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Amphipoda from depths exceeding 6,000 meters revisited 60 years on

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ABSTRACT

In the 1950s, the Danish *Galathea* Expedition undertook one of the first and most comprehensive explorations of our ocean's hadal zone, depths extending from 6,000 to nearly 11,000 m, and presented a rich collection of the diversity of Amphipoda. The subsequent papers, however, concluded that these established 'nothing essentially new' to the existing knowledge of amphipod biology. Since Dahl's foundational paper in 1959, amphipods, primarily from the superfamilies Lysianassoidea and Alicelloidea, emerged as one of the best-sampled hadal fauna, as these mobile invertebrates are readily recovered by different sampling techniques. Importantly, amphipods have become the model taxon, helping us to unlock knowledge about life in the hadal zone. In this review, we collate the knowledge gained since the *Galathea* Expedition and summarise the current understanding of how amphipods that appear during hadal exploration survive the trench environments. We discuss population structures across depth, inter-trench distribution and connectivity, applications in hadal microbiology, and, critically, how the hadal zone is being impacted by anthropogenic activity.

KEY WORDS: anthropogenic contamination, Crustacea, deep-sea biology, deep-sea ecology, deep-sea fauna, deep-sea microbiology, hadal zone, *in situ* imagery

INTRODUCTION

The first compilation of amphipods living in the hadal zone (depths > 6,000 m) was simply entitled 'Amphipoda from depths exceeding 6000 meters' by Dahl (1959). Based on the findings of the Danish *Galathea* Expedition, this account reported that despite being a comparatively rich collection, including many new species and depth records, it established 'nothing essentially new' to the existing knowledge of amphipod morphology and taxonomy compared to the works of A. Schellenberg and J.M. Pirlot in the 1920s and 30s, respectively. Based on the 15 species from three genera from *Galathea*, Dahl (1959) concluded that they conformed well to his existing understanding of structural patterns of common abyssal species. The study ultimately covered 21 species by the inclusion of various descriptions from Swedish and former Soviet Union expeditions in the 1950s. It was noted that although these species belonged to 10 different families, eight of them belonged to the superfamily Lysianassidae. Dahl (1959) also noted a high degree of endemism, with only two of these species known at the time, to reside in more

than one trench, an observation that continues to be a central focus for contemporary hadal biology.

Following the coining of the term 'hadal' by the leader of the *Galathea* Expedition (Bruun, 1956), another member of the expedition published the first concept of a 'hadal community' (Wolff, 1960). Amphipoda was listed as a dominant hadal group, alongside several others, namely holothurians, isopods, and polychaetes. The number of species known was 20–25, with 56% estimated to be endemic (Wolff, 1960). Just ten years later, Wolff (1970) re-evaluated these figures based on many other records supplied by Belyaev (1966) following the *Vitjaz* expeditions. He reported 17 hadal amphipod species, of which 14 (82.4%) were endemic, and declared that the amphipods were in the 'five significant abyssal-hadal groups' as defined by a high percentage of hadal species (alongside echinoids, polychaetes, bivalves, and holothurians). All these studies were based largely on 'rather ponderous samplers' (Hessler *et al.*, 1978), such as bottom trawling and sediment grabs and dredges, which are now known not to be the optimum method in recovering highly mobile species, such as scavenging amphipods (Jamieson *et al.* 2013a).

Following the Danish and former Soviet Union expeditions from the late 1950s to the 70s, trawling at hadal depths largely ceased. The turn of the century saw the free-fall camera and trap methods adopted more commonly for hadal research (Jamieson, 2018), although some modern trawling expeditions have occurred specifically at the Kuril-Kamchatka Trench (Northwest Pacific) (Jażdżewska & Mamos, 2019). This led to a sudden increase in the sampling of, and research, into the diversity and community structure of hadal amphipods (e.g., Thurston et al., 2002; Perrone et al., 2003, Blankenship et al., 2006; Eustace et al., 2013; Fujii et al., 2013; Lacey et al., 2016, 2018), which in turn led to molecular-based studies (e.g., Ritchie et al., 2015, 2017a, b, 2018; Lan et al., 2016, 2017; Downing et al., 2018; Zhang et al., 2018, 2019; Kobayashi et al., 2019; Li et al., 2019a, b) and their use as a model taxon in environmental pollution studies at full ocean depth (Jamieson et al., 2017, 2019; Blum et al., 2020; Cui et al., 2020; Sun et al., 2020; Weston et al., 2020).

The relative ease and frequency of sampling and the scale and breadth of studies is such that hadal amphipods have now been used as a model taxon and have resulted in a disproportionate level of knowledge on this group compared to any other hadal group, including those identified by Wolff (1960, 1970) as being of 'great ecological significance'. Here, we revisit the Amphipoda from depths exceeding 6,000 meters' (sensu Dahl, 1959) and offer a review contrary to the concept of amphipods originally offering "\'nothing essentially new', but rather have since provided some of the greatest insights into life at the deepest places in the ocean.

We review herein this important hadal group from how they appear in situ during sampling and hadal exploration, to how they survive the trench environments (pressure adaptation and trophic ecology), how their populations are structured (community structure and life history), inter-trench distribution (phylogenetics and connectivity), their usage in hadal microbiology, and how they provide a warning that the hadal zone is impacted by anthropogenic activity. We finally reflect on outstanding questions and how amphipods can continue to illuminate mysteries of the hadal zone.

BIODIVERSITY AND ENDEMISM

In the 50 years since Wolff (1970) reported 17 species of hadal species of amphipods, the number of known species now exceeds 100 (Table 1, Fig. 1). This expansion of known diversity

Table 1. Summary of records of hadal amphipod to family level, including the number of records and locations. Numbers in parentheses represent uncertain identifications.

| Suborder	Superfamily	Family	Number of genera	Number of species	Number of records	Number of locations
Amphilochidea	Alicelloidea	Alicellidae	2 (+1)	2 (+8)	30	14
		Valettiopsidae	1	1 (+1)	5	4
	Dexaminoidea	Pardaliscidae	3	9 (+2)	34	13
		Atylidae	2	4	5	5
		Lepechinellidae	1	1	1	1
	Eusiroidea	Eusiridae	4 (+1)	4 (+4)	11	9
	Haustorioidea	Phoxocephalidae	3	2 (+1)	3	3
	Iphimedioidea	Stilipedidae	1	1	1	1
		Epimeriidae	1	0 (+2)	3	3
	Liljeborgioidea	Liljeborgiidae	1	1	1	1
	Lysianassoidea	Lysianassidae	4 (+1)	4 (+2)	7	5
		Tryphosidae	2 (+3)	1 (+6)	9	7
		Eurytheneidae	1	6 (+4)	14	9
		Hirondelleidae	1	5 (+1)	34	16
		Cyclocaridae	1	1 (+2)	3	3
		Scopelocheiridae	2	2	25	16
		Uristidae	4	5 (+3)	11	6
	Stegocephaloidea	Stegocephalidae	3(+1)	4 (+4)	9	8
		Andaniexinae	1	1	1	1
	Synpioidea	Ampeliscidae	1	1	1	1
		Synopiidae				
Hyperiidea	Lanceoloidea	Lanceolidae	2	3	6	5
	Scinoidea	Scinidae	2	2	4	3
Hyperiopsidea	Hyperiopsoidea	Hyperiopsidae	2	6	11	6
		Vitjazianidae	1	1	1	1
Senticaudata	Calliopioidea	Pontogeneiidae	1	1	1	1
	Gammaroidea	Gammaridae	1	1	1	1
	Photoidea	Ischyroceridae	1	1	1	1
	Hadzioidea	Maeridae	2	2	6	6
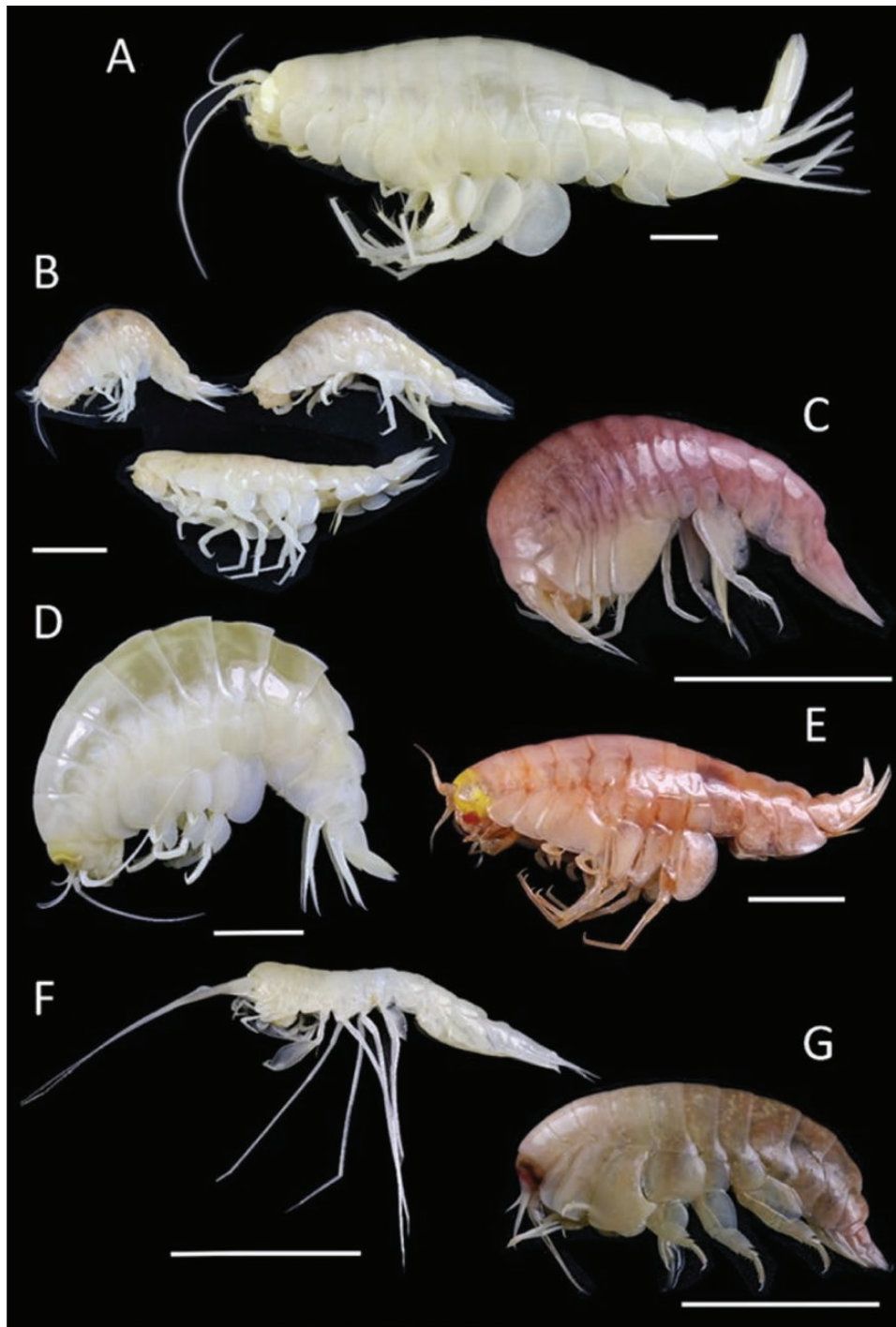
Figure 1. Hadal amphipods. *Alicella gigantea* from 7094 m in the Mariana Trench (**A**). *Bathycallisoma schellenbergi* from 8,370 m in the Puerto Rico Trench (**B**). Stegocephalidae gen. sp. from 8,380 m in the Puerto Rico Trench (**C**). *Eurythenes magellanicus* (H. Milne Edwards, 1848) from 8094 m in the Mariana Trench (**D**). *Hirondellea gigas* from 10,936 m in Mariana Trench (**E**). *Hyperiopsis laticarpa* from 10,936 m in the Mariana Trench (**F**). Undescribed species of *Stephonyx* from 8380 m in the Puerto Rico Trench (**G**). Scale bars are 1 cm.

can be attributed to a combination of increased sampling, both geographically and bathymetrically, the subsequently increased number of specimens for comparison and study, and the rise in the application of the integrative taxonomy, whereby morphological assessments are combined with DNA barcoding (Jażdżewska & Mamos, 2019; Weston *et al.*, 2021a, b). Based on

the published and available records to date, amphipods are represented at hadal depths by four suborders, 16 superfamilies, and 28 families, of which 25% are in the superfamily Lysianassoidea (Table 1). The significant families, in terms of diversity and known locations, are Alicellidae, Pardaliscidae, Hirondellidae, and Scopelocheiridae, followed by others such as Eusiridae,
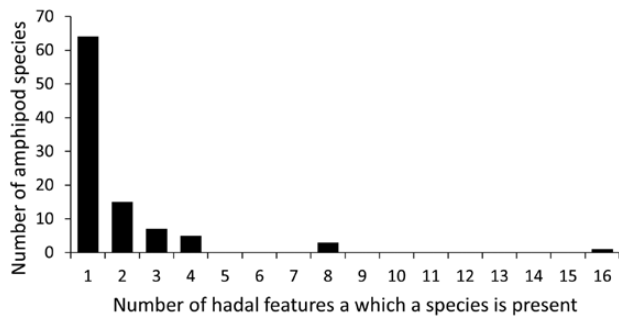
Figure 2. Most amphipod species have been found at one hadal feature, thus driving the concept of hadal endemism.

Uristidae, Hyperiopsid, and Eurytheneidae, with the latter being quite conspicuous in some trenches, particularly in the upper trench depths (< 7,000 m).

Strikingly, 83% of the known species are recorded only from one to two hadal features (Fig. 2). With the expansion of hadal exploration, this statistic has remained relatively constant, and it has given rise to the notion that the hadal zone is home to high levels of endemic diversity. This endemism is considered to be of species found to reside predominantly at hadal depths and/or at one or several neighbouring hadal features. Yet, endemism or restricted distribution to one hadal feature is not absolute. Several species challenge this notion by being found in multiple trenches, specifically *Halice aculeata* Chevreux, 1912, *Halice quarta* Birstein & M. Vinogradov, 1955, *Halice subquarta* Birstein & M. Vinogradov, 1960, *Hyperiopsis laticarpa* Birstein & M. Vinogradov, 1955, *Metaceradocoides vitjazi* Birstein & Vinogradov, 1960 at four, and *Hirondellea gigas* (Birstein & Vinogradov, 1955) and *Princaxelia abyssalis* at eight Dahl, 1959 (Fig. 2, Table 2). Some species are recorded from multiple hadal feature among several oceans, specifically, *Paralicella caperesca* Shulenberger & Barnard, 1976 at six features, *Alicella gigantea* Chevreux 1899 at seven features, and *Paralicella tenuipes* Chevreux, 1908 at eight features. Two species are considered to have a global distribution, *Hirondellea dubia* Dahl, 1959 at eight features (Weston & Jamieson, 2022) and *Bathycallisoma schellenbergi* (Birstein & Vinogradova, 1958) at 16 features (Weston et al., 2022). With increased sampling, the true distribution of particular species is becoming better known and recent work can address questions of biogeography and population connectivity across the inherently disjunct hadal zone.

While early thoughts on species endemism concentrated on whether there was a distinct hadal fauna, *Hirondellea gigas*, for example, was noted to be endemic to hadal depths but in multiple trenches from the Northwest Pacific Ocean (Hessler et al., 1978). France (1993) examined the morphologies of *H. gigas* from the Mariana, Philippine, and Palau trenches (Pacific) and concluded that these geographically isolated populations may have reduced levels of gene flow causing them to diverge morphologically. Patterns emerged within specific genera, such as *Hirondellea* Chevreux, 1899 whereby the Peru-Chile Trench (Southeast Pacific) had three species (*H. sonnei* Kilgallen, 2014, *H. wagner* Kilgallen, 2014, and *H. thurstoni* Kilgallen, 2014, whereas multiple trenches in the Southwest Pacific only had *H. dubia* (Lacey et al., 2016; Wilson et al., 2018). Since then,

H. dubia is being found in other more distant trenches, such as the Mariana ((Northwest Pacific), South Sandwich (Southern Ocean), and Puerto Rico trenches (North Atlantic), yet still at largely hadal depths (Weston & Jamieson 2022). Other families, such as Pardaliscidae contain four species of *Princaxelia* Dahl, 1959 at hadal depths, out of which, *P. stephenseni* Dahl, 1959 is also known from bathyal depths, *P. magna* Kamenskaya, 1977 is known only from the Yap Trench (West Pacific), *P. jamiesoni* Lörz, 2010 is known from the adjoined Japan and Izu-Bonin trenches (Northwest Pacific), yet *P. abyssalis* Dahl, 1959 is known from eight of the West Pacific trenches (Kamenskaya, 1981; 1995). Another species, *Bathycallisoma schellenbergi*, is now known from 16 hadal features spanning four oceans (Kilgallen & Lowry 2015; Lacey et al., 2016; Jażdżewska & Mamos, 2019; Chan et al., 2020; Weston et al., 2021b, 2022; Jamieson et al., 2022), and all but one record of 5,600 m in the New Hebrides Trench (South Pacific) (Lacey et al., 2016) have been hadal. Population genomics has uncovered that while *B. schellenbergi* does have a global distribution at the species level, populations are highly restricted to the individual features (Weston et al., 2022), with evidence for limited gene flow between neighbouring features on a shared convergence zone.

Assigning a meaningful value to levels of endemism is difficult due to many specimens having been described either from a single record or those with uncertain identification (see Table 1). Moreover, many records are not corroborated with molecular taxonomy, and therefore some species may have been misidentified, such as those highlighted by Ritchie et al. (2015) that await reclassification. Such was the case with Scopelocheiridae (Kilgallen & Lowry, 2015), or uncovered as a cryptic species complex, like *Eurythenes* S.I. Smith in Scudder, 1882 and *Paralicella caperesca* (Havermans et al., 2013; Jażdżewska et al., 2021). With these caveats in mind, of the 119 species listed in Table 1, 95 species (79.8%) are currently recorded as endemic to hadal depths.

IN SITU IMAGERY

Perhaps one of the most striking aspects of hadal amphipods is the visual imagery recorded when the bait is placed on the trench floor in front of a camera (Fig. 3). The first *in situ* images of hadal amphipods were taken in the Romanche Fracture Zone (Atlantic Ocean) at 7,500 m (Edgerton, et al., 1957; Cousteau, 1958). These two photographs showed amphipods active on the seafloor with other faunal groups, such as ophiuroids, anemones, and isopods. This *in situ* imagery gave a window into a dynamic hadal community.

The 1970s saw an increase in the use of baited cameras and traps, which revealed often very dense aggregations of deep-sea amphipods at simulated carrion falls (Paul, 1973; Shulenberger & Hessler, 1974). Hessler et al. (1978) first demonstrated the significance of amphipods at hadal depths by deploying a camera with traps to 9,600 and 9,800 m in the Philippine Trench (Pacific). These first glimpses demonstrated their ability to locate bait rapidly, aggregate in large numbers, consume the bait in a matter of hours then disperse, indicating an ecological function of rapidly dispersing organic matter.

One of the first dramatic features of these observations is the gigantism, or large body size, of some species. Hessler et al.

