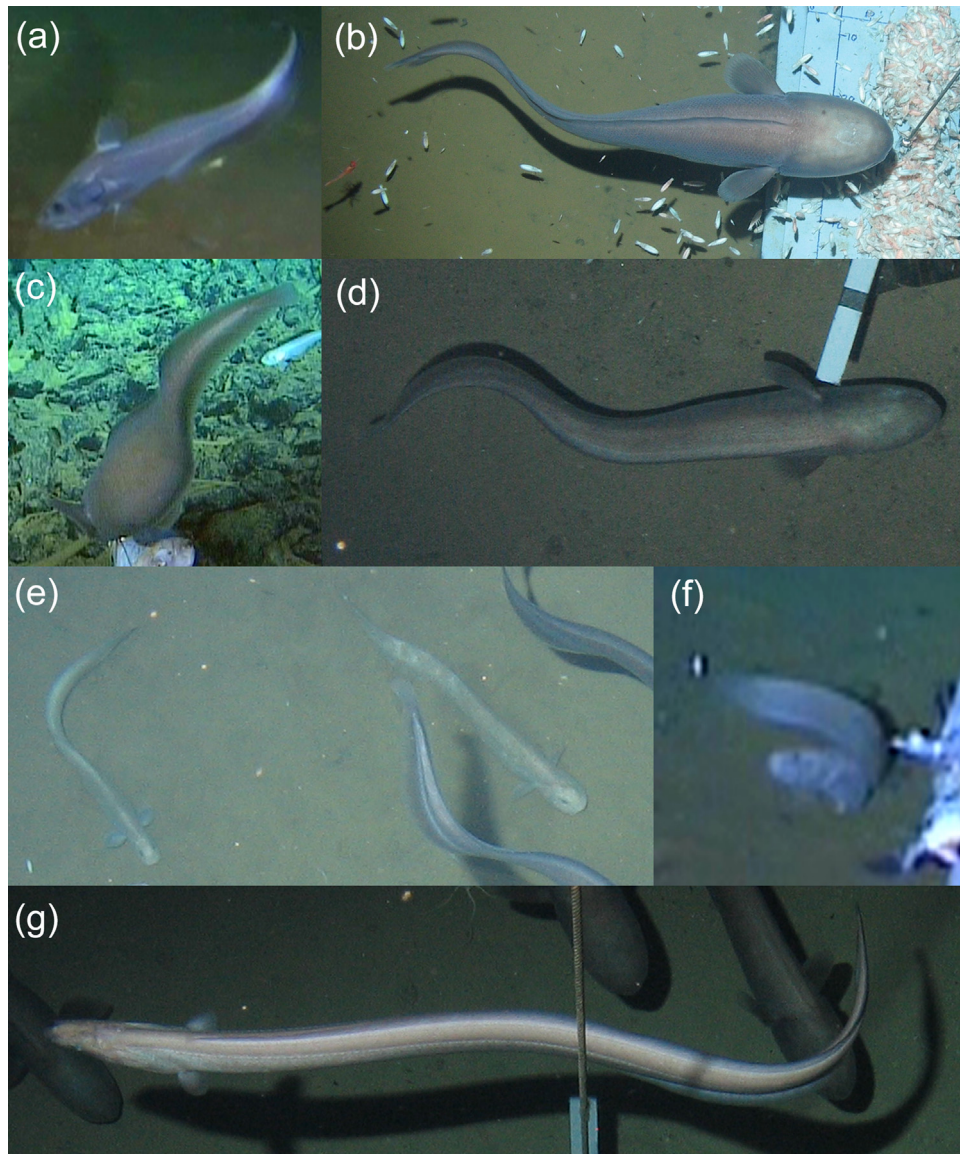
Fig. 3. New deepest records for *Coryphaenoides yaquinae* (Macrouridae) (a) 7012 m Mariana Trench; *Bassozetus sp.* (Ophidiidae) (b) 6898 m New Hebrides Trench, (c) 6750 m Kermadec Trench, (d) 6198 m Mariana Trench; unknown eel pout (Zoarcidae) (e) species 1 and species 2 6162 m New Hebrides Trench, (f) species 3 6145 m Mariana Trench; *Ilyophis robinsae* (Synaphobranchidae) (g) 6068 m Kermadec Trench.

2.4. TMAO and osmolality analyses

On the ship, osmolalities were measured with Wescor vapor-pressure osmometers in blood and pericardial fluids after centrifugation for 30 min at maximum speed in a small microcentrifuge (MyFuge; Benchmark Scientific, USA). For muscle, pieces were first mechanically homogenized with a Teflon pestle in a microcentrifuge tube, then centrifuged as above. Ten microliters of supernatant were taken for the osmometer.

Once delivered to Whitman College, frozen weighed muscle samples were processed as previously described (Kelly and Yancey, 1999). In short, they were homogenized in 7% (vol/vol) perchloric acid to remove proteins by precipitation, followed by centrifugation. Then TMAO concentrations of the supernatants were measured using an iron-EDTA reagent and a colorimetric reaction with picric acid, with appropriate standards.

3. Results

3.1. Abyssal-hadal transition fishes

Macrouridae were not seen deeper than 2087 m in the New Hebrides Trench, but were recorded from 997 m to 5879 m (observed 997–5879 m, trapped 3268–5242 m) in the Kermadec Trench and from 4441 m to 7012 m (observed 4506–7012 m, trapped 4441–6081 m) in the Mariana Trench. In both instances the deepest species was *Coryphaenoides yaquinae* (Fig. 3(a)) and the deepest of these Mariana Trench observations represents a new depth record for Macrouridae; previously 6945 m in the Japan Trench (Jamieson et al., 2009).

Ophidiidae were recorded in all three trenches; New Hebrides Trench: 2087–6898 m (observed 2087–6898 m, trapped 4700–5300 m), Kermadec Trench: 1473–6750 m (observed 1473–6750 m, trapped 1980–4204 m) and Mariana Trench 4506–6198 m (observed 4506–6198 m, not trapped) (Fig. 3(b)-(d)). The deepest species seen were visually identified to genus level as *Bassozetus* sp. This genus is difficult to identify to species level by external
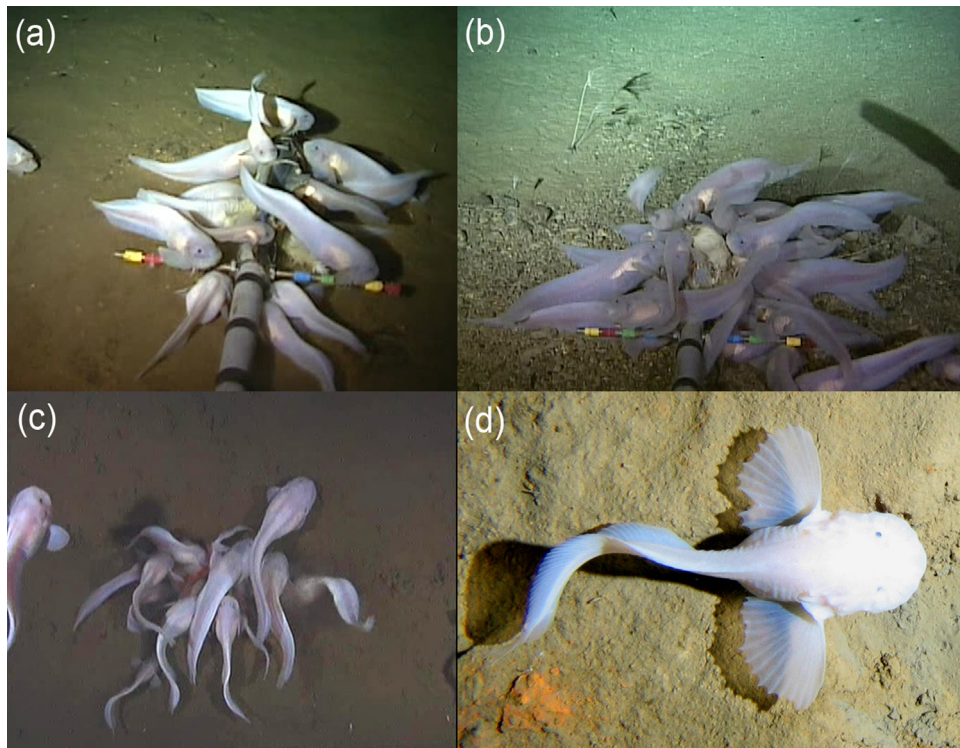
Fig. 4. Examples of hadal Liparidae from around the Pacific trenches, where (a) is the (undescribed) Mariana snailfish at 7415 m in the Mariana Trench, (b) is *Notoliparis kermadecensis* at 7243 m in the Kermadec Trench, (c) is *Pseudoliparis belyaevi* from 7703 m in the Japan Trench (Fujii et al., 2010) and (d) is the (undescribed) Peru-Chile snailfish at 7049 m in the Peru-Chile Trench (Jamieson, 2015).
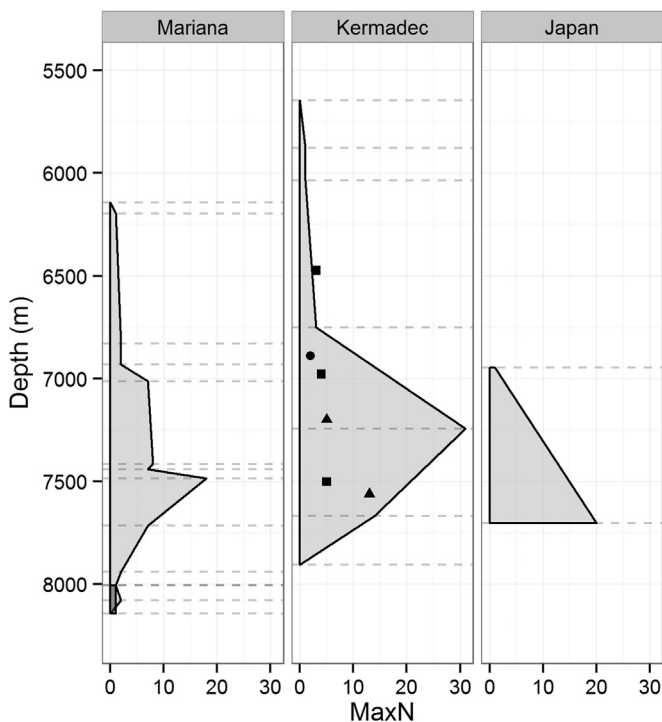