Table 2. All known records of amphipods collected from hadal depths including general location, depth, and record reference. Location abbreviations: AT, Aleutian Trench; BT, Banda Trench (also known as Weber Basin); BVT, Bougainville Trench; DFZ, Diamantina Fracture Zone; IBT, Izu–Bonin Trench (also known as Izu-Ogasawara Trench); JT, Japan Trench; JVT, Java Trench (also known as Sunda Trench); KT, Kermadec Trench; KKT, Kuril-Kamchatka Trench; MST, Massau Trench; MT, Mariana Trench; NBT, New Britain Trench; NHT, New Hebrides Trench; NPAC, Pacific Ocean; PCT, Peru Chile Trench; PHT, Philippine Trench; PLT, Palau Trench; PRT, Puerto Rico Trench; SCBT, San Cristobal Trench; SCZT –Santa Cruz Trench, SOT, South Orkney Trench; SST, South Sandwich Trench; TT, Tonga Trench; VT(MT), Volcano Trench (part of Mariana Trench); WZFZ, Wallaby Zenith Fracture Zone; YT, Yap Trench. All names and species authorities are consistent with the accepted classifications available on the World Register of Marine Species (WoRMS; Horton *et al.*, 2017; World Register of Marine Species (WoRMS Editorial Board), 2023).

	Location	Depth (m)	Record Reference
SUBORDER: Amphilochidea Boeck, 1871			
SUPERFAMILY: Alicelloidea Lowry & De Broyer 2008			
FAMILY: Alicellidae Lowry & De Broyer, 2008			
Alicella gigantea Chevreux, 1899	JVT	6,957–7,176	Jamieson *et al.*, 2022
	KT	6,265–7,000	Jamieson *et al.*, 2013b
	MT	6,846–7,507	AJJ, unpublished data
	NBT	8,225–8,903	Shi *et al.* 2018
	NPAC	6,000	Barnard & Ingram, 1986
	SCBT	6,515	AJJ, unpublished data
	SCZT	7,431	AJJ, unpublished data
	TT	6,253–6,256	Wilson *et al.*, 2018
Alicellidae sp. 1	MT	7,949–9,059	AJJ, unpublished data
Alicellidae sp. 2	MT	7,888	AJJ, unpublished data
Paralicella caperesca Shulenberger & Barnard, 1976	KT	4,329–6,007	Jamieson *et al.*, 2011
	MT	5,156–6,142	AJJ, unpublished data
	NHT	2,000–6,228	Lacey *et al.*, 2016
	PCT	4,602–6,173	Fujii *et al.*, 2013
	TT	6,256	Wilson *et al.*, 2018
	WZFZ	4,932–6,537	Weston *et al.*, 2021b
Paralicella cf. fusiformis	TT	6,253–6,256	Wilson *et al.*, 2018
Paralicella microps (Birstein & Vinogradov, 1958)	IBT	8,480	Belyaev, 1989
	JT	6,580	Belyaev, 1989
	KKT	8,000	Belyaev, 1989
Paralicella tenuipes Chevreux, 1908	KT	4,786–7,000	Belyaev, 1989
	KT	5,242–7,291	Lacey *et al.*, 2016
	MT	5,156–7,507	AJJ, unpublished data
	NHT	3,400–6,228	Lacey *et al.*, 2016
	PCT	6,173–7,050	Fujii *et al.*, 2013
	TT	7,300	Belyaev, 1989
	TT	6,256	Wilson *et al.*, 2018
	WZFZ	4,932–6,546	Weston *et al.*, 2021b
Paralicella cf. tenuipes	DFZ	7,009	AJJ, unpublished data
	SCBT	6,515	AJJ, unpublished data
Valettietta anacantha (Birstein & Vinogradov, 1963) (was *Valettiopsis*)	KT	6,007	Jamieson *et al.*, 2011
	KT	2,197–7,000	Lacey *et al.*, 2016
	MT	6,010–6,865	AJJ, unpublished data
	NHT	5,300–6,228	Lacey *et al.*, 2016
Valettietta sp.	WZFZ	4,932–6,546	Weston *et al.*, 2021b
SUPERFAMILY: Dexaminoidea Leach, 1814			
FAMILY: Pardaliscidae Boeck, 1871			
Halice aculeata Chevreux, 1912	BVT	6,500	Belyaev, 1989
	IBT	4,000–6,500	Belyaev, 1989
	KKT	4,200–8,050	Belyaev, 1989
	TT	7,100–10,500	Belyaev, 1989
Halice quarta Birstein & Vinogradov, 1955	IBT	8,480–9,000	Belyaev, 1989
	KKT	6,000–8,500	Belyaev, 1989

Table 2. Continued

	Location	Depth (m)	Record Reference
	KKT	8,183–9,574	Jażdżewska & Mamos, 2019
	MT	10,000	Belyaev, 1989
	MT	10,877–10,925	AJJ, unpublished data
	TT	9,120–9,120	Belyaev, 1989
Halice rotunda Birstein & Vinogradov, 1960	BVT	4,050–8,400	Belyaev, 1989
	TT	9,120	Belyaev, 1989
Halice secunda (Stebbing,1888) (was *Synopioides*)	KT	6,960–7,000	Dahl, 1959
	PHT	10,150–10,190	Dahl, 1959
Halice subquarta Birstein & Vinogradov, 1960	KT	9,400	Belyaev, 1989
	PHT	7,420–7,880	Belyaev, 1989
	TT	10,500	Belyaev, 1989
	YT	7,190–7,250	Belyaev, 1989
Halice sp. 1	KKT	8,183–8,743	Jażdżewska & Mamos, 2019
Pardaliscoides longicaudatus Dahl, 1959	KT	6,180	Dahl, 1959
	PHT	9,820–10,000	Dahl, 1959
Princaxelia abyssalis Dahl, 1959	AT	6,965–7,000	Belyaev, 1989
	BVT	7,974–8,006	Belyaev, 1989
	IBT	6,770–8,830	Belyaev, 1989
	JT	6,380–7,370	Belyaev, 1989
	KKT	6,435–9,530	Belyaev, 1989
	KT	6,620–8,300	Dahl, 1959
	PHT	7,420–7,880	Belyaev, 1989
	YT	7,190–8,720	Belyaev, 1989
Princaxelia jamiesoni Lörz, 2010	IBT	9,316	Lörz, 2010
	JT	7,703	Lörz, 2010
Princaxelia cf. *jamiesoni*	KKT	7,110–9,574	Jażdżewska & Mamos, 2019
Princaxelia magna Kamenskaya, 1977	JT	7,190–7,250	Belyaev, 1989
	MT	8,098–8,942	AJJ, unpublished data
	TT	7,354–8,411	Belyaev, 1989
Princaxelia sp.	DFZ	7,009	AJJ, unpublished data
aff. *Princaxelia*	JVT	5,760–6,957	Jamieson *et al.*, 2022
FAMILY: Atylidae Lilljeborg,1865			
Aberratylus aberrantis (J.L. Barnard, 1962) (was *Atylus, Lepechinella*)	VT(MT)	6,330	Belyaev, 1989
FAMILY: Lepechinellidae Schellenberg, 1926			
Lepechinella ultraabyssalis Birstein & Vinogradova, 1960	KKT	6,475–8,015	Belyaev, 1989
	JT	7,370	Belyaev, 1989
Lepechinella cf. *ultraabyssalis*	KKT	5,152–7,119	Jażdżewska & Mamos, 2019
Lepechinella vitrea Kamenskaya, 1977	YT	7,190–7,250	Belyaev, 1989
Lepechinella wolffi Dahl, 1959	KT	6,660–6,770	Dahl, 1959
SUPERFAMILY: Eusiroidea Stebbing, 1888			
FAMILY: Eusiridae Stebbing, 1888			
Cleonardo sp.	WZFZ	6,162	Weston *et al.*, 2021b
Eusiridae sp.	NHT	6,228	Lacey *et al.*, 2016
Eusirella longisetosa Birstein & Vinogradov, 1960	BVT	8,500	Belyaev, 1989
Eusirus bathybius Schellenberg, 1955	BVT	7,500	Belyaev, 1989
	PHT	7,625–7,900	Belyaev, 1989
	PRT	7,625–7,900	Belyaev, 1989
Eusirus fragilis Birstein & Vinogradov, 1960	TT	9,120	Belyaev, 1989
Rhachotropis flemmingi Dahl, 1959	KKT	6,090–6,135	Belyaev, 1989
	JVT	6,820–7,160	Dahl, 1959
Rhachotropis saskia Lörz & Jażdżewska, 2018	KKT	4,903–8,183	Lörz *et al.*, 2018
Rhachotropis sp.	PHT	7,420–7,880	Belyaev, 1989
Rhachotropsis sp.	KT	6,960–7,000	Belyaev, 1989

Table 2. Continued

	Location	Depth (m)	Record Reference
SUPERFAMILY: Haustorioidea Stebbing, 1906			
FAMILY: Phoxocephalidae G.O. Sars, 1891			
Harpiniopsis spaercki (Dahl, 1959) (was *Harpinia*)	BT	6,580–7,270	Dahl, 1959
Metaphoxus sp.	JT	7,550	Belyaev, 1989
Pseudharpinia abyssalis (Pirlot, 1932) (was *Harpinia*)	PCT	6,324–6,328	Belyaev, 1989
SUPERFAMILY: Iphimedioidea Boeck, 1871			
FAMILY: Stilipedidae Holmes, 1908			
Alexandrella carinata (Birstein & Vinogradova, 1960) (was *Astyroides*)	KKT	7,210–7,230	Belyaev, 1989
FAMILY: Epimeriidae Boeck, 1871			
Epimeria sp. Kamenskaya, 1977	JT	6,156–6,207	Belyaev, 1989
	KKT	7,210–7,230	Belyaev, 1989
Epimeria sp.	PRT	6,954–8,380	AJJ, unpublished data
SUPERFAMILY: Liljeborgioidea Stebbing, 1899			
FAMILY: Liljeborgiidae Stebbing, 1899			
Liljeborgia caeca Birstein & Vinogradova, 1960	JT	6,156–6,207	Belyaev, 1989
SUPERFAMILY: Lysianassoidea Dana, 1849			
FAMILY: Lysianassidae Dana, 1849			
Bathyschraderia fragilis Kamenskaya, 1981	PHT	7,000–9,990	Belyaev, 1989
Bathyschraderia magnifica Dahl, 1959	KT	6,960–9,174	Belyaev, 1989
	TT	7,354–9,875	Belyaev, 1989
Galathella galatheae (Dahl, 1959)	KT	6,960–7,000	Belyaev, 1989
Onesimoides carinatus Stebbing, 1888 (was *Onesimoides cavimanus* Pirlot, 1934)	BT	6,490-6,650	Belyaev, 1989
Lysianassidae sp.	MT	7,507	AJJ, unpublished data
Lysianassoidea	KKT	5,000–6,560	Jażdżewska & Mamos, 2019
Orchomene sp.	MT	10,500	Belyaev, 1989
FAMILY: Tryphosidae Lowry & Stoddart, 1997			
Bruunosa bruuni (Dahl, 1959) (was *Tryphosa*)	KT	6,660–6,770	Dahl, 1959
Tryphosella sp. 2	KT	6,007	Jamieson *et al.*, 2011
Tryphosella sp.	PCT	7,050	Fujii *et al.*, 2013
Tryphosella sp.	SST	7,400–7,439	Jamieson *et al.*, 2021
aff. *Tryphosella* sp.	PCT	8,074	Fujii *et al.*, 2013
aff. *Tryphosella* sp.	MT	7,949–9,059	AJJ, unpublished data
Tryphosidae gen. sp.	SCBT	7,200–8,407	AJJ, unpublished data
	SCZT	6,844–8,428	AJJ, unpublished data
FAMILY: Eurytheneidae Stoddart & Lowry, 2004			
Eurythenes atacamensis Weston & Espinosa–Leal, 2021 [Weston *et al.*, 2021a]	PCT	4,971–8,081	Eustace *et al.*, 2016
Eurythenes atacamensis (as *E. gryllus*)	PCT	7,800	Thurston *et al.*, 2002
Eurythenes andhakarae D'Udekem d'Acoz & Havermans, 2015	SST	6,044–7,099	Jamieson *et al.*, 2022
Eurythenes sigmiferus D'Udekem d'Acoz & Havermans, 2015 (or also *E. gryllus*)	TT	6,253–6,256	Wilson *et al.*, 2018
Eurythenes gryllus (Lichtenstein in Mandt, 1822) (more likely *Eurythenes gryllus* s.l.)	IBT	6,770–7,850	Belyaev, 1989
	NHT	2,000–6,948	Lacey *et al.*, 2016
	TT	5,155–6,252	Blankenship *et al.*, 2006
Eurythenes magellanicus (H. Milne Edwards, 1848)	MT	7,094	AJJ, unpublished data
Eurythenes maldoror D'Udekem d'Acoz & Havermans, 2015	WZFZ	4,932–6,546	Weston *et al.*, 2021b
Eurythenes plasticus Weston, 2020	MT	6,010–6,949	Weston *et al.*, 2020
Eurythenes sp. PCT 'Abyssal'	PCT	4,602–6,173	Eustace *et al.*, 2016
Eurythenes sp.	KT	4,329–6,007	Jamieson *et al.* 2011
Eurythenes sp.	SCBT	6,515	Weston & Jamieson, 2022
FAMILY: Hirondelleidae Lowry & Stoddart, 2010			
Hirondellea dubia Dahl, 1959	KT	7,640–7,680	Dahl, 1959
	KT	6,709–9,908	Lacey *et al.*, 2016
	KT	6,000–7,966	Jamieson *et al.*, 2011
	KT	9,104–9,856	Blankenship *et al.*, 2006

Table 2. Continued

	Location	Depth (m)	Record Reference
	MT	5,641–8,942	Weston & Jamieson, 2022
	NHT	6,000–6,948	Lacey *et al.*, 2016
	PRT	6,954–8,380	Weston & Jamieson, 2022
	SCBT	6,515–8,407	Weston & Jamieson, 2022
	SCZT	6,844–8,428	Weston & Jamieson, 2022
	SST	6,640–8,266	Jamieson *et al.*, 2022
	TT	7,349–10,787	Blankenship *et al.*, 2006
	TT	6,253–10,807	Wilson *et al.*, 2018
	TT	6,793–10,823	Weston & Jamieson, 2022
Hirondellea gigas (Birstein & Vinogradov, 1955) (was *Tetronychia*)	IBT	6,770–8,900	Belyaev, 1989
	IBT	8,172–9,316	Eustace *et al.*, 2013
	JT	7,703	Jamieson *et al.*, 2019
	KKT	7,250–9,345	Belyaev, 1989
	KKT	8,183–9,574	Jażdżewska & Mamos, 2019
	MT	7,218–9,144	France, 1993
	MT	10,897	Kobayashi *et al.*, 2012
	MT	10,897	Kobayashi *et al.*, 2019
	MT	10,890	Jamieson *et al.*, 2019
	MT	6,864–10,925	AJJ, unpublished data
	MT	10,840	Shi *et al.*, 2018
	PHT	8,467–9,604	France, 1993
	PHT	10,020–10,190	Dahl, 1959
	PLT	7,970–8,035	Belyaev, 1989
	PLT	7,997	France, 1993
	VT(MT)	8,530–8,540	Belyaev, 1989
	YT	8,560–8,720	Belyaev, 1989
Hirondellea sonne Kilgallen, 2014	PCT	7,050	Kilgallen, 2014
Hirondellea wagneri Kilgallen, 2014	PCT	6,173	Kilgallen, 2014
Hirondellea thurstoni Kilgallen, 2014	PCT	6,173–8,072	Kilgallen, 2014
	PCT	7,800	Perrone *et al.*, 2003
Hirondellea sp.	TT	6,256	Wilson *et al.*, 2018
FAMILY: Cyclocaridae Lowry & Stoddart, 2011			
Cyclocaris tahitensis Stebbing, 1888	KT	6,007	Jamieson *et al.*, 2011
Cyclocaris sp. (*cf. tahitensis*)	TT	6,253–6,256	Wilson *et al.*, 2018
Cyclocaris sp.	WZFZ	4,932–6,546	Weston *et al.*, 2021b
FAMILY: Scopelocheiridae Lowry & Stoddart, 1997			
Bathycallisoma schellenbergi (Birstein & Vinogradov, 1958) (was *Scopelocheirus*)	AT	6,965–7,200	Belyaev, 1989
	DFZ	7,009	Weston *et al.*, 2022
	JT	6,380–7,370	Belyaev, 1989
	JVT	6,935–7,060	Belyaev, 1989
	KKT	6,000–7,000	Belyaev, 1989
	KT	9,104	Blankenship *et al.*, 2006
	KT	6,097–8,487	Lacey *et al.*, 2016
	KT	6,007–6,890	Jamieson *et al.*, 2011
	MST	6,990	Shi *et al.*, 2018
	MT	6,010–7,507	AJJ, unpublished data
	NHT	6,680–8,000	Belyaev, 1989
	NHT	5,600–6,948	Lacey *et al.*, 2016
	PCT	5,920–6,714	Weston *et al.*, 2022
	SOT	6,820	Vinogradov & Vinogradov, 1993
	PRT	7,625–7,900	Belyaev, 1989
	PRT	8,000	Lacey *et al.*, 2013
	PRT	6,954–8,380	Weston *et al.*, 2022

Table 2. Continued

	Location	Depth (m)	Record Reference
	SCBT	7,200–8,407	Weston *et al.*, 2022
	SCZT	6,844–8,428	Weston *et al.*, 2022
	SST	6,640–8,266	Jamieson *et al.*, 2021
	TT	6,252–8,723	Blankenship *et al.*, 2006
	TT	6,253–6,256	Wilson *et al.*, 2018
	TT	6,793–7,928	Weston *et al.*, 2022
	WZFZ	6,537–6,546	Weston *et al.*, 2021b
Bathycallisoma schellenbergi (as *B. pacifica*)	KT	6,960–7,000	Dahl, 1959
Scopelocheirus hopei (Costa in Hope, 1851) (was *S. pacifica*)	KT	6,960–7,000	Belyaev, 1989
FAMILY: Uristidae Hurley, 1963			
Abyssorchomene abyssorum (Stebbing, 1888) (as *Orchomene*)	KT	8,210–8,300	Dahl, 1959
Abyssorchomene chevreuxi (Stebbing, 1906)	PCT	6,173	Fujii *et al.*, 2013
Abyssorchomene distinctus (Birstein & Vinogradov, 1960)	TT	6,253–6,256	Wilson *et al.*, 2018
Abyssorchomene gerulicorbis (Shulenberger & Barnard, 1976)	KT	5,173–6,007	Jamieson *et al.*, 2011
	KT	1,488–6,968	Lacey *et al.*, 2016
	WZFZ	5,990–6,546	Weston *et al.*, 2021b
Abyssorchomene sp.	DFZ	7,009	Unpublished, A., Jamieson
Galathella galatheae (was *Schisturella*)	KT	6,960–7,000	Dahl, 1959
Stephonyx sp.	PRT	8,280–8,370	AJJ, unpublished data
Uristes sp.	KT	9,104	Blankenship *et al.*, 2006
	TT	7,349–9,273	Blankenship *et al.*, 2006
SUPERFAMILY: Stegocephaloidea Dana, 1852			
FAMILY: Stegocephalidae Dana, 1852			
Andaniexis australis K.H. Barnard, 1932	PCT	6,324–6,328	Belyaev, 1989
Andaniexis stylifer Birstein & Vinogradov, 1960	BVT	6,500–8,500	Belyaev, 1989
Andaniexis sp.	IBT	6,770–6,890	Belyaev, 1989
Stegocephalus nipoma (J.L. Barnard, 1961)	PHT	6,290–6,330	Belyaev, 1989
Stegocephalus sp.	KKT	7,600–7,710	Belyaev, 1989
	KKT	7,795–8,015	Belyaev, 1989
Stegocephalus sp.	JT	6,380–6,380	Belyaev, 1989
Steleuthera maremboca J.L. Barnard, 1964	PCT	6,324–6,380	Belyaev, 1989
Stegocephalidae	JVT	6,957–7,176	Jamieson *et al.*, 2022
FAMILY: Andaniexinae Berge & Vader, 2001			
Andaniexis subabyssi Birstein & Vinogradov, 1955	KKT	6,000–8,500	Belyaev, 1989
SUPERFAMILY: Synopioidea Dana, 1852			
FAMILY: Ampeliscidae Krøyer, 1842			
Byblisoides arcillis J.L. Barnard, 1961	KKT	6,272–6,571	Belyaev, 1989
FAMILY: Synopiidae Dana, 1853			
Synopiidae	KKT	5,300–6,163	Jażdżewska & Mamos, 2019
SUBORDER: Hyperiidea H. Milne Edwards, 1830			
SUPERFAMILY: Lanceoloidea Bovallius, 1887			
FAMILY: Lanceolidae Bovallius, 1887			
Lanceola clausii gracilis Vinogradov, 1956	KKT	4,200–8,000	Belyaev, 1989
	PHT	6,200–6,750	Belyaev, 1989
Lanceola sphaerica Vinogradov, 1970	KKT	7,800	Belyaev, 1989
Metalanceola chevreuxi Pirlot, 1931	BVT	6,500–8,500	Belyaev, 1989
	KT	9,400	Belyaev, 1989
	TT	9,100–10,500	Belyaev, 1989
SUPERFAMILY: Scinoidea Stebbing, 1888			
FAMILY: Scinidae Stebbing, 1888			
Scina chelata Vinogradov, 1970	KKT	7,750	Belyaev, 1989
Scina wagleri abyssalis Vinogradov, 1957	IBT	8,500	Belyaev, 1989
	KKT	6,000–8,500	Belyaev, 1989