Fig. 5. Maximum number (MaxN) after 10 h across the known bathymetric range of snailfish in the Mariana Trench, Kermadec Trench and Japan Trench. Dashed lines indicate exact depth of observation. The deepest and shallowest deployment without snailfish is also included except for the next deeper deployment lacking the Ethereal snailfish as this is beyond the presented scale. Mariana and Kermadec data taken from this study. The Japan Trench data is from Jamieson et al., (2009; shallower), Fujii et al., (2010; deeper). Previous studies in the Kermadec Trench have been superimposed: square; unpublished data from 2011, 2012, triangle; Jamieson et al. (2009) and squares; Jamieson et al. (2011).
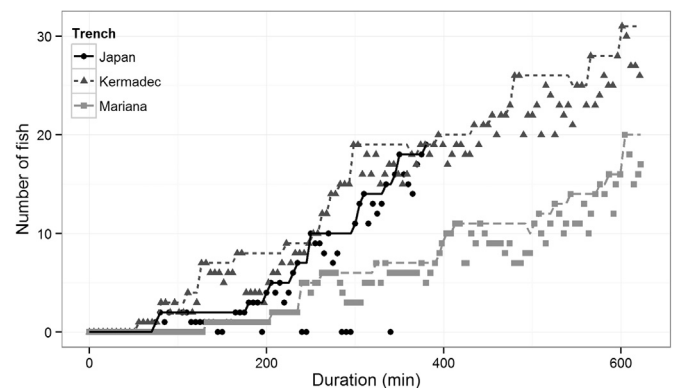
Fig. 6. Number of snailfish present around the bait over time in the Mariana, Kermadec and Japan trenches, from depths of 7485, 7243, and 7703 m respectively (respective depths where snailfish were the most abundant in each trench). Data taken from this study except the Japan Trench from Fujii et al. (2010). Data truncated to 10 h for Kermadec and Mariana, whereas Japan Trench data is only 6.5 h long. Trends lines represent a rolling maximum number per hour.

morphology, so species level identification was not possible. More than one species may have been present. In the absence of any physical sample to confirm the species, these are hereafter referred to simply as *Bassozetus* sp.

Zoarcidae are hitherto not known from hadal depths, but at 6162 m (observed 3424–6162 m, trapped 4100 m) up to nine individuals of two visually distinct species where seen simultaneously in the New Hebrides Trench. A Zoarcid was also seen at 6145 m in the Mariana Trench (observed 5055–6145 m, not trapped). These represent the first finding of Zoarcidae at such depths (Fig. 3(e)-(f)). They were also recorded from 3039 to 4989 m in the Kermadec Trench (observed 3039–4953 m, trapped 4193–4989 m). Specimens caught from 4100 to 4193 m in the Kermadec Trench, New Hebrides Trench and adjoining South Fiji Basin were
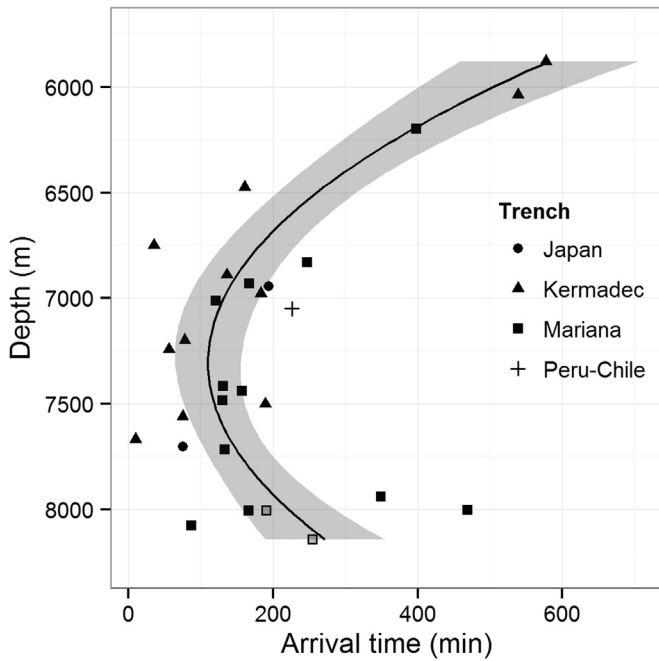
Fig. 7. First Arrival time (T_{arr}, min) of snailfish in the Japan Trench (circle; Fujii et al., 2010; Jamieson et al., 2009), Kermadec Trench (triangle; data from this study and supplemented with Jamieson et al., 2011, 2009 and unpublished data), and Mariana Trench (square; data from this study). As the Mariana Trench contained two species, the Ethereal snailfish is indicated by grey squares. The regression line is fitted to all snailfish arrival times and is highly significant (adj-R2=0.604, $F_{2,25}$=21.61, p < 0.001). The shaded area represents the 95% confidence interval of this model.

identified as *Pachycara moelleri* Shinohara, 2012. Specimens from 4204 to 4989 m in the Kermadec Trench contain at least one additional, potentially undescribed, species. These specimens are currently under assessment.

Synaphobranchidae are also unreported from hadal depths. They were notably absent in the Mariana Trench. However, they were recorded from 997 to 6068 m in the Kermadec Trench (observed 997–6068 m, trapped 1013–1980 m; Fig. 3(g)) and 2087–5344 m in the New Hebrides Trench (observed 2087–5344 m,
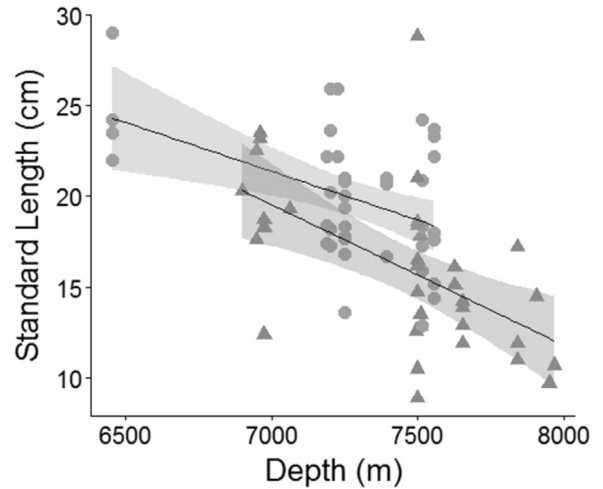
Fig. 8. Standard lengths of hadal snailfish by depth for Kermadec (circles), and Mariana (triangles) Trenches. Linear regression is shown for each population with 95% confidence interval illustrated by shading. Relationships are significant for both trenches (p=0.002 for Kermadec, p < 0.001 for Mariana).

trapped 5180 m). The specimen trapped in the New Hebrides Trench was identified as *Ilyophis robinsae*. The *in situ* photography in the Kermadec and New Hebrides trenches and the South Fiji Basin frequently observed a large *syn*aphobranchid eel resembling *I. robinsae* at abyssal depth (crossing the hadal boundary in the Kermadec Trench). Eels viewed in profile possessed pale lateral line pores, a lower jaw that does not appear to protrude beyond the upper, a dorsal fin origin in line with the pectoral fin origin and small pectoral fins supporting that this is an *Ilyophis* rather than a *Histiobranchus* species (Sulak and Shcherbachev, 1997) as previously thought (Jamieson et al., 2011).
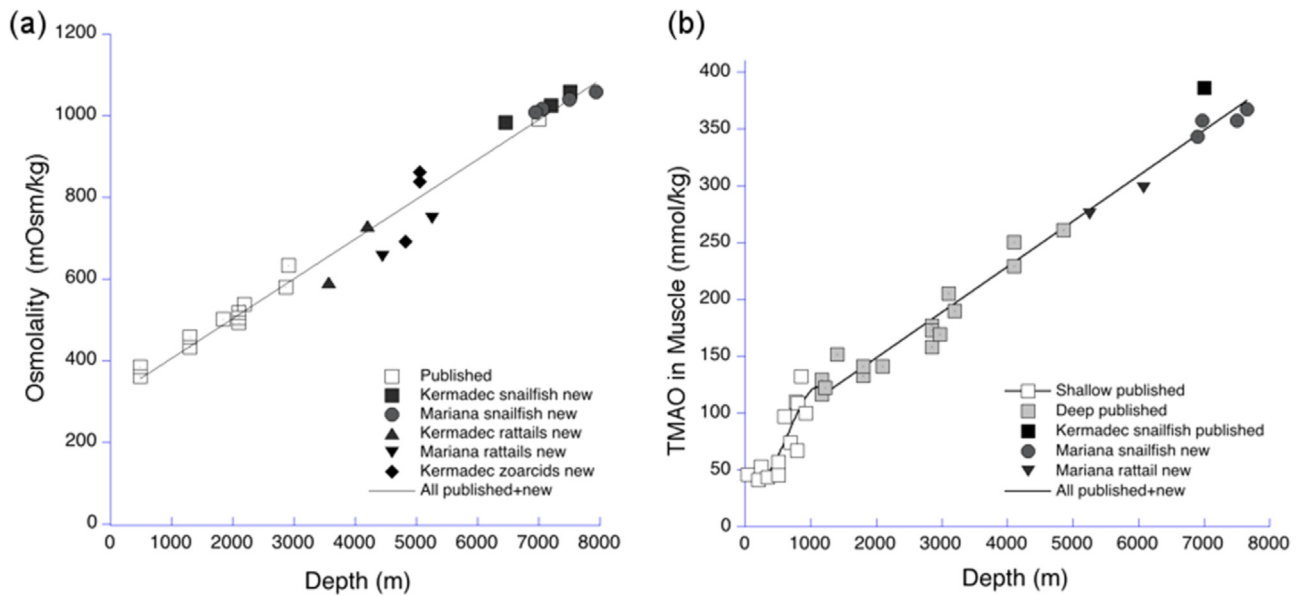
3.2. Hadal snailfishes

Liparidae were by far the dominant fish family at hadal depths in the Kermadec and Mariana trenches, but were not observed in the New Hebrides Trench. They were observed *in situ* between 5879 and 7669 m in the Kermadec Trench (over three

Table 1

Arrival times, maximum numbers and percentage of frames/video sequences of *Notoliparis kermadecensis*, the Mariana snailfish and the Ethereal snailfish, where Kerm = Kermadec Trench, Mar=Mariana Trench, Al=Abyssal-lander and HL=Hadal-lander. To account for different durations, the MaxN of the first 10 h is included in parentheses if it differs from MaxN of the entire deployment.