Table 2. Continued

	Location	Depth (m)	Record Reference
	KT	9,400	Belyaev, 1989
SUBORDER: Hyperiopsidea Bovallius, 1886			
SUPERFAMILY: Hyperiopsoidea Bovallius, 1886			
FAMILY: Hyperiopsidae Bovallius, 1886			
Hyperiopsis anomala Birstein & Vinogradov, 1960	TT	6,900	Belyaev, 1989
Hyperiopsis laticarpa Birstein & Vinogradov, 1955	BVT	8,500	Belyaev, 1989
	IBT	8,480	Belyaev, 1989
	KKT	6,000–8,500	Belyaev, 1989
	MT	10,925	AJJ, unpublished data
Protohyperiopsis affinis (Birstein & Vinogradov, 1960) (as *Parargissa*)	BVT	8,150–8,500	Belyaev, 1989
	IBT	6,500	Belyaev, 1989
Protohyperiopsis arquata Birstein & Vinogradov, 1955 (as *Parargissa*)	KKT	4,200–8,500	Belyaev, 1989
Protohyperiopsis curticornis (Birstein & Vinogradov, 1960) (as *Parargissa*)	NHT	7,000	Belyaev, 1989
Protohyperiopsis longipes (Birstein & Vinogradov, 1960) (as *Parargissa*)	BVT	8,500	Belyaev, 1989
FAMILY: Vitjazianidae Birstein & Vinogradov, 1955			
Vitjaziana gurjanovae Birstein & Vinogradov, 1955	IBT	4,200–8,480	Belyaev, 1989
SUBORDER: Senticaudata Lowry & Myers, 2013			
SUPERFAMILY: Calliopioidea G.O. Sars, 1895			
FAMILY: Pontogeneiidae Stebbing, 1906			
Bathyschraderia magnifica Dahl, 1959	KT	6,960–7,000	Dahl, 1959
SUPERFAMILY: Gammaroidea Latreille, 1816 (Bousfield, 1977)			
FAMILY: Gammaridae Latreille, 1816			
Bathyceradocus stephenseni Pirlot, 1934	BT	7,250–7,290	Dahl, 1959
SUPERFAMILY: Photoidea Boeck, 1871			
FAMILY: Ischyroceridae Stebbing, 1899			
Bonnierella linearis J.L. Barnard, 1964	PCT	6,342–6,328	Belyaev, 1989
SUPERFAMILY: Hadzioidea S. Karaman, 1943 (Bousfield, 1983)			
FAMILY: Maeridae Krap-Schickel, 2008			
Bathyceradocus stephenseni Pirlot, 1934	BT	7,250–7,340	Belyaev, 1989
	BVT	6,920–7,652	Belyaev, 1989
Metaceradocoides vitjazi Birstein & Vinogradov, 1960	IBT	8,900	Belyaev, 1989
	JT	6,600–7,370	Belyaev, 1989
	MT	8,215–8,225	Belyaev, 1989
	YT	7,190–7,250	Belyaev, 1989

(1972) published a record of a very large lysianassoid amphipod from the abyssal plains of the North Pacific (5,304 m) that was twice as big as any known species at that time, estimated to be 282 mm long. A similar, albeit smaller individual, was recorded by Lemche *et al.* (1976) at 6,758–6,776 m in the New Hebrides Trench. The Hessler *et al.* (1972) specimens were later identified as the 'supergiant' amphipod *Alicella gigantea* (Barnard & Ingram 1986), while the Lemche *et al.* (1976) individual was only 4 cm long and may have been *Eurythenes* sp. or a juvenile *A. gigantea,* now both known from that trench (Lacey *et al.*, 2016). An impressively large *A. gigantea* was later filmed, and recovered, from hadal depths (6,265–7,000 m) in the Kermadec Trench (South Pacific) (Jamieson *et al.*, 2013b) and is now known to be present at seven hadal features across Pacific, Indian, and Atlantic oceans (Table 2). Characterised by their elongated, articulate body, larger body size, and behaviour that differs from the scavenging lysianassoids, the princaxelids (Pardaliscidae) comprise another easily identifiable hadal amphipod group (Lörz, 2010).

These amphipods predate on the scavenging lysianassoids that gather at bait (Jamieson *et al.*, 2012), and are present in most trenches studied so far (AJJ, personal observation).

As striking as some of the larger species are on camera, the large aggregations of more typical-sized lysianassoid species, < 20 mm, at the bait is perhaps the most impressive. Since the black and white still images of Hessler *et al.* (1978), technology has progressed to permit full colour high-definition video and high-resolution still recording of this activity (Jamieson, 2015). The small body size of these species makes identifications and diversity assessments nearly impossible. The size of the aggregations also increases with time on the bottom, culminating in feeding frenzies that can fill the field of view of a camera making quantifying their numbers difficult (Fig. 3). The time of arrival and time of peak numbers decreases and increases respectively with depth, which results in impressive displays of bait consumption at the deepest parts of a trench (Figs. 4, 5). Although imaging these responses is mostly qualitative and unquantifiable, it
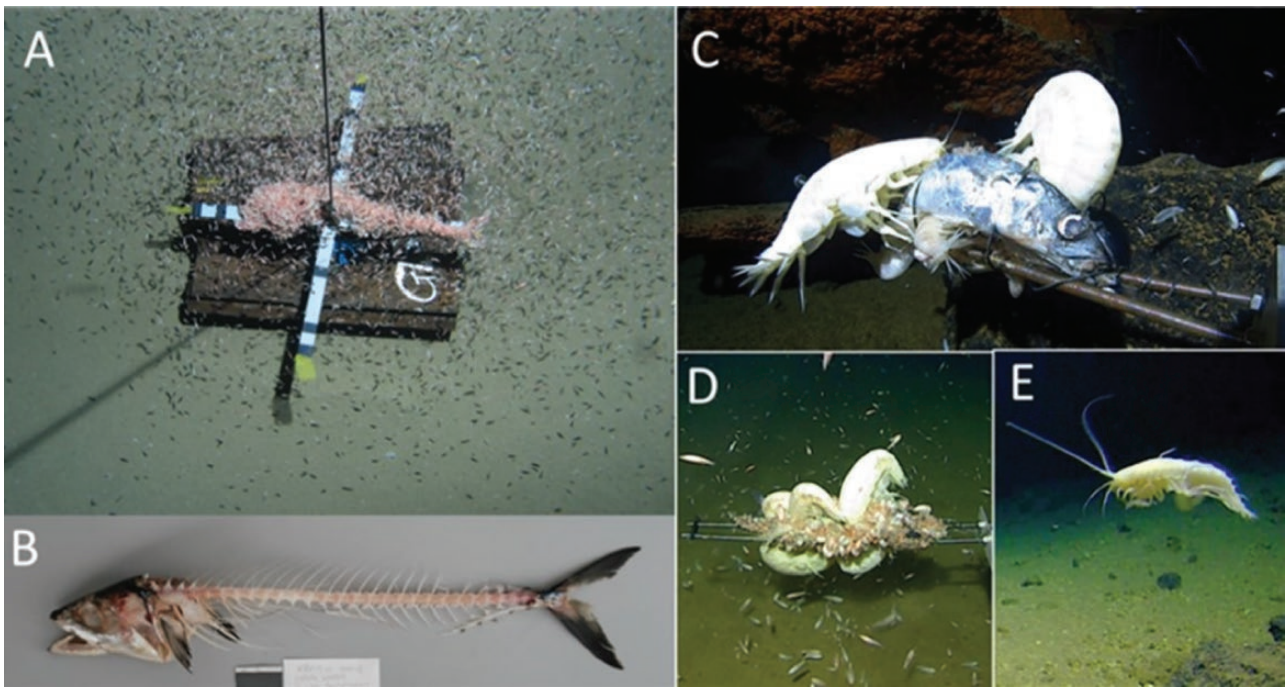
Figure 3. Large aggregation of *Hirondellea dubia* at 8,000 m in the Kermadec Trench after one hour on the seafloor (white reference cross is 50 cm) (**A**). Remains of the bait after 8 hours on the seafloor showing the efficiency with which amphipods can remove flesh from carrion (**B**). *Alicella gigantea*, a.k.a. 'the supergiant,' feeding at 5,900 m in the Mariana Trench (**C**), and with large aggregations of *Bathycallisoma schellenbergi* in the San Cristóbal Trench (7,220 m) (**D**). *Princaxelia* cf. *magna* at 7,542 m in the Mariana Trench (**E**).

FEEDING AND TROPHIC ECOLOGY

The success of the Amphipoda at hadal depths may also be a virtue of adaptations for a low food environment, as similar for amphipods inhabiting other rare food habitats like Lake Baikal (Mekhanikova, 2010) and subterranean systems (Hutchins *et al.*, 2014). Many of the well-known hadal species are recovered by baited traps and therefore belong to the scavenging guild. Although not all hadal amphipods are scavengers, with predator species like *Princaxelia jamiesoni* Lörz, 2010 and *Rhachotropis saskia* Lörz & Jażdżewska, 2018 [Lörz *et al.*, 2018], scavengers in low-food environments, such as the trenches, must adapt to detecting, intercepting, and rapidly consuming large carrion falls, which can be unpredictable both in space and time, while supplementing potentially long intermediate periods with alternative sources of nutrition (Dahl, 1979). Hadal amphipods exhibit effective strategies such as localizing potential food sources, feeding on large muscular food parcels, consuming large quantities of food in relatively short periods of time, storage of this energy for gradual utilization over extended periods of starvation and supplementing their diet with alternative food sources, such as wood (Kobayashi *et al.*, 2012), that become available between large carrion falls.

Chemosensory adaptations are evident in many key deep-sea amphipods. For example, chemosensory stimulation is used to detect the odour plume emanating from a food fall (e.g., Tamburri & Barry, 1999). These amphipods typically have short and stout antennae, with an array of chemosensory setae on the ventral side of the first flagellar article, which is kept depressed to increase exposure to stimuli. When swimming, these sensors are prominently exposed to the surrounding body of water (Dahl, 1979). Some species sweep water over the proximal part of the antennule, mouthparts, and into the branchial region when beating their pleopods, presumably to maximise the chance of detecting chemical stimuli (Dahl, 1977).

Other methods of food detection may include sound and 'mechano-reception.' Such hydroacoustic stimuli could occur as a large carcass impacts the seafloor or during potentially 'noisy' feeding bouts (Klages *et al.*, 2002). Smith & Baldwin (1984) estimated the spherical spreading of noises created by *Eurythenes gryllus* s.l. during feeding could potentially produce 15 dB which can be heard for up to 1 km. The augmentation of hydroacoustic stimuli may attract further visitors to the carrion-fall, although chemoreception appears the most likely the primary detection method.

Hadal amphipods are often observed in mass aggregations at baited cameras where bait carcasses are typically stripped of every visible shred of flesh within 10 h. This efficient consumption of food is a result of highly adapted mouth morphology (Fig. 6). The basic gammaridean amphipod has strongly and irregularly serrated incisors with well-developed lacinia mobilis on both mandibles (Dahl, 1979). When biting, the left incisor passes in front of the right incisor which, in turn, moves between the left lacinia mobilis, which then positions in front of the right one. This feeding motion, however, is slightly different for three common hadal amphipod genera (*Eurythenes, Hirondellea,* and *Paralicella* Chevreux, 1908). The right incisor slides in behind the left and the 'shape' of the bite is bowl-shaped, which allows these genera to remove larger pieces of food than those with a
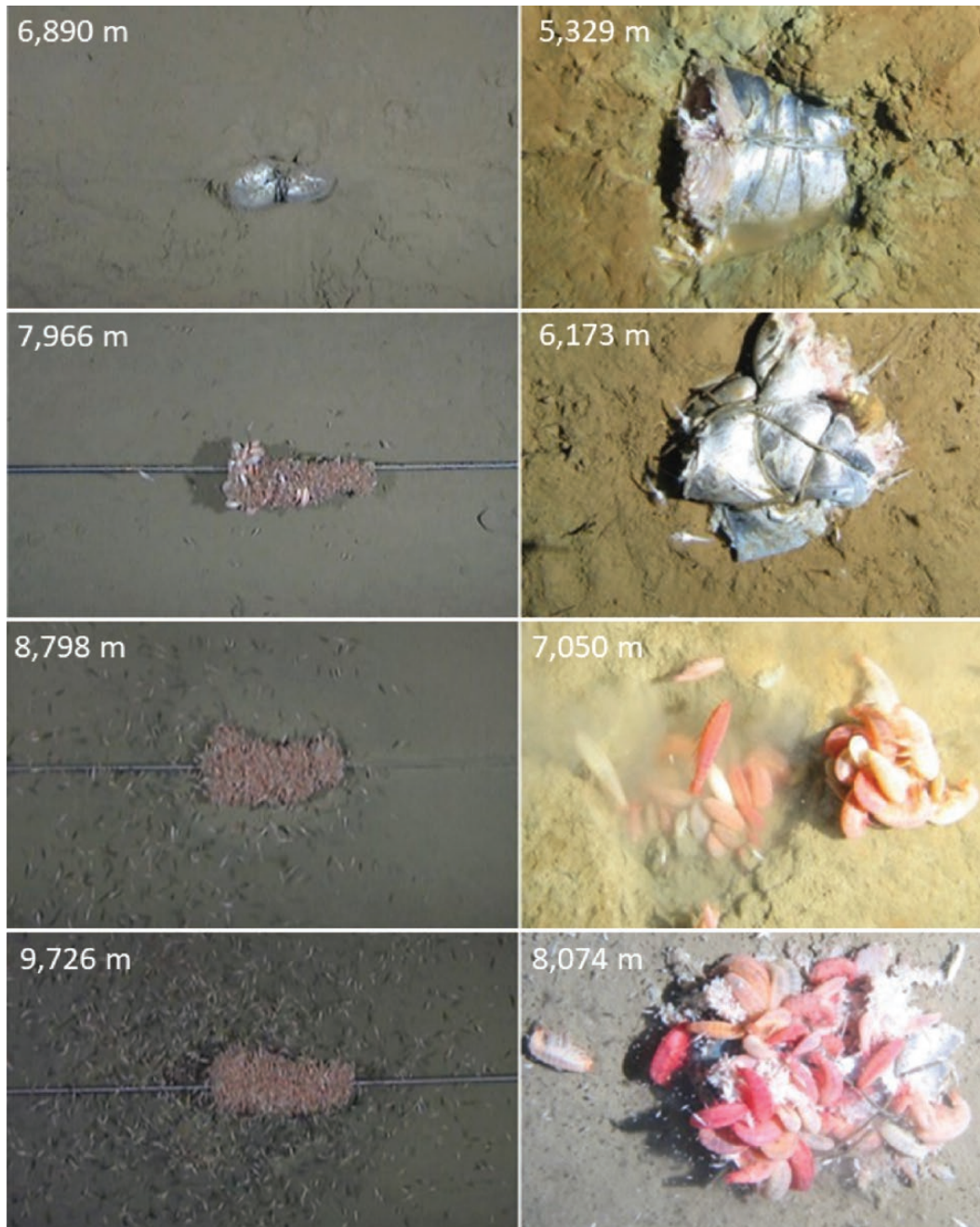
Figure 4. *In situ* images showing increasing numbers of scavenging amphipods with increasing depth, from the Tonga Trench (left) and the Peru-Chile Trench (right), all images are from three hours after landing on the seafloor.

flattened mandible (Dahl, 1979). Furthermore, *Eurythenes* and *Hirondellea gigas* have distinctively shaped molars, such that when they are closed, they form an almost complete funnel from the mouth to the stomach, thought to aid in guiding larger food particles to the digestive tract. Amphipods may also be capable of characterizing, or 'tasting,' the food source upon contact, via chemical and physical gustatory seta on the gnathopods and pereopods (Kaufmann, 1994). This selectivity of food items, or anatomical parts of the food, that differ either chemically or texturally is supported by observations of selective feeding on livers and gonads during necrophagy (Scarratt, 1965), presumably to maximise energetic intake per unit feeding (Kaufmann, 1994).

The enhanced consumption rates are complemented further by their ability to ingest large volumes of food. The alimentary tracts of *Eurythenes, Hirondellea, Paralicella,* and *Bathycallisoma* Dahl, 1959 are adapted for the accumulation and storage of large volumes of food relative to their body size. The food is stored in the midgut, which can expand to fill the entire body cavity and are therefore capable of ingesting more food than their shallower water counterparts. *Paralicella* can extend ventrally to two or three times its body size (Shulenberger & Hessler, 1974; Thurston, 1979). These 'capacious guts' and high consumption rates, enable them to survive prolonged periods of starvation (Sainte-Marie, 1992) (Fig. 6).
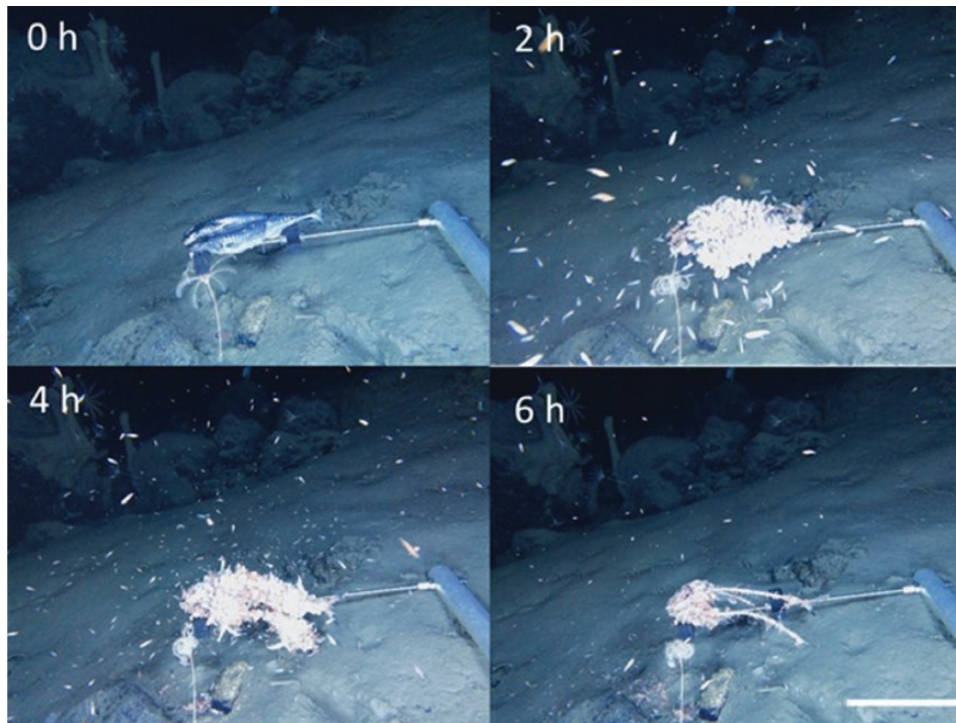
Figure 5. Time course of bait consumption, exclusively by amphipods, mostly *Hirondellea dubia* at 7,000 m in the South Sandwich Trench. Scale bar = 20 cm.

The diets of most hadal amphipods are not well known, but most of the better-known species are scavengers. The concept of obligate scavengers has been debated for some time (Britton & Morton, 1994; Kaiser & Moore, 1999), and it now seems evident that many hadal amphipods are indeed facultative scavengers. In low-food environments, obligate scavenging is inhibited by the unpredictable disparate nature of carrion-fall occurrence and thus an additional strategy is trophic plasticity, whereby carrion-based scavenging is supplemented with alternative food items. Blankenship & Levin (2007) reported high trophic plasticity of three lysianassoid amphipod species from the Tonga Trench, namely *Eurythenes gryllus* s.l., *Bathycallisoma schellenbergi*, and *Hirondellea dubia*. A combination of gut content metabarcoding and stable isotope analysis further indicated that these amphipods supplement necrophagy with detrivory, predation, and cannibalism. In the absence of carrion *Eurythenes gryllus* s.l., and *Bathycallisoma schellenbergi*, for example, were predatory and possibly detrivores, having digested tunicates, ascidians, pelagic salps, or larvaceans as well as other amphipods. Shi *et al.* (2018) found that *Alicella gigantea* from the New Britain Trench was dependent on high-quality organic matter such as carrion, whereas *Hirondellea gigas* from the Mariana Trench and *Bathycallisoma schellenbergi* from the Massau Trench favored more detritus and bacterial organic matter as supplementary food.

The diet and feeding strategies may also vary by age, depth, and sex. For example, Shi *et al.* (2020) demonstrated that *Alicella gigantea* from the New Britain Trench (South Pacific) consumed more bacteria and zooplankton debris in early developmental stages before shifting to carrion consumption, and later stages adopting a more diverse diet of benthic fauna, algae, and carrion.

Females were also found to be more reliant on carrion from higher trophic organisms than males. This strong dependency on surface-derived material, whatever that form may be, was further expanded by Tokuda *et al.* (2020) who when describing trophic interactions in the Mariana and Kermadec trenches found that amphipods consumed infauna, carrion, terrestrial plant debris, older material from turbidity flows, and perhaps even seep-derived organic material. Functional classification of gut bacteria from *Hirondellea gigas* also implies heterotrophic utilization of a variety of carbon sources (Zhang *et al.*, 2018). These trophic linkages to the surface are perhaps best demonstrated by Kobayashi *et al.* (2012), who showed that *Hirondellea gigas* from 10,897 m in the Mariana Trench, have a unique digestive enzyme capable of digesting wood debris. These studies support the notion that amphipods are one of the most trophically diverse taxa in the marine environment (Nyssen *et al.*, 2002).

In addition to facultative scavenging and trophic plasticity, there are further strategies to overcome what could be long periods before the next major feeding opportunity, metabolic reduction, and long-term energy cache. Energy management is demonstrated by drastically reducing metabolic activity during starvation periods (Smith & Baldwin, 1984). Tamburri & Barry (1999) demonstrated that an abyssal amphipod, *Orchomene obtusus* G.O. Sars, 1895, could survive without food for four to six weeks in laboratory conditions. This strategy is complemented by rapidly converting the food to lipids (triacylglycerols, wax esters, phospholipids, and diacylglycerol ether) for long-term energy storage (Lee *et al.*, 2006). Upon sequencing the transcriptome of *Hirondellea gigas*, Lan *et al.* (2016) suggested that six key genes directly participating in energy metabolites are positively selected suggesting these relate to food utilization and
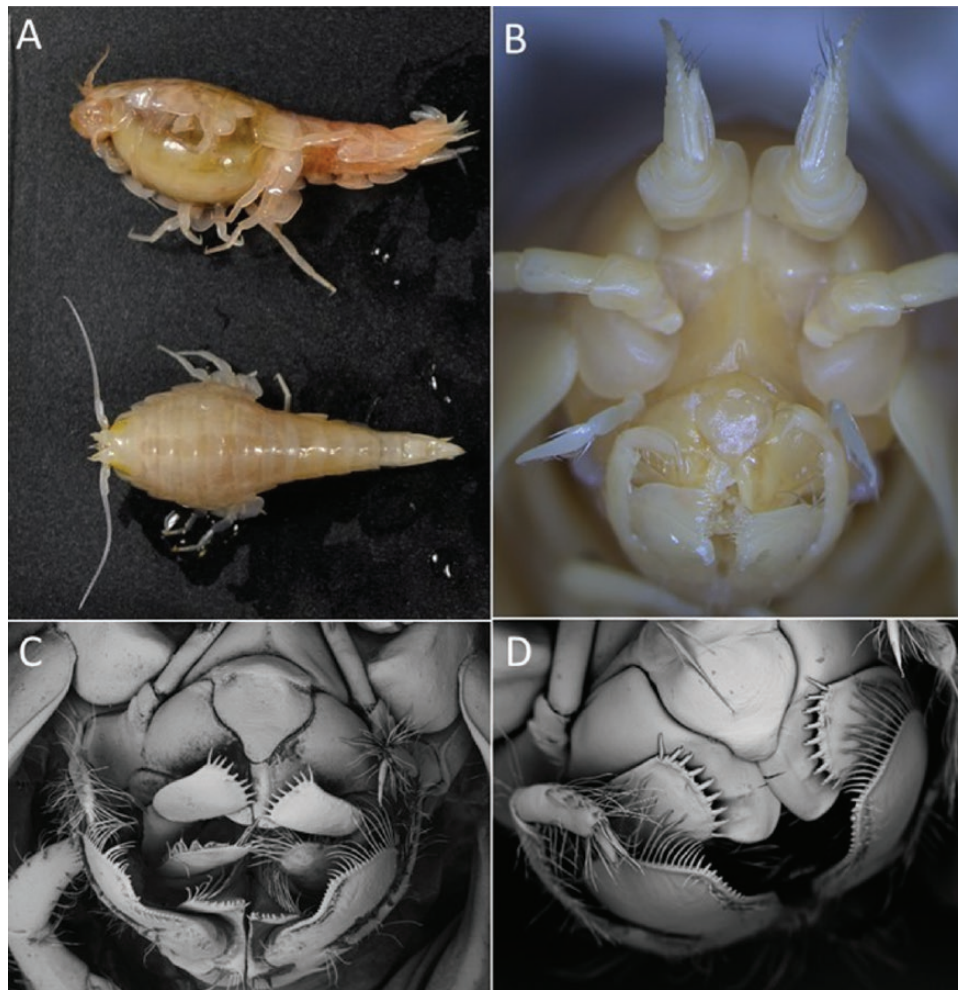
Figure 6. Feeding adaptations of hadal *Bathycallisoma schellenbergi*: The expansion of the capacious gut following feeding (**A**), the feeding morphologies (**B**), and the mandibles as seen using a low vacuum environmental scanning electron microscope (SEM) (**C**–**D**).

efficient energy storage. This implies a novel genetic adaptation strategy for *Hirondellea gigas,* at least, to sustain starvation periods when food is scarce. Yayanos & Nevenzel (1978) found that *H. gigas* specimens from the Philippine Trench had appreciable stores of lipids in their bodies, presumably a large energy cache to cope with long periods of starvation. Lipid concentrations of the necrophagous *Eurythenes gryllus* s.l. (now *E. atacamensis* Weston & Espinosa–Leal, 2021 [Weston *et al.,* 2021a]) from the Atacama Trench (Eastern Pacific) accounted for 7–18% of the dry weight and were dominated by monounsaturated fatty acids, suggesting that these hadal amphipods are more dependent upon lipid reserves than similar shallower water amphipods (Perrone *et al.,* 2003).

The high lipid content of amphipods gave rise to the 'rising particle hypothesis' (Yayanos & Nevenzel, 1978), which postulated that the high lipid content of benthic amphipods could generate particles that could rise into the water column. They found the lipid content of *Hirondellea gigas* from 9,600 m in the Philippine Trench to be as high as 26.1% dry weight. While these concentrations of lipids were likely in a solid phase at ambient deep-sea temperatures and pressures, they speculated that lipids could be released to the environment by several mechanisms, including natural decay and animal mortality, cannibalism, predation, and

the debris generated during mass feeding bouts. They estimated that lipid particles from 5,000 m depth could reach the surface within a week. Such a mechanism, although never truly investigated, could explain why the largest amphipod, *Alicella gigantea*, estimated to be 340 mm in length, was an adult female regurgitated by an albatross on Laysan Island in the Hawaiian Islands (Harrison *et al.,* 1983). Given all records of *Alicella gigantea* are ~5,000 m deep or more (except for one at 1,720 m; Barnard & Ingram, 1986) it is difficult to explain how else a mature adult ended up being consumed by an albatross.

The significance of the hadal Amphipoda goes beyond their ability to consume bait but also their consumption by predatory species, particularly in the upper trenches. Linley *et al.* (2017) documented the feeding strategies of fishes spanning the bathyal, abyssal, and hadal depths of three Pacific trenches and found that the bathyal and abyssal fish communities were almost exclusively necrophagous. The fish species (mostly Ophidiidae and Macrouridae) that inhabited the abyssal-hadal transition zone comprised predatory and generalist feeders; however, the characteristically hadal fishes, the snailfishes (Liparidae), were exclusively predators. Similar patterns are observed in the large crustacean decapods, most common at the lower abyssal and upper hadal depths. The Decapoda are largely represented by

the Penaeidae (Jamieson et al., 2009; Swan et al., 2021) whereby the shallower abyssal species *Cerataspis* c.f. *monstrosus* Gray, 1828 is largely necrophagous while the deeper abyssal and hadal *Benthesicymus crenatus* Spence Bate, 1881 appears to be entirely predatory. Scavenging in these groups therefore decreases with increasing depth, whereas predation appears to increase, and the preferred prey is the abundance of amphipods.

Gerringer et al. (2017a) analysed the stomach contents of hadal snailfishes, from the Mariana and Kermadec trenches. Amphipods comprised 95.8% of the items (84.6% of the weight) of the stomach contents of *Notoliparis kermadecensis* (Nielsen, 1964) and 97.3% of the items (87.7% of the weight) in *Pseudoliparis swirei* Gerringer & Linley, 2017 [Gerringer et al. 2017b] from the Mariana Trench. All other sources (decapods, polychaetes, squids, and fish-carrion remnants) were only minor dietary components, which demonstrates the importance of amphipods as a source of food to larger hadal organisms, although they are limited to depths of ~8,100 and ~7,700 m, respectively in the case of fishes and decapods (Yancey et al., 2014; Swan et al., 2021). This means that beyond 8,000 m, hadal amphipods are free from larger predators, which also coincides with a large increase in baited trap yields and the aggregation density filmed by baited cameras.

PRESSURE ADAPTATION

High hydrostatic pressure is perhaps the most conspicuous environmental gradient of the hadal trenches and is a key physical influence on the evolution and distribution of both micro- and macro-organisms (Bartlett, 2002). Piezophily (high-pressure adaptation) is an essential prerequisite for survival at hadal depths as pressure increases by 1 atmosphere (atm) for every 10 m depth (Jamieson et al., 2010). Hadal amphipods, therefore, occupy depths with ambient hydrostatic pressures from ~600–1,100 atm (~60–110 MPa). Some amphipods, particularly in Hirondelleidae, exhibit extraordinarily large depth ranges. *Hirondellea dubia*, for example, is known from 4,700–10,817 m (range 6, 117 m) (Weston & Jamieson, 2022). This pressure-tolerant characteristic and ease of capture have made amphipods the model taxa in many key pressure-related physiological studies (MacDonald & Gilchrist, 1980, 1982; Yayanos, 1978, 1981; Downing et al., 2018).

During decompression (equating to vertical migrations), amphipods are 'relatively hardy in this respect' and the decompression tolerance is species-specific (MacDonald, 1997). Yayanos (2009) recalls how amphipods from the Mariana and Philippine trenches may be capable of significant decompression and that the pressure tolerance of amphipods increases with the depth of capture. Individuals of *Paralicella caperesca* from 5,900 m were recovered to the surface at ambient pressure (~600 atm) and decompressed to atmospheric pressure. Loss of locomotor activity occurred at 215 atm but was regained following recompression, thus suggesting that this species is capable of over 3,500 m of vertical migration (Yayanos, 1981). Other species such as *Eurythenes gryllus* s.l. from as deep as 4,000 and 5,900 m have been readily resuscitated by recompression following decompression paralysis (MacDonald & Gilchrist, 1980; Yayanos, 1981).

MacDonald (1997) described the effects on shallow-water species when exposed to increasing pressure. In amphipods, relatively slow dorsally directed spasms of the longitudinal musculature are elicited at high pressure. At higher pressure still, a progressive immobilisation begins, eventually culminating in mortality. Some deep-water species, however, exhibit no hyperexcitability at pressures higher than their natural depth range (MacDonald, 1997). MacDonald & Gilchrist (1982) recovered amphipods in a pressure retaining trap at 394–442 atm (~4,000 m) and pressurised the specimens to 700 atm (~7,000 m) and found the amphipods did not convulse, albeit mild hyperexcitability was observed. The failure to convulse at higher pressures suggests that specimens from 4,000 m had a greater pressure tolerance than those captured at 2,700 m. Likewise, Yayanos (1981) demonstrated that hadal amphipods had a greater pressure tolerance than those from 5,800 m, which again suggested that for some amphipod species at least, the deeper their natural depth range, the greater their pressure tolerance.

These high pressures can have profound biochemical perturbations. For example, pressure can disrupt protein conformations and ligand binding and can encourage protein aggregate damage (Yancey, 2020). Downing et al. (2018) analyzed a variety of amphipod species spanning the intertidal to full ocean depths, including the Mariana and Kermadec trenches. They concluded that shallow osmolytes (i.e., taurine, glycine, and betaine) decreased with depth while potential piezolytes or pressure counteractants increased with depth. These piezolytes include trimethylamine oxide (TMAO), glycerophosphorylcholine, proline betaine (all methylamine chaperones), glycerophosphorylethanolamine, and scyllo-inositol, which is a polyol chaperone that differs from methylamines by avoiding damaging protein aggregations. Although TMAO is known for its piezolyte properties (Yancey et al., 2001), the other solutes found in hadal amphipods may explain how they can thrive at depths beyond other organisms, such as teleost fishes (Yancey et al., 2014), cephalopods (Jamieson & Vecchione, 2020), and decapods (Swan et al., 2021), that appear restricted to maximum depths of ~7,000–8,200 m.

Other mechanisms in the adaptation to high pressure have been found within the exoskeletons of *Hirondellea gigas* (Kobayashi et al., 2019; Okada et al., 2022). One adaption suggested was an 'aluminum gel shield' found on the surface of the exoskeleton of *H. gigas* to prevent the dissolution of calcitic exoskeleton below the carbonate compensation depth (Kobayashi et al., 2019); however, this aluminum shield may be an artefact in the analysis of the signals in energy-dispersive X-ray spectroscopic analysis (Okada et al., 2022). Okada et al. (2022) found that contrary to an aluminum accumulation, that many parts of the body, most extensively the gastric ossicles and setae, are enriched with bromine. Further, to limit exoskeleton dissolution below the carbonate compensation depth, magnesium is particularly substituted for calcite. Together, these studies present a window into physical pressure adaptions.

How organisms have adapted to extreme environmental stressors, such as high pressure, is an important and enduring theme in evolutionary biology. Heat-shock proteins (HSPs) are a prominent family of cellular chaperones that are involved in the folding, assembly, and degradation of cellular proteins,

cell-cycling, and signal transduction. Ritchie *et al.* (2018) characterised two key heat-shock protein genes (hsp70 and hsp90) in abyssal and hadal Lysianassoidea and Alicelloidea amphipods. Four phylogenetically distinct isoforms were resolved for both hsp70 and hsp90, with one isoform in each gene being exclusive to the hadal genus *Hirondellea*. They concluded that increased hydrostatic pressure was important environmental stress that shaped the adaptation of heat-shock protein genes in deep-sea amphipods. DNA damage can occur due to high hydrostatic pressure (Rothschild & Mancinelli, 2001), therefore, hadal organisms may require high frequencies of DNA repair (Dixon *et al.*, 2004). Lan *et al.* (2017) observed a positive selection in the *H. gigas* Replication Factor A1 (RFA1) gene, known to aid in DNA replication, DNA repair, and chromosomal stability, implying a role in counteracting the negative effects of high hydrostatic pressure on DNA.

COMMUNITY STRUCTURE

Identification of patterns in community structure has been common practise in ecological research for decades. Until the turn of the last century, however, hadal sampling was sporadic and often lacked replication at a given depth, or sufficient sampling from multiple depths within a trench to conclude structural patterns. It was not until Blankenship *et al.* (2006) developed the methods of Hessler *et al.* (1978) in the Philippine Trench and repeated them across the entire hadal depth range of the Tonga Trench (central Pacific). Thirteen baited trap hauls between 5,155–10,787 m revealed that the now recognised three main species, all lysianassoids, exhibited distinct vertical zonation ranging from a small overlap of the abyssal *Eurythenes* spp. in the upper trench to the dominance of large numbers of *Hirondellea dubia* at the deepest depths, and populations of *Bathycallisoma schellenbergi* at the mid-depths, with the latter two species being endemic to hadal depths (Blankenship *et al.*, 2006). Further, the *H. dubia* and *B. schellenbergi* populations showed the first indications of ontogenetic structuring with depth and were consistent across species (see below).

Such approach was then taken by Jamieson *et al.* (2011), who focussed on the community structure as it transitioned from the abyssal plains to the trenches. At seven sampling sites in the Kermadec Trench between 4,329 to 7,966 m, they recovered 14 species and demonstrated a marked, statistically significant compositional change (ecotone) across the abyssal–hadal boundary, shifting at depths between 6,007 and 6,890 m, indicating that there is an ecologically distinct amphipod community at hadal depths in this trench. These data were then compared to five stations sampled across similar depths in the Peru-Chile Trench (Eastern Pacific) to test the abyssal-hadal ecocline over two trenches on either side of the South Pacific (Fujii *et al.*, 2013). The abyssal communities were very similar in that they were dominated by cosmopolitan species of *Paralicella*, *Abyssorchomene* De Broyer, 1984 and *Eurythenes*. Two very dissimilar groups were identified, the hadal Kermadec sites (6,890 to 7,966 m) dominated by *Hirondellea dubia*, and the hadal Peru-Chile sites (7,050 to 8,074 m). While the Kermadec hadal group was very similar to that in the Tonga Trench (Blankenship *et al.*, 2006), the Peru-Chile hadal group was characterised by the presence of *Eurythenes* and *Hirondellea*, later described as *Eurythenes atacamaensis* (Weston *et al.*, 2021a), and *Hirondellea sonnei*, *H. wagneri*, and *H. thurstoni* (Kilgallen, 2014). Fujii *et al.* (2013) demonstrated vast abyssal cosmopolitanism in contrast to trench-specific hadal endemism and that the environmental gradients of depth and geographic isolation (or dispersal distance) best explained these variations in the amphipod assemblage structure. Lacey *et al.* (2016) expanded both the sampling rate and the bathymetric and geographic reach of this approach by analysing amphipod community composition from the Kermadec Trench (1,490–9,908 m), the New Hebrides Trench (2,000–6,948 m), and the Peru-Chile Trench (4,602–8,074 m).