Trench	Gear	Depth (m)	Station	Arrival times (min)			Maximum number			Percentage of frames (%)		
				Notoliparis kermadecensis	Mariana snailfish	Ethereal snailfish	*Notoliparis kermadecensis*	Mariana snailfish	Ethereal snailfish	*Notoliparis kermadecensis*	Mariana snailfish	Ethereal snailfish
Kerm	AL	5879	LA10	577			1			0.8		
Kerm	AL	6037	LA11	539			1			1.6		
Kerm	HL	6750	LH12	35			3			42.7		
Kerm	HL	7243	LH10	56			31			92.9		
Kerm	HL	7669	LH11	10			15(14)			87.2		
Mar	AL	6198	LA03		398			1			0.3	
Mar	HL	6831	LH05		247			2			35.8	
Mar	HL	6931	LH06		167			2			7.6	
Mar	HL	7012	LH12		121			7			58.8	
Mar	HL	7415	LH07		131			11(8)			92.1	
Mar	HL	7440	LH08		157			7			71.8	
Mar	HL	7485	LH13		130			20(18)			78.2	
Mar	HL	7716	LH23		133			13(7)			80.1	
Mar	HL	7941	LH09		349			4(4)			57.1	
Mar	HL	8004	LH18		469			2(1)			29.1	
Mar	HL	8007	LH10		166	191		7(1)	1		69.8	19.5
Mar	HL	8078	LH11		87			2			15.5	
Mar	HL	8145	LH22			255			1			12.7

Fig. 9. Datasets from Yancey et al. (2014) updated with new data from this study for a) osmolalities of muscle fluid and b) muscle TMAO content with depth of capture.

deployments), and 6198 and 8145 m in the Mariana Trench (over 13 deployments). The former were identified as *Notoliparis kermadecensis* (Nielsen, 1964) and the latter comprise two new species of snailfish. The first is currently being described and for clarity is hereafter referred to as the 'Mariana snailfish'. This was a predicted discovery based on consistent observations in the

Kermadec Trench (Jamieson et al., 2011, 2009), Japan Trench (Fujii et al., 2010; Jamieson et al., 2009), Peru-Chile Trench (Jamieson, 2015), and written observations in the Puerto-Rico Trench (Pérês, 1965). Also, anecdotal reports of a snailfish at 7000 m were reported from test dives of the Chinese *Jiaolong* submersible (Cui, 2013). The 'Mariana snailfish' was observed in 12 lander
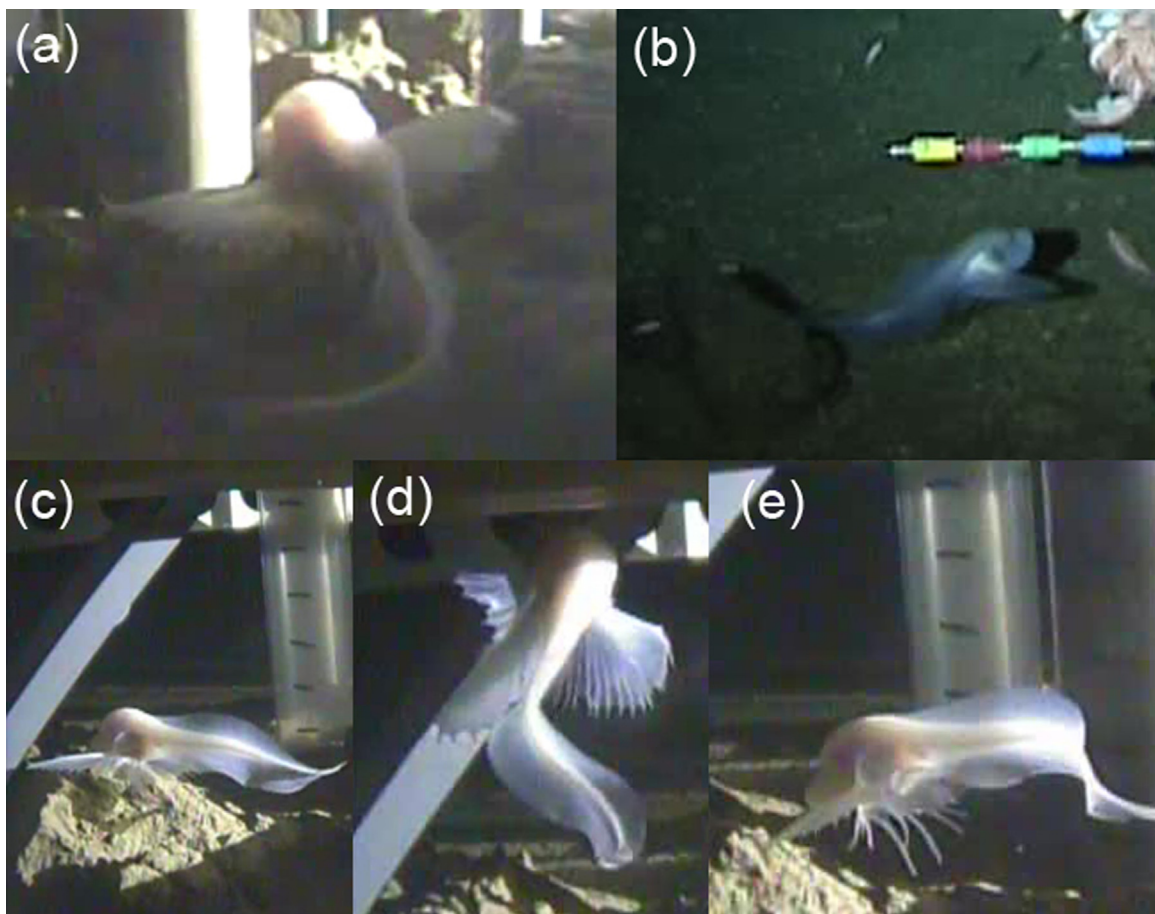
Fig. 10. In situ observations of the Ethereal snailfish as recorded by (a) the FVCR at 7939 m and (b) the Hadal-lander at 8145 m. Images (c), (d) and (e) show details for the caudal fin, pectoral fins and filamentous fin-rays on the lower lobe respectively.

deployments between 6198 and 8076 m and captured in 15 trap deployments between 6898 and 7966 m. The second new species was an unexpected, solitary snailfish observed as deep as 8145 m over two deployments in the Mariana Trench.