While hadal ecological research has been focused largely on subduction trenches, non-subduction features like fracture zones and troughs are begin to be explored and studied to access how community structure may be influenced by topography. As an initial investigation of hadal fracture zones, Weston *et al.* (2021b) analysed the change in community composition from 4,932 m of the Zenith Plateau to 6,546 m at the flat-bed trough of the Wallaby-Zenith Fracture Zone (East Indian Ocean). Eleven species were identified across the abyssal-hadal transition zone, and the community composition gradually changed from an entirely abyssal community to a largely abyssal community with key hadal fauna at hadal depths. This pattern contrasted with the ecotone shift characteristic of subduction trenches, suggesting that the community is influenced not solely by pressure but also by the topography and depositional environments. The work by Weston *et al.* (2021b) highlights the importance of expanding expeditions to understand the ecosystem role and dynamics of other hadal depth geomorphology features.

LIFE HISTORY

As with all Malacostraca, amphipods are brooders, where females carry their fertilised eggs in an external brood pouch until the fully formed juveniles emerge. Beyond that, there is little understanding of the life cycle and life history of hadal amphipods. Research within the hadal zone has focused on accounting for patterns in the distribution of males, females, and juveniles (ontogenetics). The first account of ontogenetics in hadal amphipods was from Hessler *et al.* (1978), who identified seven to eight female instars and four male instars within the populations of *Hirondellea gigas* from 9,600–9,800 m in the Philippine Trench. These instars represent a particular stage of maturity based on primary and secondary sexual characters that exhibit a relatively constant growth ratio. An exception to the growth ratio was found in females, where it decreased markedly at the stage coinciding with an accumulation of reproductive products suggesting that females breed only once with a total fecundity of approximately 97 oocytes per female. These data, however, were from a limited depth range, representing the deepest population of what would turn out to be a species that typically spans the entire hadal depth range.

Vertical ontogenetic stratification across the hadal depth range was later found in the congener of *Hirondellea gigas*, *H. dubia* from the Tonga and Kermadec trenches, as well as in *Bathycallisoma schellenbergi* (Blankenship *et al.*, 2006; Wilson *et al.*, 2018). These two studies found that early instars tended to

reside in the shallower depths of each species' depth range, with size and instar (as a proxy for age) increasing with increasing depth. This trend was later found by the expansion of the capture depth of *Hirondellea gigas* from additional samples in the Izu-Bonin Trench (Eustace *et al.*, 2013), *Bathycallisoma schellenbergi* in the New Hebrides and Kermadec trenches (Lacey *et al.*, 2018), and *Eurythenes atacamensis* in the Atacama Trench (Thurston *et al.*, 2002; Eustace *et al.*, 2016; Weston *et al.*, 2021a). Together, these studies suggest that the increased juvenile presence around the upper trench could be driven by reduced competition and relaxation of pressure effects on metabolism. This in turn shows that females descend deeper with age, culminating in a stage of reproduction preparation at the deepest depths (also coinciding with the absence of males).

The vertical ontogenetic stratification has also been found to scale to the topography of the trench (Lacey *et al.*, 2018), i.e., the patterns are the same but the actual depth across which it occurs depends on the depth of the trench. These observations suggests that the population structure is more affected by trench topography and how it may influence resource distribution and ecological interactions, rather than simply by the effects of hydrostatic pressure. Perhaps the most striking example of this condition is *Bathycallisoma schellenbergi*. This characteristically hadal amphipod has a typical depth range of 6,000 to 9,000 m in the trenches, with distinct vertical ontogenetic stratification (Blankenship *et al.*, 2006; Lacey *et al.*, 2016). Weston *et al.* (2021b), however, found them in a hadal feature that reached only 6,625 m in depth, the Wallaby-Zenith Fracture Zone. The species was found within a very narrow depth range of 6,537–6,546 m in the fracture zone, where the population showed no apparent stratification as it comprised a mix of both adults and juveniles. This distribution revealed that a population that normally spans over 3,000 m in depth range was residing in a shallower, albeit hadal, feature in the bottom 100 m, which suggests that while the minimum depth of occurrence could be driven by hydrostatic pressure, the maximum depth and ontogenetic structuring therein, are not, and are more likely linked to topography.

VISION AND COLOUR

Perhaps one of the most striking characteristics of freshly recovered amphipods is their eyes (Senna, 2009; Narahara-Nakano *et al.*, 2018). The often vividly yellow or orange sessile compound eyes typically occupy a large surface area of the head, extending from the dorsal to the ventral side as an irregular band (Hallberg *et al.*, 1980) (Fig. 7). Eyes are, however, quickly lost upon preservation in ethanol and their descriptions are therefore lacking in many species (see Stoddart & Lowry, 2004; Horton & Thurston, 2013). Eye morphology can be characterised by the constellation and consistency of several features. There are four main sub-categories of eyes: the ampeliscid, hyperiid, gammarid, and lysianassid types, with the latter being the most common at hadal depths (Hallberg *et al.*, 1980). The lysianassid type has a reduced or no dioptric apparatus and hypertrophied (enlarged) rhabdoms, therefore differing from that of littoral species (Strauss, 1926 as quoted in Hallberg *et al.*, 1980). Few studies on the eye morphology of deep-water amphipods have been undertaken, but for *Eurythenes gryllus* s.l. there are at least no traces

of the crystalline cone, except for some flattened cells distal to the rhabdom that may represent the remnants of the cone cells (Hallberg *et al.*, 1980). While these organs do not appear capable of generating an image, they may provide crude directional information given that they extend dorsally to ventrally. The organs, however, appear to be adapted to detecting low ambient light intensities (Hallberg *et al.*, 1980).

Like many crustaceans, amphipods are often orange-pink-red pigmentation except for species, such as *Alicella gigantea*, or genera, such a *Princaxelia*, that appear uniformly white. This colouration is a result of carotenoid pigments, which are synthesised by higher plants, mosses, bacteria, algae, and fungi (Gaillard *et al.*, 2004) and acquired by amphipods through their diet, likely through phytoplankton-derived particulate organic matter (Repeta & Gagosian, 1984). These carotenoids serve an important function in deep and low-light environments in terms of camouflage. Given the quick attenuation of red wavelengths through water, a uniformly red exoskeleton provides valuable camouflage against predators and exposure by illumination from bioluminescent light (Johnsen, 2005). Many species of amphipods vary across a spectrum of the white-orange-pink-red and sometimes deep red, with individuals of the same species from the same haul, or filmed *in situ*, being quite different (e.g., white *vs.* deep red) (Fig. 8). Earlier studies of the abyssal *Eurythenes gryllus* in the North Pacific indicated an increase in colour intensity with age and sexual maturation (Smith & Baldwin, 1984; Charmasson & Calmet, 1987). Similarly, Arctic populations of *E. gryllus* showed an increase in colour intensity correlated with body size (Thoen *et al.*, 2011). The amount of pigmentation continues to increase as growth ceases or slows down at a certain size or stage, but variations in pigment composition are probably affected by both diet and moulting/growth patterns or other factors like metabolic pathways or reproduction (Thoen *et al.*, 2011). The absence of this pigmentation in *Alicella gigantea* and *Princaxelia* spp. may be a result of a lack of predation with the former, and the latter consisting of predatory species.

MICROBIOME AND PARASITISM

The first study of bacteria associated with hadal Amphipoda came from a specimen of *Hirondellea gigas* from 10,476 m in the Mariana Trench (Yayanos *et al.*, 1981). The specimen was incubated at close to ambient pressure and temperature where the bacterial strain 'MT-41' (later assigned to *Colwellia*; DeLong *et al.*, 1997) was isolated and partially characterised and deemed an obligately piezophilic bacterium. The generation time of 'MT-41' was three times longer than a similar abyssal strain, 'CNPT-1.' The 'CNPT-1' abyssal strain did not grow at pressures beyond ~8,500 m, while the 'MT-41' strain ceased growing at pressures less than those found shallower than ~5,000 m. DeLong *et al.* (1997) also demonstrated that samples from 3,500 m at the rim of the Mariana Trench, just 28 km from the 10,476 m 'MT-41' sample site, also could not survive beyond 8,500 m. This observation suggested for the first time that the microbiome of the hadal bacteria may be as endemic to hadal depths as the amphipod itself. A similar strain, *Colwellia marinimaniae* strain 'MTCD1^{T}' was more recently isolated using the same amphipod species from the Mariana Trench and was found to be the
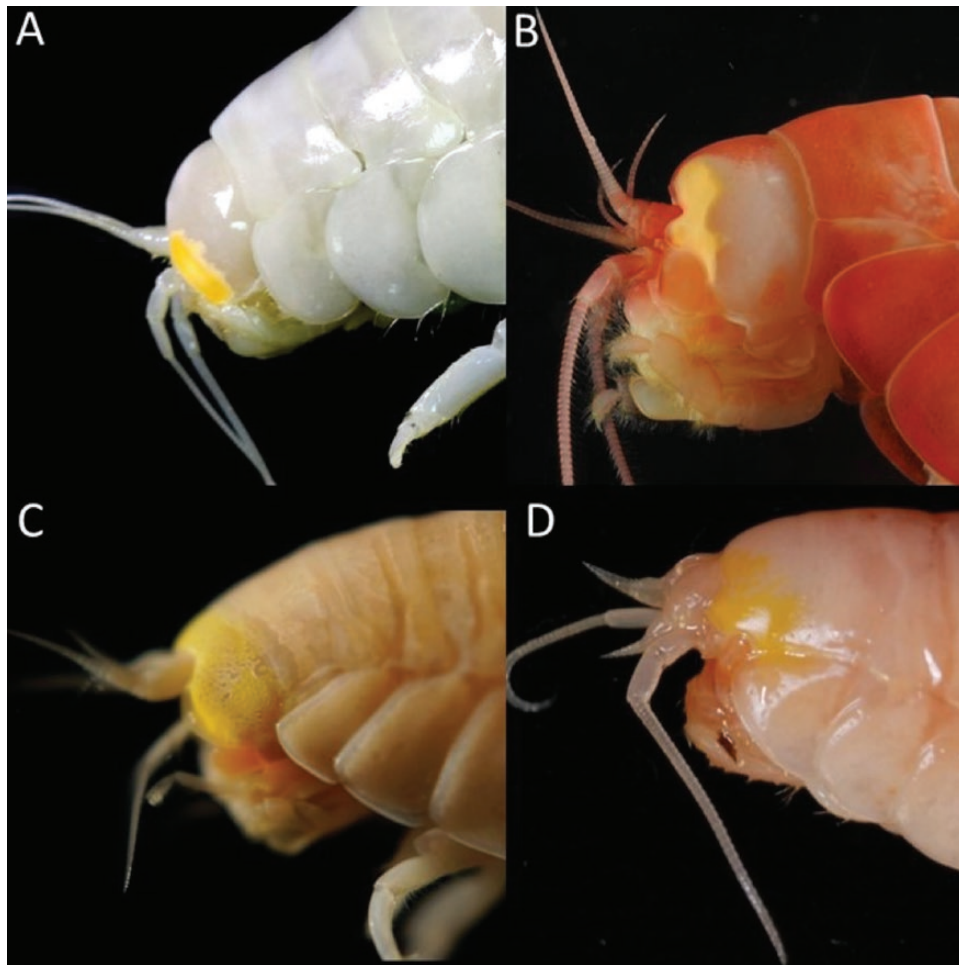
Figure 7. The eyes of common hadal species prior to fixation: *Alicella gigantea* (**A**), *Eurythenes atacamensis* (**B**), *Hirondellea gigas* (**C**), and *Bathycallisoma schellenbergi* (**D**).

most piezophilic organism ever described, with a growth pressure range of 80–140 Mpa and an optimum of 120 Mpa at 6 °C (Kusube *et al.*, 2017). Strains were also isolated from *Hirondellea dubia* from the Kermadec Trench (South Pacific) from a depth of 9,856 m (Lauro *et al.*, 2007). Both isolates, 'KT27' and 'KT99', were piezophilic and represented the first psychropiezophiles from the Southern Hemisphere. The closest cultured relatives of 'KT27' and 'KT99' were the isolates *Colwellia* sp. strain 'MT-41' (Yayanos, 1986) and *Shewanella* sp. strain 'PT99' (DeLong *et al.*, 1997), respectively.

Gut microbiotas are known to play a crucial role in organismal health, including pathogen defence, environmental adaptation, and digestion (Cheng *et al.*, 2019), and are becoming increasingly more appreciated in their critical role in assisting the host to adapt to hadal environments (He *et al.*, 2018; Zhang *et al.*, 2018, 2019). Studies are emerging on the gut microbiota of hadal amphipods, again centred on *Hirondellea gigas* from the Mariana Trench. The most dominant bacterium was found to be *Psychromonas* sp., of which Zhang *et al.* (2018) successfully recovered a nearly complete genome (designated 'CDP1'). This strain was found to have a reduced genome, consistent with the hypothesis that in some ecosystems the bacteria are subject to strong selection to minimise the material costs of growth (Giovannoni *et al.*, 2005). The genome reduction in CDP1 was posited to reflect a

long-term series of strategic adaptations within the gut of *Hirondellea gigas* through a long history of coevolution.

A comparative analysis of the gut microbiota between *Hirondellea gigas* from the Mariana and Japan trenches revealed significant differences in the composition of the gut microbes such as variation in abundance of *Psychromonas*, *Propionibacterium*, and *Pseudoalteromonas* species of bacteria (Zhang *et al.*, 2019). The comparative metagenomics suggested that the gut microbial compositions of the two populations have undergone significant divergence and might be a result of selective factors, such as environmental variations and microbial interactions. Cheng *et al.* (2019) compared the gut microbial composition and diversity of two distinct species of amphipods, *Hirondellea gigas* and *Halice* sp. from the Mariana Trench. The genera '*Candidatus* Hepatoplasma' dominated overall, followed by *Psychromonas* in *Hirondellea gigas* and *Psychrobacter* in *Halice* sp. These two hadal species shared the predominant symbiont of '*Ca.* Hepatoplasma' but were classified into two different operational taxonomic units (OTU), suggesting host-specific colonization of symbionts. In terms of diversity and abundance, there was a significant divergence of gut microbiota found between the two species, both which came from the same environment. Comparison between the microbiomes of *Alicella gigantea*, *Bathycallisoma schellenbergi*, and *Hirondellea gigas* from the New Britain
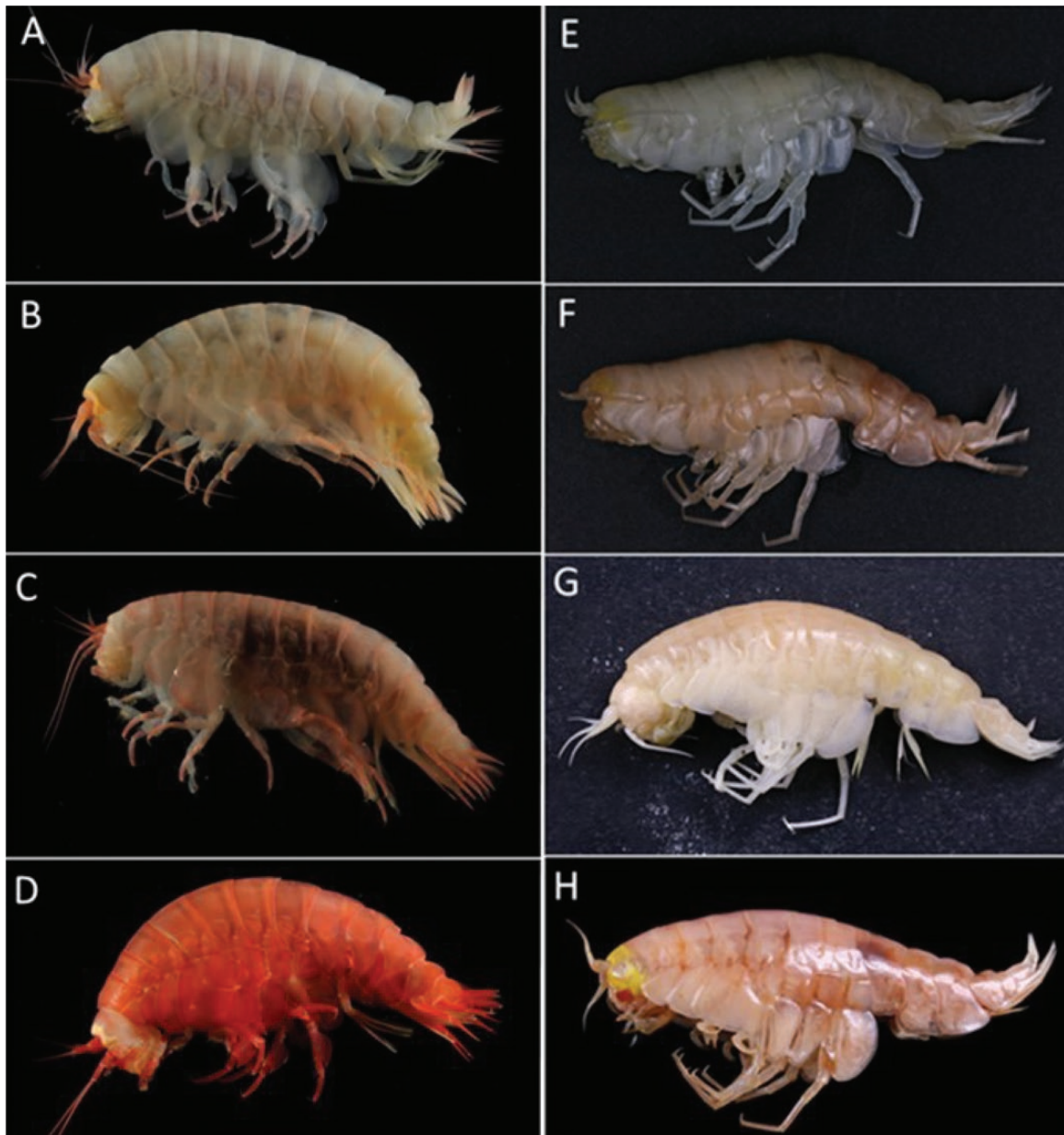
Figure 8. Colour variation in freshly caught amphipods: *Eurythenes atacamensis* from 8,074 m in the Atacama Trench (**A–D**), *Bathycallisoma schellenbergi* from 7,000 m in the South Sandwich Trench (**E, F**), and *Hirondellea gigas* from 10,900 m in the Mariana Trench (**G, H**).

Trench further strengthens the evidence that gut microbiomes at hadal depths are species-specific (Chan *et al.*, 2021). Whether the host-microbe associations are a result of vertical transmission (where microbes pass from the parents and not from the environment) or horizontal transmission (acquisition from the environment) is yet to be resolved (Zhang *et al.*, 2018).

Records of parasitic nematodes at hadal depths are rare and mostly known from free-living adult stages living in the sediments (Leduc, 2015). Leduc & Wilson (2016), however, described the benthimermithid nematode *Trophomera* cf. *marionensis* from the body cavity of *Hirondellea dubia* from the Kermadec Trench at depths of 7,018 to 10,005 m. Although morphologically identical, the nematodes were about twice the length of *Trophomera marionensis* recorded from shallower areas. The prevalence of these parasites among the *Hirondellea dubia* populations was

estimated to be < 1 %. The ecological role that these parasitic interactions play is largely unknown.