The baited camera observations of snailfish from the Mariana and Kermadec trenches were surprisingly similar in terms of depth distribution, optimum depth (as inferred from peak numbers), accumulation rates and behaviour at the bait. They are similar also to those in the Japan Trench (Fujii et al., 2010) and to other studies in the Kermadec Trench (Jamieson et al., 2011), despite the geographic isolation of these trenches. Furthermore, the snailfish morphology is very similar between these sites and also to the images of the Peru-Chile snailfish (Jamieson, 2015; Fig. 4). All have soft pinkish-white bodies covered in a gel layer sufficiently translucent to make the liver visible by camera. They have small black eyes and were observed suction feeding on amphipods.

The Mariana snailfish and *N. kermadecensis* share many similar attributes such as depth range (6198–8078 m and 5879–7669 m respectively) and depth of greatest relative abundance (7485 m, MaxN=20 and 7243 m, MaxN=31 respectively; Fig. 5). These in turn are similar to those of *P. belyeavi* from the Japan Trench (7703 m, MaxN=20; Fujii et al., 2010). Few fish are observed at the shallower and deeper end of the depth ranges but there is a marked peak in numbers in between. The aggregation patterns at depth of greatest relative abundance also revealed a distinct similarity (Fig. 6). Likewise, their arrival times (T_{arr}) also showed a degree of similarity over their known depth ranges, showing a decrease with depth to a minimum at ~7300 m after which it increases with depth (Fig. 7). Using this study's data from the Mariana and Kermadec Trenches, where the methodology has remained consistent, a 2nd order polynomial model best represented the relationship of both MaxN (up to 10 hr) and T_{arr} (Figs. 5 and 7) to depth with trench as a covariate. Depth has a highly significant effect on both metrics ($F_{2,15}=6.552$, p=0.009 and $F_{2,15} = 20.484$, p < 0.001 respectively). A significant effect of trench (Mariana and Kermadec) was detected in MaxN, and T_{arr} also approached significance ($F_{1,15}=7.519$, p=0.015, $F_{1,15}=3.459$, p=0.083 respectively). The lower MaxN of snailfish in the Mariana Trench relative to the Kermadec Trench would suggest a lower snailfish population density in the Mariana Trench. A summary of arrival times, maximum numbers and the percentage of frames containing snailfish from baited camera data are listed in Table 1.

The baited traps recovered 41 specimens of *N. kermadecensis* and 37 specimens of the Mariana snailfish. These collections more than quadruple the number of hadal snailfish that have been collected worldwide. *Notoliparis kermadecensis* were collected from depths 6456–7554 m. Standard lengths ranged from 12.9 to 29 cm and total weights from 20 to 230 g. 19 females, 14 males and 3 juveniles were collected. The Mariana snailfish was captured between 6898 and 7966 m. Standard lengths ranged 8.9–28.8 cm and total weights from 7 to 160 g. 14 females, 5 males, and 7 juveniles were collected. In both trenches, body size of hadal snailfish decreased with depth of capture (Fig. 8), perhaps suggesting ontogenetic movement upslope.

3.3. TMAO Contents and Osmolalities

Osmolalities were obtained for rattails (*C. yaquinae*) from Kermadec and Mariana trenches, zoarcids (*Pachycara* spp.) from the Kermadec, and *N. kermadecensis* and Mariana snailfish. As shown in Fig. 9(a) along with our previously published data (see Yancey et al., 2014), these osmolalities fit well with the existing depth trend.

TMAO contents were also determined in some of the same species, and found that they too correspond well with our published depth trend (Fig. 9(b)).

Table 2

Updated assessment of the fish found reported from hadal depths. * likely a pelagic capture (Markle and Olney, 1990; Nielsen et al., 1999).

Species	Depth (m)	Trench	Record
Synaphobranchidae (Cutthroat eels)			
cf. *Ilyophis robinsae*	6068	Kermadec	This study
Macrouridae (Grenadiers)			
Coryphaenoides yaquinae	6000	Kermadec	Jamieson et al., 2011
	6160	Japan	Horibe, 1982
	6945	Japan	Jamieson et al., 2009
	6380–6450	Japan	Endo and Okamura, 1992
	6008–7012	Mariana	This Study
Carapidae (Pearl fish)			
*Echiodon neotes**	8200–8300	Kermadec	Markle and Olney, 1990
Ophidiidae (Cusk-eels)			
Bassozetus zenkevitchi	0–6930	Not specified	Rass, 1955
Bassozetus sp.	6116–6750	Kermadec	Jamieson et al., 2013, This study
	4506–6198	Mariana	This Study
	5329–6173	Peru-Chile	Jamieson, 2015
	2086–6898	New Hebrides	This Study
Leucicorus atlanticus	4580–6800	Cayman	Nielsen, 1975
Barathrites sp.	6173	Peru-Chile	Jamieson, 2015
Barathrites iris	6116	Kermadec	Jamieson et al., 2013
Abyssobrotula galatheae	3110–8370	Puerto Rico	Nielsen, 1977
Holcomycteronus profundissimus	5600–7160	Sunda	Roule, 1913
Liparidae (Snailfish)			
Notoliparis antonbruuni	6150	Peru-Chile	Stein, 2005
Notoliparis kermadecensis	6660–6770	Kermadec	Nielsen, 1964
	6890	Kermadec	Jamieson et al., 2009
	6474–7501	Kermadec	Jamieson et al., 2013
	5879–7669	Kermadec	This study
	7199–7561	Kermadec	Jamieson et al., 2011a
Pseudoliparis amblystomopsis	7210–7230	Kurile-Kamchatka	Andriashev, 1955
	7420–7450	Japan	Horikoshi et al., 1990
Pseudoliparis belyaevi	7565–7587	Japan	Andriashev and Pitruk,1993
	6945	Japan	Jamieson et al., 2009
	7703	Japan	Fujii et al., 2010
The Mariana snailfish	6198–8078	Mariana	This study
The Ethereal Snailfish	8007–8145	Mariana	This study
The Peru-Chile Snailfish	7049	Peru-Chile	Jamieson, 2012
Unknown Liparid	7300	Puerto-Rico	Pérès, 1965
Zoarcidae (eel pouts)			
Zoarcid 1	6162	New Hebrides	This study
Zoarcid 2	6162	New Hebrides	This study
Zoarcid 3	6145	Mariana Trench	This study