ANTHROPOGENIC SIGNATURES

The hadal zone is remote, understudied, and rarely visited, and as such one might easily assume it to be pristine and free from signatures of anthropogenic impacts. In recent years, however, hadal amphipods have been used in multiple studies as a model taxon in which to demonstrate the extent of anthropogenic contamination at extreme depths. As in shallower systems, amphipods function as biomonitors for anthropogenic influences, such as heavy metals. Reid *et al.* (2018) provided an initial baseline for examining trace-metal variability. Amphipods can also be used for a signal of contamination. The range of contamination sources

is as alarmingly widespread as contamination levels are high. For example, Wang *et al.* (2019), for example, detected 'bomb ^{14}C' radiocarbon in *Hirondellea gigas* and *Alicella gigantea*, a radiocarbon resulting from thermonuclear tests during the 1950s and 1960s that doubled the amount of ^{14}C in the atmosphere (Hua & Barbetti, 2004). The bomb ^{14}C is mixed with ocean and terrestrial carbon pools that are then transported to the trenches via particulate organic matter (POM). Similarly, Oguri *et al.* (2013) demonstrated that the cesium (^{137}Cs) fallout following the 2011 Tohoku-Oki Earthquake and Tsunami induced Fukushima Dai-ichi nuclear disaster could reach the Japan Trench communities in < 100 d as it binds to, and descends, with POM. While it is not yet been recorded in amphipods, it appears ^{137}Cs is likely to be present, as it was shown to have penetrated both the POM and seafloor sediment.

Other anthropogenic pollutants include persistent organic pollutants (POPs), such as polychlorinated biphenyls (PCBs, used as dielectric fluid) and polybrominated diphenyl ethers (PBDEs, used as flame retardants). POPs are highly detrimental to organismal health through their endocrine disrupting properties (Rhind, 2012) and possess an inherent hydrophobicity therefore a high binding affinity to POM descending in the water column. They also have inherent lipophilicity, so these compounds readily bioaccumulate in organisms, with cumulative increases at each trophic level (Ballschmiter *et al.*, 1983). Both man-made PCBs and PBDEs were detected in all amphipods studied across the entire depths range of both the Mariana and Kermadec trenches (*Hirondellea gigas, H. dubia*, and *Bathycallisoma schellenbergi*, respectively; Jamieson *et al.*, 2017). The Mariana Trench amphipods had the highest levels of PCBs (147.3–905 ng g^{-1} lw), which were fifty times more contaminated than crabs from paddy fields fed by the Liaohe River, one of the most polluted rivers in China, while the Kermadec Trench amphipods showed very high levels of PBDEs (13.75–31.02 ng g^{-1} lw). In addition to these POPs, Cui *et al.* (2020) also detected high concentrations (up to 1343 ng g^{-1} lw) of chlorinated pesticides, such as dichlorodiphenyltrichloroethanes (DDT) and chlordanes as well as four brominated natural products (BNPs) that resembled methoxylated brominated diphenyl ethers or polybrominated biphenyls, from specimens of *Hirondellea gigas*, *Bathycallisoma schellenbergi*, and *Alicellea gigantea* from the Mariana, Mussau (Southwest Pacific), and New Britain trenches, respectively.

Monomethyl mercury (MMHg) is a globally distributed neurotoxic pollutant also known to biomagnify in marine food webs. Mercury isotope measurements in hadal amphipods have been used to demonstrate the extent to which surface-ocean-derived mercury has infiltrated the hadal zone (Sun *et al.*, 2020). When surface-dwelling organisms and POM sink, large amounts of mercury are transferred to the underlying trench fauna, as demonstrated by high concentrations of MMHg in amphipods from both the Mariana and Kermadec trenches (1.49‰ ± 0.28, *N* = 13 and 1.57‰ ± 0.14, *N* = 12, respectively; Blum *et al.*, 2020).

The occurrence of microplastics (< 5 mm in size) in the deep sea has seen a rapidly growing realisation (Van Cauwenberghe *et al.*, 2013, Taylor *et al.*, 2016). Peng *et al.* (2018) documented microplastic abundances in hadal sediments of the Mariana Trench varying from 200 to 2200 pieces per litre, values that are much higher than those in typical deep-sea sediments, making it available through detritivory (Blankenship & Levin, 2007). Jamieson *et al.* (2019) detected ingested microplastics in the hindguts of lysianassoid amphipod populations in six trenches around the Pacific Rim (Japan, Izu-Bonin, Mariana, Kermadec, New Hebrides, and Japan-Chile trenches), at depths ranging from 7,000 m to 10,890 m. They found that 72% of individuals examined across all sites contained at least one microparticle. The number of microparticles ingested per individual across all trenches ranged from 1 to 8. The average microparticle per specimen varied per trench, from 0.9 ± 0.4 SD (New Hebrides Trench) to 3.3 ± 0.7 SD (Mariana Trench).

One species encapsulates the sober fact of the extent of marine plastic pollution in the hadal zone, *Eurythenes plasticus* Weston, 2020 [Weston *et al.*, 2020]. A new hadal amphipod species from 6,010 and 6949 m deep in the Mariana Trench was found to have ingested polyethylene terephthalate (PET) and was named *'plasticus'* to highlight the extent of the plastic problem (Weston *et al.*, 2020). *Eurythenes plasticus* was used in a campaign to raise awareness about the problem of marine plastics in collaboration between Newcastle University (UK), Worldwide Fund for Nature (Germany), and the advertising agency BBDO-Dusseldorf (Fig. 9). The 2020 campaign led to 120,000 signatures across 94 countries on a petition to end marine plastics, > 500,000 visitors to exhibitions in UK and German museums and amassed a global reach of 1.4 billion people. It was awarded the Guinness World first for the first new species already found to have been contaminated with plastic as of 2021.

HADAL AMPHIPODS – 60 YEARS ONWARDS

The ability to sample such high numbers and species of any hadal organismal group still makes the Amphipoda highly significant in the study of hadal ecosystems. While many questions have been answered, there is still a wealth of knowledge to be gained and questions that could be addressed over the next 60 years, ranging from taxonomy to the biology of individual species to global population and evolution. As new technology is developed and expeditions intensify, the work already done on the hadal Amphipoda should serve as a framework to be applied to other crustacean orders and invertebrate phyla. Such a multi-disciplinary approach to other taxa, exemplified by the work on hadal amphipods, will be required to disentangle trends across multiple hadal habitats, species, higher taxonomic ranks, and functional groups.

DIVERSITY AND TAXONOMY

Only a fraction of the hadal zone has been explored, and similarly, as this review demonstrates, only a fraction of specimens recovered from hadal depths have a scientific name. Specifically, 71 species are assigned to a valid genus, while at least another 40 records have uncertain identification (Table 1). This gap represents both a taxonomic impediment and highlights that much work is still required for fundamental taxonomy and the study of biodiversity in the hadal zone. This gap is the widest for pelagic and non-benthic scavenger amphipods, which is largely derived
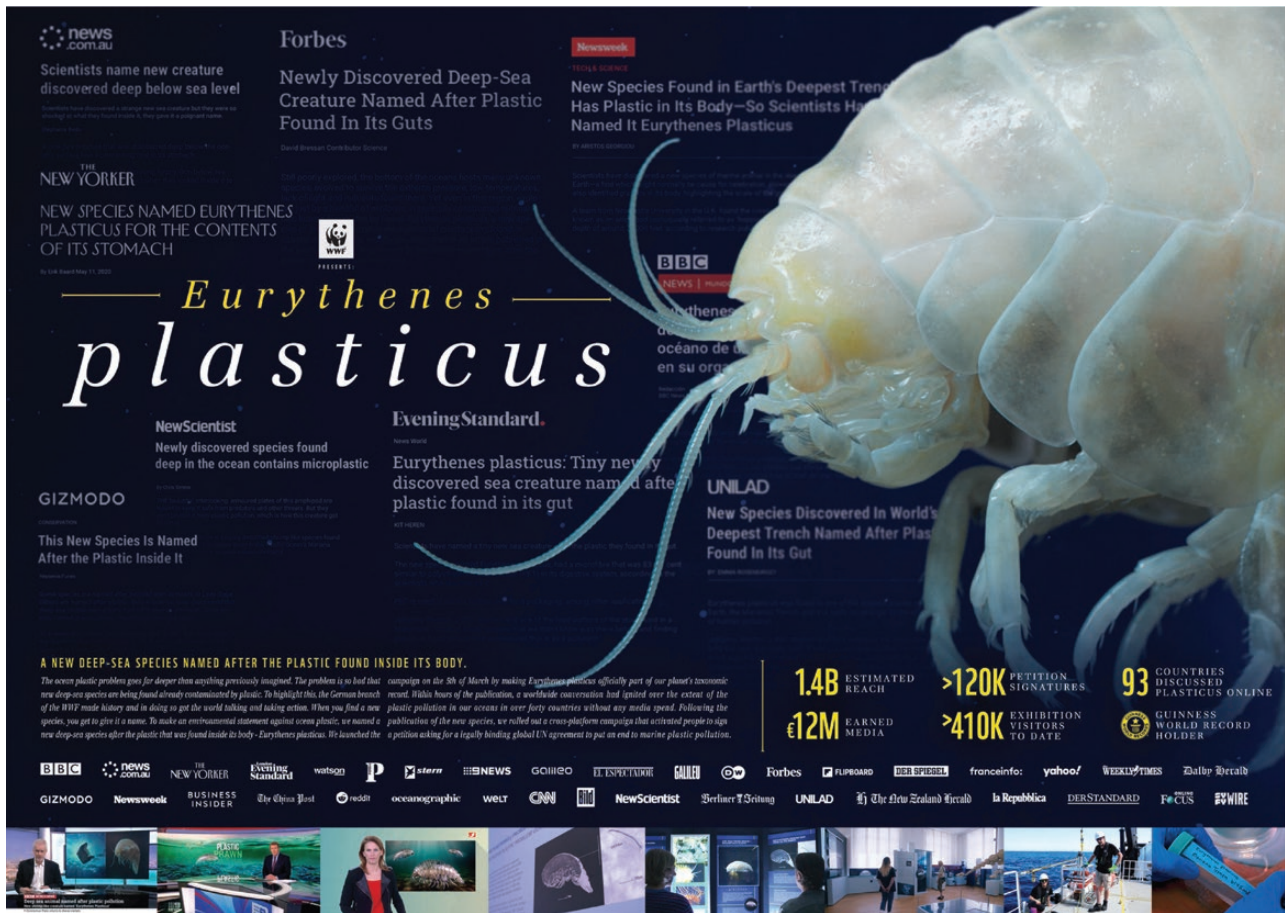
Figure 9. A promotional poster of *Eurythenes plasticus* from the 'Call It Plastic' marine plastic awareness campaign in 2020. Credit: Worldwide Fund for Nature (Germany)/Batten, Barton, Durstine & Osborn (BBDO).

from the predominate use of landers. As more technologies, such as suction samplers on submersibles, come available and are deployed to hadal depths our understanding of the occurrence and distribution of non-scavenging fauna can be expected to expand.

Once specimens are on land, focus on fundamental taxonomy remains necessary for the progression of the understanding of hadal biology, particularly to provide identitifications, understand distributions, unravel biogeographic patterns, understand evolutionary histories and relationships, discover new biodiversity, and track long-term changes to anthropogenic stressors. One approach to supporting this progression is by applying an integrative taxonomic approach, of coupling morphological taxonomy with DNA barcoding, to gain robust identifications (see Page *et al.*, 2005; Padial *et al.*, 2010). This approach is being well applied to document diversity at hadal features (e.g., Jażdżewska & Mamos, 2019; Weston *et al.*, 2021b), resolve identities within the cryptic genera of *Eurythenes* (e.g., Havermans *et al.*, 2013; Weston *et al.*, 2021a) and *Paralicella* (e.g., Jażdżewska *et al.*, 2021), and illuminate cosmopolitan distributions within the species of *Bathycallisoma schellenbergi* (e.g., Weston *et al.*, 2020) and *Hirondellea dubia* (e.g., Weston & Jamieson, 2022). While successful DNA barcoding is not possible for all specimens, potentially due to preservation type, age, substantial degradation during repair, or a myriad of other possibilities, future works should prioritise

an integrative taxonomic approach to overcome taxonomic impediments and achieve robust identifications that provide the foundation for other questions.

Physiology and chronobiology

Marine organisms, much like their terrestrial counterparts, exhibit cyclic behaviour that has been the focus of chronobiological research for many years (Naylor, 1996, Last *et al.*, 2009). The marine environment is subject to tidal (~12.4 h), daily (~24 h), lunar-day (~24.8 h), semi-lunar (~15 d), and lunar cycles (~28 d) that constitute only the main environmental cycles present at full ocean depth (Taira *et al.*, 2004). While circadian clocks are principally governed by the light/dark cycle, tidal clocks are entrained by a suite of cycles associated with the predictable inundation and exposure of the shore. These tidal cycles (unlike circadian) can include hydrostatic pressure, among other parameters (Reid & Naylor, 1990).

On a cellular level, pressure changes of less than 20 kPa (equivalent to ≤ 2m depth), trigger perturbations in cell growth and/ or metabolism (MacDonald & Fraser, 1999). It is unclear how amphipods sense pressure. Identification of hydrostatic pressure receptors in marine organisms without a gas phase has proved elusive until it was found that thread hair receptors in the statocyst of decapod Crustacea responded to small changes in hydrostatic pressure (Fraser & MacDonald, 1994; Fraser, 2001; Fraser

& Takahata, 2002). It is now presumed that amphipods detect pressure using statocysts much in the same way as decapod crustaceans (Platvoet *et al.*, 2006) and are therefore likely to detect minute variations in hydrostatic pressure. The location of a statocyst nevertheless remains elusive within hadal amphipods.

If the statocysts are sensitive enough to detect tidal fluctuations present at depth (Jamieson *et al.*, 2020), are the amphipods exhibiting chronobiological behaviour? Observations have shown that in some deep-sea organisms there is an apparent synchronisation of activity (Guennegan & Rannou, 1979; Wagner *et al.*, 2007). Amphipod fluctuations at 4,855 m in the North Atlantic have been attributed to current and pressure changes, although these parameters were not measured (Thurston, 1979). Synchronization of an organism's endogenous biological oscillators, of tidal and/or daily to annual periodicities, is fundamental to optimal physiological performance, life history, and ultimately survival. How hadal amphipods can naturally detect and respond to small fluctuations such as tidal cycles or even large seismic events and perturbations is an important but unresolved issue.

Reproduction and life history

All studies that have examined the life histories of hadal amphipods across a wide depth range of a trench have identified a clear pattern of juveniles at the shallower depths and mature females at the deeper depths (Blankenship *et al.*, 2006; Eustace *et al.*, 2013; Lacey *et al.*, 2018; Weston *et al.*, 2021a). As the females descend deeper with age, culminating in the reproduction preparation stage at the deepest depths, they are seldomly recovered in baited traps as they likely no longer feed to prevent the expulsion of eggs. This results in the last stage of the females going unsampled using the most successful sampling methods for amphipods. This prevents a 'closed loop' analysis of the reproduction cycle that leaves large unresolved questions regarding how the juveniles end up at the shallower depth of the trench, which can be nearly 5,000 m shallower than the deepest point where the large females were last reported. Do these brooding females suddenly ascend back up 5,000 m to the top of the trench to release their brood, or is there a pelagic stage and they float up as larvae? Or do the juveniles hatch and make the ascent themselves? As challenging as all these options appear to be, some mechanism must exist to explain the gap in observations.

Other intriguing questions in the study of the life history are the age and life span of species and the timing of reproduction. While we know they make the depth-maturity descent during their lifetime, there are currently no estimates of how long this cycle takes to complete. Ingram & Hessler (1987) estimated that the *Eurythenes gryllus* s.l. (Lichtenstein in Mandt, 1822) age to maturity to be 7.9–12.8 y for females and 3.5–5.6 y for males based on instar analysis calculation; however, this remains unresolved at hadal depths. Gerringer *et al.* (2018) posited that the relatively young age of reproductively mature hadal snailfishes may be due to long-lived species more typical of the relatively stable aseismic abyssal plains being highly susceptible to disturbances in seismically active trenches. Perhaps the reason for a sudden shift in amphipod diversity in the upper trenches is related to population resilience to seismically induced disturbance events such as burial or smothering, following a mass wasting event (Oguri *et al.*, 2013).

Ecology beyond the trenches

Although hadal amphipods are principally known for inhabiting large subduction trenches, other geomorphologies are hadal but not trenches. Jamieson & Stewart (2021) analysed bathymetric data from the Northwest Pacific where a large majority of hadal features occur and concluded that trenches only accounted for 32% of the 2.1 million km^2 of seafloor greater than 6,000 m. The remaining comprised basins and fracture zones, *albeit* generally shallower. Weston *et al.* (2021b) reported finding quintessentially hadal amphipods within the bottom 100 m of a flat-bottomed fracture zone that was only 6,625 m deep. *Bathycallisoma schellenbergi* is well documented from the larger subduction trenches (Weston *et al.*, 2022) and typically exhibits ontogenetic stratification (Lacey *et al.*, 2018), which it did not in this shallower fracture zone. Similarly, the hadal species *Hirondellea gigas* has been found in in the Sui Shin Hole, an equally shallow location in the Philippine Plate (AJJ, unpublished data). These observations suggest that these amphipods are indeed 'hadal' amphipods and not 'trench' amphipods, and much of their global footprint may well be in non-trench hadal zones such as basins and fracture zones that are relatively under-sampled.

Connectivity and speciation

The hadal zone represents an intriguing seafloor landscape, as inverted island-like habitats. Recent population genomic analysis is dually highlighting that the seafloor separating hadal features does pose reproductive barriers to population connectivity but also that the distribution of hadal fauna is more complex than one species per trench. For example, Weston *et al.* (2022) showed that *Bathycallisoma schellenbergi* has a cosmopolitan distribution at hadal depths, but populations were highly restricted to individual features with only limited gene flow between topographically connected features. Weston & Jamieson (2022), however, showed that *Hirondellea dubia*, while largely present in the Southwest Pacific, is not present in the Indian Ocean but is present in the Southern and North Atlantic Oceans, with evidence of co-inhabiting the Mariana Trench with the congener *H. gigas*. *Hirondellea gigas*, does not appear to exhibit such a global distribution and is so far known to be confined to the Northwest Pacific. All three species appear to not inhabit the Atacama Trench where three other *Hirondellea* species are known (Kilgallen, 2014) and a closely related potential cryptic linage of *Bathycallisoma schellenbergi* (Weston *et al.*, 2022). These results represent three dominant hadal species from two genera, none of which exhibit the same biogeographic pattern. This suggests that there is more research to be done with regards to population connectivity and phylogeography which would benefit from considerations of the non-trench hadal features and life history stages described above and historical conditions of the deep ocean that may provide insight into how and when an individual hadal feature is being populated and are connected.

Omics and the hadal zone

The hadal zone represents an extreme point for understanding rules of the life and the final terminus for pathways in the deep ocean. With abundant diversity, recovery in high numbers, and shallower comparative species, hadal amphipods represent

model taxa to determine the fundamentals of cellular organization, evolutionary adaptions, and protein functions required to thrive at full ocean depth. At present, the number of available 'omics resources are in its infancy, with only three mitogenomes (Lan *et al.*, 2016; Li *et al.*, 2019a, b) and three transcriptomes (Lan *et al.*, 2017; Li *et al.*, 2021) available. One of the limits to the number of genomic resources is the extreme estimated size of genome size hadal amphipods, ranging from 4–34 Gb (Ritchie *et al.*, 2017b). With the exponential rise in next-generation sequencing technologies, particularly with long-read capabilities, coupled with the steady decline in sequencing costs and increase in bioinformatic capabilities, genomic, transcriptomic, and epigenetic research of hadal amphipods is primed for explosive growth over the next several decades. This will enable the continued discovery of hadal diversity, novel pressure adaption, and genetic resources to uncover how and when life evolved to the hadal zone.

CONCLUSIONS

Since their initial discovery in the hadal zone, amphipods have become a model taxon in understanding life at great depth. While Dahl (1959) mused that hadal amphipods established 'nothing essentially new,' they have since become central to contemporary hadal science, from anthropogenic contaminants to evolutionary genetics. Their extraordinary responses to artificial food-falls, and ease of capture in large numbers have put amphipods at the centre of many hadal science studies. This ecological trait has resulted in a disproportionately greater number of studies, discoveries, and insights than the others in the 'five significant abyssal-hadal groups' reported by Belyaev (1966). It is therefore arguable that the Amphipoda are any more important ecologically than other hadal groups but have been and will likely continue to be highly important scientifically.

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REFERENCES

Ballschmiter, K., Buchert, H., Scholz, C. & Zell, M. 1983. Baseline studies of the global pollution. VI: The pattern of pollution by chlorinated hydrocarbons in the Caspian Sea. *Fresenius' Zeitschrift für analytische Chemie*, **316**: 242–246.

Barnard, K.H. 1932. Amphipoda. *Discovery Reports*, **5**: 1–326.

Barnard, J.L. 1961. Gammaridean Amphipoda from depths of 400-6000 meters. *Galathea Report*, **5**: 23–128.

Barnard, J.L. 1962. *South Atlantic abyssal amphipods collected by R.V." Vema". Abyssal Crustacea. Vema Research Series 1*. Columbia University Press, New York.

Barnard, J.L. 1964. Deep-sea Amphipoda (Crustacea) collected by R.V. "Vema" in the eastern Pacific Ocean and the Caribbean and Mediterranean Seas. *Bulletin of the American Museum of Natural History*, **127**: 3–46.

Barnard, J.L. & Ingram, C.L. 1986. The supergiant amphipod, *Alicella gigantea* Chevreux from the North Pacific Gyre. *Journal of Crustacean Biology*, **6**: 825–839.

Bartlett, D.H. 2002. Pressure effects on *in vivo* microbial processes. *Biochimica et Biophysica Acta*, **1595**: 367–381.

Belyaev, G.M. 1966. *Bottom fauna of the ultra-abyssal depths of the world ocean*. Nauka Publishing House, Moscow [in Russian].

Belyaev, G.M. 1989. *Deep-sea ocean trenches and their fauna*. Nauka Publishing House, Moscow.

Berge, J. & Vader, W. 2001. Revision of the amphipod (Crustacea) family Stegocephalidae. *Zoological Journal of the Linnean Society*, **133**: 531–592.

Blankenship, L.E. & Levin, L.A. 2007. Extreme food webs: Foraging strategies and diets of scavenging amphipods from the ocean's deepest 5 kilometers. *Limnology and Oceanography*, **52**: 1685–1697.

Blankenship, L.E., Yayanos, A.A., Cadien, D.B. & Levin, L.A. 2006. Vertical zonation patterns of scavenging amphipods from the Hadal zone of the Tonga and Kermadec Trenches. *Deep Sea Research Part I: Oceanographic Research Papers*, **53**: 48–61.

Blum, J.D., Drazen, J.C., Johnson, M.W., Popp, B.N., Motta, L.C. & Jamieson, A.J. 2020. Mercury isotopes identify near-surface mercury in deep-sea trench biota. *Proceedings of the National Academy of Sciences of the United States of America*, **117**: 29292–29298.

Birstein, Y.A. & Vinogradov, M.E. 1955. Pelagicheskie gammaridy (Amphipoda, Gammaridea) Kurilo-Kamchatskoi Vpadiny [Pelagic gammarids (Amphipoda, Gammaridea) at the Kourilo-Kamtchatka Trench]. *Trudy Instituta Okeanologii Akademija Nauk S.S.S.R.*, **12**: 210–287 [in Russian].

Birstein, Y.A. & Vinogradov, M.E. 1958. Pelagicheskie gammaridy (Amphipoda, Gammaridea) severo-zapadnoi chasti Tikhogo Okeana [Pelagic Gammaridea from the northwestern Pacific Ocean]. *Trudy Instituta Okeanologii Akademija Nauk S.S.S.R.*, **27**: 219–257 [in Russian].

Birstein, Y.A. & Vinogradov, M.E. 1960. Pelagischeskie gammaridy tropischeskoi chasti Ticogo Okeana [Pelagic Gammaridea of the tropical part of the Pacific Ocean]. *Trudy Instituta Okeanologii Akademija Nauk S.S.S.R.*, **34**: 165–241 [in Russian].

Birstein, Y.A. & Vinogradov, M.E. 1963. The deep-sea pelagic amphipods of the Philippine Trench. *Trudy Instituta Okeanologii Akademi Nauk S.S.S.R.*, **71**: 81–93 [in Russian].

Birstein, Y.A. & Vinogradova, N.G. 1960. Bottom ultra-abyssal Gammaridea of the north-western part of the Pacific Ocean. I. Families Lilljeborgiidae, Astyridae, Lepechinellidae, Gammaridae. *Trudy Instituta Okeanologii Akademi Nauk S.S.S.R.*, **34**: 147–164.

Boeck, A. 1871. *Crustacea Amphipoda borealia et Arctica*. Trykt hos Brøgger & Christie, Christiania [= Oslo].

Bousfield, E.L. 1977. A new look at the systematics of gammaridean amphipods of the world. *Crustaceana*, Supplement, **4**: 282–316.

Bousfield, E.L. 1983. An updated phyletic classification and palaeohistory of the Amphipoda. In: F.R. Schram (ed.). *Crustacean phylogeny*. San Diego: Museum of Natural History, San Diego, CA, USA.

Bovallius, C. 1886. Amphipoda Synopidea. *Nova Acta Regiae Societatis Scientarum Upsaliensis*, Series 3, **13**: 9, 36.

Bovallius, C. 1887. Systematical list of the Amphipoda Hyperiidea. *Bihang till Kungliga Vetenskaps-Akademiens Handlingar*, **11**: 1–50.

Britton, J.C. & Morton, B. 1994. Marine carrion and scavengers. *Oceanography and Marine Biology Annual Review*, **32**: 369–434.

Bruun, A.F. 1956. The abyssal fauna: Its ecology, distribution and origin. *Nature*, **177**: 1105–1108.

Chan, J., Geng, D., Pan, B., Zhang, Q. & Xu, Q. 2021. Gut microbial divergence between three hadal amphipod species from the isolated hadal trenches. *Microbial Ecology*, **84**: 627–637.

Chan, J., Pan, B., Geng, D., Zhang, Q., Zhang, S., Guo, J. & Xu, Q. 2020. Genetic diversity and population structure analysis of three deep-sea

Amphipod species from geographically isolated hadal trenches in the Pacific Ocean. *Biochemical Genetics*, **58**: 157–170.

Charmasson, S.S. & Calmet, D.P. 1987. Distribution of scavenging Lysianassidae amphipods *Eurythenes gryllus* in the northeast Atlantic: comparison with studies held in the Pacific. *Deep Sea Research*, **34**: 1509–1523.

Cheng, X.Y., Wang, Y., Li, J.Y., Yan, G.Y. & He, L.S. 2019. Comparative analysis of the gut microbial communities between two dominant amphipods from the Challenger Deep, Mariana Trench. *Deep Sea Research Part I: Oceanographic Research Papers*, **151**: 103081 [https://doi.org/10.1016/j.dsr.2019.103081].

Chevreux, E. 1899. Sur deux espèces géantes d'amphipodes provenant des campagnes du yacht Princesse Alice. *Bulletin de la Société Zoologique de France*, **24**: 152–158.

Chevreux, E. 1908. Diagnoses d'amphipodes nouveaux provenant des campagnes de la "Princesse-Alice" dans l' Atlantique nord. *Bulletin de l'Institut Océanographique* (Monaco), **117**: 1–13.

Chevreux, E. 1912. Description d'un amphipode nouveau provenant de la campagne de l' "Hirondelle II" en 1911. *Bulletin de l'Institut Océanographique* (Monaco), **233**: 1–4.

Costa, A. 1851. *Catalogo dei crotacei Italiani e di moltri altri del Mediterraneo per Fr. Gugl. Hope*. F. Azzolino, Naples.

Cousteau, J.Y. 1958. Calypso explores an undersea canyon. *National Geographic*, **133**: 373–396.

Cui, J., Yu, Z., Mi, M., He, L., Sha, Z., Yao, P., Fang, J. & Sun, W. 2020. Occurrence of halogenated organic pollutants in hadal trenches of the Western Pacific Ocean. *Environmental Science & Technology*, **54**: 15821–15828.

Dahl, E. 1959. Amphipoda from depths exceeding 6000 meters. *Galathea Report*, **1**: 211–242.

Dahl, E. 1977. The amphipod functional model and its bearing upon systematics and phylogeny. *Zoologica Scripta*, **6**: 221–228.

Dahl, E. 1979. Deep-sea carrion feeding amphipods: Evolutionary patterns in niche adaptation. *Oikos*, **33**: 167–175.

Dana, J.D. 1849. Synopsis of the genera of Gammaracea. *The American Journal of Science and Arts*, **8**(22): 135–140.

Dana, J.D. 1852. On the classification of the Crustacea Choristopoda or Tetradecapoda. *The American Journal of Science and Arts, Second Series*, **14**: 297–316.

Dana, J.D. 1853. Crustacea. Part II. In: *United States Exploring Expedition. During the years 1838, 1839, 1840, 1841, 1842. Under the command of Charles Wilkes. U. S. N. C.*, **Vol 14**. Sherman. Philadelphia.

De Broyer, C. 1984. Evolution du Complexe Orchomene Boeck (Amphipoda, Lysianassidae). *Annales de la Société Royale Zoologique de Belgique*, **114**: 197–198.

DeLong, E.F., Franks, D.G. & Yayanos, A.A. 1997. Evolutionary relationships of cultivated psychrophilic and barophilic deep-sea bacteria. *Applied and Environmental Microbiology*, **63**: 2105–2108.

Dixon, D.R., Pruski, A.M. & Dixon, L.R. 2004. The effects of hydrostatic pressure change on DNA integrity in the hydrothermal-vent mussel *Bathymodiolus azoricus*: Implications for future deep-sea mutagenicity studies. *Mutation Research/Fundamental and Molecular Mechanisms of Mutagenesis*, **552**: 235–246.

Downing, A.B., Wallace, G.T. & Yancey, P.H. 2018. Organic osmolytes of amphipods from littoral to hadal zones: Increases with depth in trimethylamine N-oxide, scyllo-inositol and other potential pressure counteractants. *Deep Sea Research Part I: Oceanographic Research Papers*, **138**: 1–10.

D'Udekem d'Acoz, C. & Havermans, C. 2015. Contribution to the systematics of the genus *Eurythenes* S.I. Smith in Scudder, 1882 (Crustacea: Amphipoda: Lysianassoidea: Eurytheneidae). Zootaxa. **3971**: 1–80.

Edgerton, H.E., Cousteau J.Y., Brown J.B. & Hartman R.H. 1957. Nylon rope for deep-sea instrumentation. *Deep-Sea Research*, **4**: 287.

Eustace, R.M., Kilgallen, N.M., Lacey, N.C. & Jamieson, A.J. 2013. Population structure of the hadal amphipod *Hirondellea gigas* (Amphipoda: Lysianassoidea) from the Izu-Bonin Trench. *Journal of Crustacean Biology*, **33**: 793–801.

Eustace, R.M., Ritchie, H., Kilgallen, N.M., Piertney, S.B. & Jamieson, A.J. 2016. Morphological and ontogenetic stratification of abyssal and hadal *Eurythenes gryllus* sensu lato (Amphipoda: Lysianassoidea) from the Peru–Chile Trench. *Deep Sea Research Part I: Oceanographic Research Papers*, **109**: 91–98.

France, S.C. 1993. Geographic variation among three isolated populations of the hadal amphipod *Hirondellea gigas* (Crustacea: Amphipoda: Lysianassoidea). *Marine Ecology Progress Series*, **92**: 277–277.

Fraser, P.J. 2001. Statocysts in crabs: short-term control of locomotion and long-term monitoring of hydrostatic pressure. *Biological Bulletin*, **200**: 155–159.

Fraser, P.J. & Macdonald, A.G. 1994. Crab hydrostatic pressure sensors. *Nature*, **371**: 383–384.

Fraser, P.J. & Takahata, P.M. 2002. Statocysts and statocyst control of motor pathways in crayfish and crabs. In: *Crustacean experimental systems in neurobiology* (K. Wiese, ed.), pp. 89–108. Springer, Berlin & Heidelberg.

Fujii, T., Kilgallen, N.M., Rowden, A.A. & Jamieson, A.J. 2013. Deep-sea amphipod community structure across abyssal to hadal depths in the Peru-Chile and Kermadec trenches. *Marine Ecology Progress Series*, **492**: 125–138.

Gaillard, M., Juillet, C., Cézilly, F. & Perrot-Minnot, M. 2004. Carotenoids of two freshwater amphipod species (*Gammarus pulex* and *G. roeseli*) and their common acanthocephalan parasite *Polymorphus minutus*. *Comparative Biochemistry and Physiology Part B*, **139**: 129–136.

Gerringer, M.E., Popp, B.N., Linley, T.D., Jamieson, A.J. & Drazen, J.C. 2017a. Comparative feeding ecology of abyssal and hadal fishes through stomach content and amino acid isotope analysis. *Deep Sea Research Part I: Oceanographic Research Papers*, **121**: 110–120.

Gerringer, M.E., Linley, T.D., Jamieson, A.J., Goetze, E., Drazen, J.C. 2017b. *Pseudoliparis swirei* sp. nov.: A newly-discovered hadal snailfish (Scorpaeniformes: Liparidae) from the Mariana Trench. *Zootaxa*, **4358**: 161–177.

Gerringer, M.E., Andrews, A.H., Huss, G.R., Nagashima, K., Popp, B.N., Linley, T.D., Gallo, N.D., Clark, M.R., Jamieson, A.J. & Drazen, J.C. 2018. Life history of abyssal and hadal fishes from otolith growth zones and oxygen isotopic compositions. *Deep Sea Research Part I: Oceanographic Research Papers*, **132**: 37–50.

Giovannoni, S.J., Tripp, H.J., Givan, S., Podar, M., Vergin, K.L., Baptista, D., Bibbs, L., Eads, J., Richardson, T.H., Noordewier, M. & Rappé, M.S. 2005. Genome streamlining in a cosmopolitan oceanic bacterium. *Science*, **309**: 1242–1245.

Gray, J.E. 1828. *Spicilegia Zoologica; or original figures and short systematic descriptions of new and unfigured animals*, **Part I**. Treüttel, Würtz, London.

Guennegan, Y. & Rannou, M. 1979. Semi-diurnal rhythmic activity in deep-sea benthic fishes in the Bay of Biscay. *Sarsia*, **64**: 113–116.

Hallberg, E., Nilsson, H.L. & Elofsson, R. 1980. Classification of amphipod compound eyes — the fine structure of the ommatidial units (Crustacea, Amphipoda). *Zoomorphologie*, **94**: 279–306.

Harrison, C. S., Hida, T.S. & Seki, M.P. 1983. Hawaiian seabird feeding ecology. *Wildlife Monographs*, **85**: 1–71.

Havermans, C., Sonet, G., d'Udekem d'Acoz, C., Nagy, Z.T., Martin, P., Brix, S., Riehl, T., Agrawal, S. & Held, C. 2013. Genetic and morphological divergences in the cosmopolitan deep-sea amphipod *Eurythenes gryllus* reveal a diverse abyss and a bipolar species. *PLoS ONE*, **8**: e74218 [https://doi.org/10.1371/journal.pone.0074218].

He, L.S., Zhang, P.W., Huang, J.M., Zhu, F.C., Danchin, A. & Wang, Y. 2018. The enigmatic genome of an obligate ancient *Spiroplasma* symbiont in a hadal holothurian. *Applied and Environmental Microbiology*, **84**: e01965–01917 [https://doi.org/10.1128/AEM.01965-17].

Hessler, R.R., Ingram, C.L., Yayanos, A.A. & Burnett, B.R. 1978. Scavenging amphipods from the floor of the Philippine Trench. *Deep Sea Research*, **25**: 1029–1047.

Hessler, R.R., Isaacs, J.D. & Mills, E.L. 1972. Giant amphipod from the Abyssal Pacific Ocean. *Science*, **175**: 636–637.

Holmes, S.J. 1908. The Amphipoda collected by the U.S. Bureau of Fisheries Steamer "Albatross" off the West Coast of North America,

in 1903 and 1904, with descriptions of a new family and several new genera and species. *Proceedings of the United States National Museum*, **35**: 489–543.

Horton, T. & Thurston, M. 2013. *Hirondellea namarensis* (Crustacea: Amphipoda: Lysianassoidea: Hirondelleidae), a new deep-water scavenger species from the Mid-Atlantic Ridge. *Marine Biology Research*, **9**: 554–562.

Horton, T., Gofas, S., Kroh, A., Poore, G.C., Read, G., Rosenberg, G., Stöhr, S., Bailly, N., Boury-Esnault, N., Brandão, S.N. & Costello, M.J. 2017. Improving nomenclatural consistency: a decade of experience in the World Register of Marine Species. *European Journal of Taxonomy*, **389**: 1–24.

Hua, Q. & Barbetti, M. 2004. Review of tropospheric bomb C-14 data for carbon cycle modeling and age calibration purposes. *Radiocarbon*, **46**: 1273–1298.

Hurley, D.E. 1963. Amphipoda of the family Lysianassidae from the west coast of North and Central America. *Allan Hancock Foundation Publications, Occasional Paper*, **25**: 1–160.

Hutchins, B.T., Schwartz, B.F. & Nowlin, W.H., 2014. Morphological and trophic specialization in a subterranean amphipod assemblage. *Freshwater Biology*, **59**: 2447–2461.

Ingram, C.L. & Hessler, R.R. 1987. Population biology of the deep-sea amphipod *Eurythenes gryllus* inferences from instar analyses. *Deep-Sea Research A*, **34**: 1889–1910.

Jamieson, A.J. 2015. *The hadal zone: Life in the deepest oceans*. Cambridge University Press, Cambridge, UK.

Jamieson, A.J. 2018. A contemporary perspective on hadal science. *Deep Sea Research Part II: Topical Studies in Oceanography*, **155**: 4–10.

Jamieson, A.J. & Stewart, H.A. 2021. Hadal zones of the northwest Pacific Ocean. *Progress in Oceanography*, **190**: 102477 [https://doi.org/10.1016/j.pocean.2020.102477].

Jamieson, A.J. & Vecchione, M. 2020. First *in situ* observation of Cephalopoda at hadal depths (Octopoda: Opisthoteuthidae: *Grimpoteuthis* sp.). *Marine Biology*, **167**: [https://doi.org/10.1007/s00227-020-03701-1].

Jamieson, A.J., Boorman, B. & Jones, D.O.B. 2013a. Deep-sea sampling. In: *Methods for the Study of Marine Benthos* (A. Eleftheriou, ed.), Edn. 4. Wiley-Blackwell, Oxford.

Jamieson, A.J., Brooks, L.S.R., Reid, W.D., Piertney, S.B., Narayanaswamy, B.E. & Linley, T.D. 2019. Microplastics and synthetic particles ingested by deep-sea amphipods in six of the deepest marine ecosystems on Earth. *Royal Society Open Science*, **6**: 180667 [https://doi.org/10.1098/rsos.180667].

Jamieson, A.J., Fujii, T., Solan, M., Matsumoto, A.K., Bagley, P.M. & Priede, I.G. 2009. First findings of decapod crustacea in the hadal zone. *Deep Sea Research Part I: Oceanographic Research Papers*, **56**: 641–647.

Jamieson, A.J., Fujii, T., Mayor, D.J., Solan, M. & Priede, I.G. 2010. Hadal trenches: the ecology of the deepest places on Earth. *Trends in Ecology and Evolution*, **25**: 190–197.

Jamieson, A.J., Kilgallen, N.M., Rowden, A.A., Fujii, T., Horton, T., Lörz, A.N., Kitazawa, K. & Priede, I.G. 2011. Bait-attending fauna of the Kermadec Trench, SW Pacific Ocean: evidence for an ecotone across the abyssal–hadal transition zone. *Deep Sea Research Part I: Oceanographic Research Papers*, **58**: 49–62.