3.4. Ethereal snailfish

The second new snailfish species was first discovered seren-dipitously on an inspection 'task' camera, on the underside of the SOI/University of Hawaii 'Free Vehicle Core Respirometer' (FVCR) at 7939 m (Fig. 10). To distinguish this deeper species from the other, more common Mariana snailfish, it is referred to hereafter by the common name coined by those present on the cruise; the Ethereal snailfish, which reflects the delicate morphology and graceful swimming gait. The individual fish swam close enough to the camera to reveal in great detail the small body form and de-licate elongate fin morphology, particularly the pectoral fins, which do not conform to any known species of snailfish. The snailfish was also observed to suction feed from surficial sediment.

Following the FVCR observation, the Hadal-lander was de-ployed and the same species of fish was observed at a further two depths (8007 and 8145 m). The latter represents the deepest fish ever seen alive, 442 m deeper than the previous record of 7703 m (Fujii et al., 2010). At its shallower depth, the Ethereal snailfish was observed simultaneously with the Mariana snailfish. In all in-stances the Ethereal snailfish was observed singly, in constant motion, close to the seafloor, circling the bait and associated am-phipod aggregation. It was observed a total of eight times to suction feed on small amphipods, in the same manner as other snailfishes observed at hadal depths. As has also been observed in other hadal snailfishes it displayed quick c-start escape responses (Weihs, 1973), presumably to dislodge amphipods irritating its skin.

At the depths where it was observed by the Hadal-lander (8007 m and 8145 m) the first arrival time and staying time were noted: At 8007 m it arrived 2 h 42 min after the lander touched down. One individual was present in view of the camera for the next 3 h 47 min, and in the following 6 h and 45 min there were another 8 intermittent appearances for no more than 1 min at a time. There is no evidence to show this was more than one in-dividual, suggesting it stayed in the vicinity of the lander for 10.5 h. At 8145 m, an Ethereal snailfish arrived at 4 h 15 min after lander touched down. There were five appearances in front of the camera over the subsequent 56 min

Despite the baited traps capturing 37 individual Mariana snailfish over 15 deployments between 6896 and 7966 m, the deeper Ethereal snailfish was not captured and thus remains undescribed.

4. Discussion

The fishes we observed can be broadly placed into two groups: the first are primarily abyssal species that can extend into the hadal habitat and the second are those that appear to be confined to the hadal zone.

These new observations extend some of the known depths and locations of the abyssal fish fauna, such as the Macrouridae and Ophidiidae further into the hadal zone. In the case of the zoarcid and synaphobranchid species this represent their first recorded hadal occurrence. An updated assessment of hadal fish species, in light of these new data and the (now corrected) misreporting of *Apagesoma edentatum* as a hadal species in Froese and Pauly (2016), is listed in Table 2.

Macrourids are an abundant and diverse family of deep-sea Gadiformes (Wilson and Waples, 1983). Two macrourid species are often observed within the vicinity of Pacific trenches; *Cor-yphaenoides yaquinae* Iwamoto and Stein, 1974, and *C. armatus* (Hector, 1875). The former is a deeper-living species restricted to the Pacific Ocean and often observed up to 5900 m on the abyssal plains (Priede et al., 1990), although on occasion reported deeper

(6000 m, Jamieson et al., 2012, 6160 m, Horibe, 1982, and 6945 m, Jamieson et al., 2009). This study reports the deepest record of Macrouridae: *C. yaquinae* at 7012 m in the Mariana Trench. Inter-estingly, Pérês (1965) reportedly saw a macrourid at ∼7000 m in the Puerto Rico Trench but did not have any recorded imagery. It is unlikely to be *C. yaquinae* given its Atlantic setting and may sug-gest that either *C. armatus* or an unknown macrourid can trans-cend the abyssal-hadal boundary in the Atlantic. In the case of the former, this would extend the known range of this species by ∼1500 m.

There are taxonomic descriptions based on caught specimens of four ophidiids with a depth range exceeding 6000 m: *Bassozetus zenkevitchi* Rass, 1955, *Leucicorus atlanticus* Nielsen, 1975, *Holco-mycteronus profundissimus* (Roule, 1913), and *Abyssobrotula ga-latheae* Nielsen, 1977. All of these are rarely encountered. Various hadal ophidiids have also been observed by baited cameras. Through lack of physical samples they have yet to be identified to species level, though most appear morphologically close to *Bas-sozetus* sp. (Jamieson et al., 2013). These were photographed *in situ* at 6116 and 6474 m in the central Kermadec Trench (Jamieson et al., 2013). This *Bassozetus* sp. is morphologically very similar to individuals photographed at 5469 m on the edge of Mariana Trench (Jamieson et al., 2009), at 5329 and 6173 m in the Peru-Chile Trench (Jamieson, 2015) and to those from this study. In-dividuals resembling *Barathrites iris* were photographed *in situ* at 6116 m in the Kermadec Trench (Jamieson, 2015) and smaller in-dividuals (potentially a different species) were photographed in large numbers at 6173 m in the Peru-Chile Trench (Jamieson, 2015). The relatively common *Bassozetus* and lesser photographed *Barathrites* are genera known to primarily inhabit abyssal depths. They are likely present in the upper hadal zone simply at the deeper end of their respective populations rather than re-presenting endemic hadal species.

The discovery of the Mariana snailfish between 6198 and 8076 m appears in keeping with many other observations of large trenches hosting relatively large, active communities of endemic snailfish between approximately 6500 and 8000 m. Their apparent absence from the New Hebrides Trench cannot be fully explained other than it being a relatively shallow trench with a maximum depth of 7156 m. This falls short of the emerging optimal hadal snailfish depth of between 7000 and 8000 m. The reasons behind the notable success of this family at hadal depths remain to be explored.

While the Mariana snailfish resembles *P. belyaevi* in the Japan Trench (Fujii et al., 2010) and *N. kermadecensis* in the Kermadec Trench (Jamieson et al., 2011; this study), the Ethereal snailfish is distinctively different in appearance; its delicate elongated pec-toral fins, filamentous fin-rays and reduced body cavity to tail ratio are apparent. The extended rays on the ventral side of the fish are likely part of a modified lower pectoral fin lobe, very distinct from the known *Notoliparis/Pseudoliparis* morphology. The markedly sloping head shape is also quite distinct from other hadal snailfish. Compared to the more common hadal snailfish form, the Ethereal snailfish also appears to have a thin body depth, with reduced epaxial and hypaxial musculature. It also has a larger proportion of gelatinous tissue, or subdermal extracellular matrix (Eastman et al., 1994; Gerringer et al., in prep) around the posterior half of the body. The presence or absence of a ventral disk could not be determined from the video collected.

According to the International Code of Zoological Nomen-clature (ICZN, 2012), attributing a species to the Ethereal snailfish is possible in the absence of a holotype as its distinctive mor-phology is more than sufficient to confirm it as a previously un-known species. As we did not recover a specimen of this new species, we have decided to not designate an official scientific name, and would rather wait until a physical type-specimen is

collected. It is also not possible to attribute a genus as the morphological characters ("extra" postcoronal and temporal cephalic pores) that distinguish *Notoliparis* from *Pseudoliparis* (Andriyashev and Pitruk, 1993) are at best cryptic in images and are undetectable following preservation or even slight decomposition after capture. The morphological differences in fin rays, head shape, and body proportion could place this fish in a new genus. Until a holotype is obtained, the Ethereal snailfish must remain undescribed.

The significance of the Ethereal snailfish is not only in its delicate and distinctive form, but in its very existence at the depths at which it was found. The TMAO hypothesis by Yancey et al. (2014) proposes a potential biochemical limit of ~8200 m for bony fish on the grounds that the relationship between hydrostatic pressure, TMAO content and osmolality results in an isosmotic state at this depth. To live deeper would require TMAO contents above isosmotic levels, requiring significant physiological reorganization of osmoregulatory systems. Yancey et al. (2014) used samples obtained from Kermadec Trench snailfish at ~7000 m to confirm this trend from data extrapolated from other shallower deep-sea fish. Our new data from depths increasingly close to the proposed maximum do not show any signs of deviation from the extrapolations for both osmolality (Fig. 9(a)) and for TMAO which is responsible for the increase in osmolality with depth (Fig. 9(b)). The presence of the Ethereal snailfish bridges the gap between the previous record of the deepest fish (7703 m; Fujii et al., 2010) and the proposed maximum limit (~8200 m; this study and Yancey et al., 2014). In fact, the deepest Ethereal snailfish observation falls ~50 m shallower than the proposed limit. It should be stressed that this is not a discrete limit and individual fish may be able to surpass this depth for short periods. The next deepest *Hadal-lander* deployment was at 8964 m, 764 m deeper than the proposed limit. At this depth and greater no other fish were observed. This trend was seen in every other trench studied using the methodology of this study (Tonga, Kermadec, Izu-Bonin and Peru-Chile trenches). Other recent studies also reported a lack of fish at 8228 m in the New Britain Trench (SW Pacific Ocean) and at 10,908 m in the Mariana Trench (Gallo et al., 2014).

The paper entitled "The deepest living fish (*Abyssobrotula galatheae*)" notes that stomach contents in all but one individual indicate a benthic origin (Nielsen, 1977), the exception being the deepest individual trawled in open pelagic gear by the *Pillsbury* (Staiger, 1972). Though questionable, the 8370 m catch record can be neither confirmed nor refuted; however, it would fall within the error range of our extrapolations in Fig. 9 and in Yancey et al. (2014). Therefore at present the capture of a Mariana snailfish from 7966 m represents the deepest vertebrate collection using benthic gear with confirmation by pressure sensor and the *in situ* observation of the Ethereal snailfish at 8145 m represents the deepest fish seen alive.

Acknowledgements

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