Jamieson, A.J., Lacey, N.C., Lörz, A-N., Rowden, A.A. & Piertney, S.B. 2013b. The supergiant amphipod *Alicella gigantea* (Crustacea: Alicellidae) from hadal depths in the Kermadec Trench, SW Pacific Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, **92**: 107–113.

Jamieson, A.J., Lörz, A.-N., Fujii, T. & Priede, I.G. 2012. In situ observations of trophic behaviour and locomotion of *Princaxelia* amphipods (Crustacea, Pardaliscidae) at hadal depths in four West Pacific Trenches. *Journal of the Marine Biology Association of the United Kingdom,* **91**: 143–150.

Jamieson, A.J., Malkocs, T., Piertney, S.B., Fujii, T. & Zhang, Z. 2017. Bioaccumulation of persistent organic pollutants in the deepest ocean fauna. *Nature Ecology & Evolution*, **1**: [https://doi.org/10.1038/s41559-016-0051].

Jamieson, A.J., Stewart, H.A., Rowden, A.A. & Clark, M.R. 2020. Geomorphology and benthic habitats of the Kermadec Trench, Southwest Pacific Ocean. In: *Seafloor geomorphology as benthic habitat* (P.T. Harris & A.K. Baker, eds.), pp, 949–966. Elsevier, Amsterdam.

Jamieson, A.J., Stewart, H.A., Weston, J.N.J. & Bongiovanni, C. 2022. Hadal fauna of the South Sandwich Trench, Southern Ocean: Baited camera survey from the Five Deeps Expedition. *Deep-Sea Research Part II: Topical Studies in Oceanography,* **94**: 104987 [https://doi.org/10.1016/j.dsr2.2021.104987].

Jażdżewska, A.M. & Mamos, T. 2019. High species richness of Northwest Pacific deep-sea amphipods revealed through DNA barcoding. *Progress in Oceanography*, **178**: 102184 [https://doi.org/10.1016/j.pocean.2019.102184].

Jażdżewska, A.M., Horton, T., Hendrycks, E., Mamos, T., Driskell, A.C., Brix, S. & Arbizu, P.M. 2021. Pandora's box in the deep sea-intraspecific diversity patterns and distribution of two congeneric scavenging amphipods. *Frontiers in Marine Science*, **8**: 750180 [https://doi.org/10.3389/fmars.2021.750180].

Johnsen, S. 2005. The red and the black: bioluminescence and the color of animals in the deep Sea. *Integrative and Comparative Biology*, **45**: 234–246.

Kaiser, M.J. & Moore, P.G. 1999. Obligate marine scavengers: do they exist? *Journal of Natural History*, **33**: 475–481.

Kamenskaya, O.E. 1977. Two new species of ultra-abyssal amphipods from Yap Trench. *Akademia Nauk SSSR*, **108**: 105–114 [in Russian].

Kamenskaya, O.E. 1981. Ultra-abyssal (hadal) amphipods from the trenches of the Pacific Ocean. *P.P. Shirshov Institute of Oceanology Academy of Sciences of the USSR Moscow*, **117218**: 40–44 [in Russian].

Kamenskaya, O.E. 1995. Gammaridean amphipods from hadal trenches of the Pacific Ocean. *Polskie Arhiwum Hydrobiologii*, **42**: 327–334.

Karaman, S.L. 1943. Die unterirdischen Amphipoden Südserbiens. *Srpska Akademya Nauka, Posebna Izdana, 135 (Prirodn'achki i Mathematichki Spici)*, **34**: 161–312.

Kaufmann, R.S. 1994. Structure and function of chemoreceptors in scavenging lysianassoid amphipods. *Journal of Crustacean Biology*, **14**: 54–71.

Kilgallen, N.M. 2014. Three new species of *Hirondellea* (Crustacea, Amphipoda, Hirondelleidae) from hadal depths of the Peru-Chile Trench. *Marine Biology Research*, **11**: 34–48.

Kilgallen, N.M. & Lowry, J.K. 2015. A review of the scopelocheirid amphipods (Crustacea, Amphipoda, Lysianassoidea), with the description of new taxa from Australian waters. *Zoosystematics and Evolution*, **91**: 1–43.

Klages, M., Muyakshin, S., Soltwedel, T. & Arntz, W.E. 2002. Mechanoreception, a possible mechanism for food fall detection in deep-sea scavengers. *Deep Sea Research Part I: Oceanographic Research Papers*, **49**: 143–155.

Kobayashi, H., Hatada, Y., Tsubouchi, T., Nagahama, T. & Takami, H. 2012. The hadal amphipod *Hirondellea gigas* possessing a unique cellulase for digesting wooden debris buried in the deepest seafloor. *PLoS ONE*, **7**: e42727 [https://doi.org/10.1371/journal.pone.0042727].

Kobayashi, H., Shimoshige, H., Nakajima, Y., Arai, W. & Takami, H. 2019. An aluminum shield enables the amphipod *Hirondellea gigas* to inhabit deep-sea environments. *PloS ONE*, **14**: e0206710 [https://doi.org/10.1371/journal.pone.0206710].

Krøyer, H. 1842. Nye nordiske slaegter og arter af amfipodernes orden, henhorende til familien Gammarina. (Forelobigt uddrag af et storre arbejde). *Naturhistorisk Tidsskrift*, Series 1, **4**: 141–166.

Kusube, M., Kyaw, T.S., Tanikawa, K., Chastain, R.A., Hardy, K.M., Cameron, J. & Bartlett, D.H. 2017. *Colwellia marinimaniae* sp. nov., a hyperpiezophilic species isolated from an amphipod within the Challenger Deep, Mariana Trench. *International Journal of Systematic and Evolutionary Microbiology*, **67**: 824–831.

Lacey, N.C., Jamieson, A.J. & Søreide, F. 2013. Successful capture of ultra-deep sea animals from the Puerto Rico Trench. *Sea Technology*, **54**: 19–21.

Lacey, N.C., Mayor, D.J., Linley, T.D. & Jamieson, A.J. 2018. Population structure of the hadal amphipod *Bathycallisoma* (*Scopelocheirus*)

schellenbergi in the Kermadec Trench and New Hebrides Trench, SW Pacific. *Deep Sea Research Part II: Topical Studies in Oceanography*, **155**: 50–60.

Lacey, N.C., Rowden, A.A., Clark, M.R., Kilgallen, N.M., Linley, T., Mayor, D.J. & Jamieson, A.J. 2016. Community structure and diversity of scavenging amphipods from bathyal to hadal depths in three South Pacific Trenches. *Deep Sea Research Part I: Oceanographic Research Papers*, **111**: 121–137.

Lan, Y., Sun, J., Bartlett, D.H., Rouse, G.W., Tabata, H.G. & Qian, P.Y. 2016. The deepest mitochondrial genome sequenced from Mariana Trench *Hirondellea gigas* (Amphipoda). *Mitochondrial DNA Part B*, **1**: 802–803.

Lan, Y., Sun, J., Tian, R., Bartlett, D.H., Li, R., Wong, Y.H., Zhang, W., Qiu, J.W., Xu, T., He, L.S. & Tabata, H.G. 2017. Molecular adaptation in the world's deepest-living animal: Insights from transcriptome sequencing of the hadal amphipod *Hirondellea gigas*. *Molecular Ecology*, **26**(14): 3732–-3743.

Last, K.S., Bailhache, T., Kramer, C., Kyriacou, C.P., Rosato, E. & Olive, P.J. 2009. Tidal, daily, and lunar-day activity cycles in the marine polychaete *Nereis virens*. *Chronobiology International*, **26**: 167–183.

Lauro, F.M., Chastain, R.A., Blankenship, L.E., Yayanos, A.A. & Bartlett, D.H. 2007. The unique 16S rRNA genes of piezophiles reflect both phylogeny and adaptation. *Applied and Environmental Microbiology*, **73**: 838–845.

Leach, W.F. 1814. Crustaceology. *The Edinburgh Encyclopaedia*, **7**: 383–434.

Leduc, D. 2015. One new genus and five new nematode species (Monhysterida, Xyalidae) from Tonga and Kermadec Trenches, Southwest Pacific. *Zootaxa*, **3964**: 501–525.

Leduc, D. & Wilson, J. 2016. Benthimermithid nematode parasites of the amphipod *Hirondellea dubia* in the Kermadec Trench. *Parasitology Research*, **115**: 1675–1682.

Lee, R.F., Hagen, W. & Kattner, G. 2006. Lipid storage in marine zooplankton. *Marine Ecology Progress Series*, **307**: 273–306.

Lemche, H., Hansen, B., Madsen, F.J. Tendal, O.S. & Wolff, T. 1976. Hadal life as analysed from photographs. *Videnskabelige Meddelelser Fra Dansk Naturhistorik Forening*. **139**: 263–336.

Li, J.Y., Song, Z.L., Yan, G.Y. & He, L.S. 2019a. The complete mitochondrial genome of the largest amphipod, *Alicella gigantea*: Insight into its phylogenetic relationships and deep-sea adaptive characters. *International Journal of Biological Macromolecules*, **141**: 570–577.

Li, J.Y., Zeng, C., Yan, G.Y. & He, L.S. 2019b. Characterization of the mitochondrial genome of an ancient amphipod *Halice* sp. MT-2017 (Pardaliscidae) from 10,908 m in the Mariana Trench. *Scientific Reports*, **9**: [https://doi.org/10.1038/s41598-019-38735-z].

Li, W., Wang, F., Jiang, S., Pan, B., Chan, J. and Xu, Q. 2021. The adaptive evolution and gigantism mechanisms of the hadal "supergiant" amphipod *Alicella gigantea*. *Frontiers in Marine Science*, **8**: 743663 [https://doi.org/10.3389/fmars.2021.743663].

Lilljeborg, W. 1865 On the *Lysianassa magellanica* H. Milne Edwards, and on the Crustacea of the suborder Amphipoda and subfamily Lysianassina found on the coast of Sweden and Norway. *Nova Acta Regiae Societatis Scientiarum Upsaliensis*, **61**: 1–38.

Linley, T.D., Stewart, A., McMillan, P., Clark, M., Gerringer, M.E., Drazen, J.C., Fujii, T. & Jamieson, A.J. 2017. 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. *Deep Sea Research Part I: Oceanographic Research Papers*, **121**: 38–53.

Lowry, J.K. & De Broyer, C. 2008. Alicellidae and Valettiopsidae, two new callynophorate families (Crustacea: Amphipoda). *Zootaxa*, **1843**: 57–66.

Lowry, J.K. & Myers, A.A. 2013. A phylogeny and classification of the Senticaudata subord. nov. (Crustacea: Amphipoda). *Zootaxa*, **3610**: 1–80.

Lowry, J.K. & Stoddart, H.E. 1997. Amphipoda Crustacea IV. Families Aristiidae, Cyphocarididae, Endevouridae, Lysianassidae, Scopelocheiridae, Uristidae. *Memoirs of the Hourglass Cruises*, **10**, 1, 148.

Lowry, J.K. & Stoddart, H.E. 2010. The deep-sea scavenging genus *Hirondellea* (Crustacea: Amphipoda: Lysianassoidea: Hirondelleidae fam. nov.) in Australian waters. *Zootaxa*, **2329**: 37–55.

Lowry, J.K. & Stoddart H.E. 2011. The new deep-sea families Cebocaridae fam. nov., Cyclocaridae fam. nov. and Thoriellidae fam. nov. (Crustacea: Amphipoda: Lysianassoidea). *Zootaxa*, **2747**: 53–68.

Lörz, A.N. 2010. Trench treasures: the genus *Princaxelia* (Pardaliscidae, Amphipoda). *Zoologica Baetica*, **21**: 65–84.

Lörz, A.N., Jażdżewska, A.M. & Brandt, A. 2018. A new predator connecting the abyssal with the hadal in the Kuril-Kamchatka Trench, NW Pacific. *PeerJ*, **6**: e4887 [https://doi.org/10.7717%2Fpeerj.4887].

MacDonald, A.G. 1997. Hydrostatic pressure as an environmental factor in life processes. *Comparative Biochemistry and Physiology Part A*, **116**: 291–297.

MacDonald, A.G. & Fraser, P.J. 1999. The transduction of very small hydrostatic pressures. *Comparative Biochemistry and Physiology Part A*, **122**: 13–36.

MacDonald, A.G. & Gilchrist, I. 1980. Effects of hydraulic decompression and compression on deep sea amphipods. *Comparative Biochemistry and Physiology Part A*, **67**: 149–153.

MacDonald, A.G. & Gilchrist, I. 1982. Pressure tolerance of deep-sea amphipods collected at their ambient pressure. *Comparative Biochemistry and Physiology Part A*, **71**: 349–352

Mandt, M.W. 1822. *Observationes in historiam naturalem et anatomiam comparatam in itinere Groenlandico factae.* Dissertation, University of Berlin [https://www.biodiversitylibrary.org/item/96152#page/2/mode/1up].

Mekhanikova, I., 2010. Morphology of mandible and lateralia in six endemic amphipods (Amphipoda, Gammaridea) from Lake Baikal, in relation to feeding. *Crustaceana*, **83**: 865–887.

Milne Edwards, H. 1830. Description des genres Glaucothoe, Sicyonie, Sergeste et Acete, de l'ordre des Crustacés Décapodes. *Annales des Sciences Naturelles*, **19**: 333–352.

Milne Edwards, H. 1848. Sur un crustacé amphipode, remarquable par sa grande taille. *Annales des Sciences Naturelles*, Zoologie, Série 3, **9**: 398.

Narahara-Nakano, Y., Nakano, T. & Tomikawa, K. 2018. Deep-sea amphipod genus *Eurythenes* from Japan, with a description of a new *Eurythenes* species from off Hokkaido (Crustacea: Amphipoda: Lysianassoidea). *Marine Biodiversity*, **48**: 603–620.

Naylor, E. 1996. Crab clockwork: the case for interactive circatidal and circadian oscillators controlling rhythmic locomotor activity of *Carcinus maenas*. *Chronobiology International*, **13**: 153–161.

Nielsen, J.G. 1964. Fishes from depths exceeding 600 meters. *Galathea Report*, **7**: 113–124.

Nyssen, F., Brey, T., Lepoint, G., Bouquegneau, J.M., De Broyer, C. & Dauby, P. 2002. A stable isotope approach to the eastern Weddell Sea trophic web: Focus on benthic amphipods. *Polar Biology*, **25**: 280–287.

Oguri, K., Kawamura, K., Sakaguchi, A., Toyofuku, T., Kasaya, T., Murayama, M., Fujikura, K., Glud, R.N. & Kitazato, H. 2013. Hadal disturbance in the Japan Trench induced by the 2011 Tohoku–Oki Earthquake. *Scientific Reports*, **3**: 1915 [https://doi.org/10.1038/srep01915].

Okada, S., Chen, C., Watanabe, H. K., Isobe, N. & Takai, K. 2022. Unusual bromine enrichment in the gastric mill and setae of the hadal amphipod *Hirondellea gigas*. *PLoS ONE*, **17**: e0272032 [https://doi.org/10.1371/journal.pone.0272032].

Padial, J.M., Miralles, A., De la Riva, I. & Vence, M. 2010. The integrative future of taxonomy. *Frontiers in Zoology*, **7**: 16 [https://doi.org/10.1186/1742-9994-7-16].

Page, T.J., Choy, S.C. & Hughes, J.M. 2005. The taxonomic feedback loop: Symbiosis of morphology and molecules. *Biology Letters*, **1**: 139–142.

Paul, A. Z. 1973. Trapping and recovery of living deep-sea amphipods from the Arctic Ocean floor. *Deep-Sea Research*, **20**: 289–290.

Peng, X., Chen, M., Chen, S., Dasgupta, S., Xu, H., Ta, K., Du, M., Li, J., Guo, Z. & Bai, S. 2018. Microplastics contaminate the deepest part of the world's ocean. *Geochemical Perspectives Letters*, **9**: [https://doi.org/10.7185/geochemlet.1829].

Perrone, F.M., Della Croce, N. & Dell'Anno, A, 2003. Biochemical composition and trophic strategies of the amphipod *Eurythenes gryllus* at hadal depths (Atacama Trench, South Pacific). *Chemistry and Ecology*, **19**: 441–449.

Pirlot, J.M. 1931. Metalanceola chevreuxi genre et espèce nouveaux d'Amphipodes Hypérides. *Bulletin de l'Institut Océanographique* (Monaco), **572**: 1–14.

Pirlot, J.M. 1932. Les amphipodes de l'expédition du Siboga. Deuxième partie: Les amphipodes gammarides. I. Les amphipodes fouisseurs. Phoxocephalidae, Oedicerotidae. *Siboga-Expeditie*, **Monographie 33b**: 57–113.

Pirlot, J.M. 1934. Les amphipodes de l'expédition du Siboga. Deuxième partie. Les amphipodes gammarides II. Les amphipodes de la mer profonde 2. (Hyperiopsidae, Pardaliscidae, Astyridae nov. fam., Tironidae, Calliopiidae, Paramphithoidae, Amathillopsidae nov. fam., Eusiridae, Gammaridae, Aoridae, Photidae, Ampithoidae, Jassidae. *Siboga-Expeditie*, **Monographie 33d**: 167–235.

Platvoet, D., Hou, Z., van der Velde, G. & Li, S.Q. 2006. Presumed statocysts in the cephalon of *Dikerogammarus villosus* (Sowinsky, 1894) (Peracarida, Amphipoda). Amphipod Pilot Species Project (AMPIS) Report 3, *Crustaceana*, **79**: 1123–1127.

Reid, D.G. & Naylor, E. 1990. Entrainment of biomodal circatidal rhythms in the shore crab *Carcinus maenus*. *Journal of Biological Rhythms*, **5**: 333–347.

Reid, W.D., Cuomo, N.J. & Jamieson, A.J. 2018. Geographic and bathymetric comparisons of trace metal concentrations (Cd, Cu, Fe, Mn, and Zn) in deep-sea lysianassoid amphipods from abyssal and hadal depths across the Pacific Ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, **138**: 11–21.

Repeta, D.J. & Gagosian, R.B. 1984. Transformation reactions and recycling of carotenoids and chlorins in the Peru upwelling region (15°S, 75°W). *Geochim Cosmochim Acta*, **48**: 1265–1277.

Rhind, S.M. 2012. Anthropogenic pollutants–an insidious threat to animal health and productivity? *Acta Veterinaria Scandinavica*, **54**: 1–7.

Ritchie, H., Jamieson, A.J. & Piertney, S.B. 2015. Phylogenetic relationships among hadal amphipods of the Superfamily Lysianassoidea: Implications for taxonomy and biogeography. *Deep Sea Research Part I: Oceanographic Research Papers*, **105**: 119–131.

Ritchie, H., Jamieson, A.J. & Piertney, S.B. 2017a. Population genetic structure of two congeneric deep-sea amphipod species from geographically isolated hadal trenches in the Pacific Ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, **119**: 50–57.

Ritchie, H., Jamieson, A.J. & Piertney, S.B. 2017b. Genome size variation in deep-sea amphipods. *Royal Society Open Science*, **4**: 170862 [https://doi.org/10.1098/rsos.170862].

Ritchie, H., Jamieson, A.J. & Piertney, S.B. 2018. Heat-shock protein adaptation in abyssal and hadal amphipods. *Deep Sea Research Part II: Topical Studies in Oceanography*, **155**: 61–69.

Rothschild, L. J. & Mancinelli, R. L. 2001. Life in extreme environments. *Nature*, **409**: 1092–1101.

Sainte-Marie, B. 1992. Foraging of scavenging deep-sea lysianassoid amphipods. In: *Deep-sea food chains in the global carbon cycle* (G.T. Rowe & V. Pariente, eds.), pp. 105–124. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Sars, G.O. 1891. Amphipoda. Part VII. Phoxocephalidae. In: *An account of the Crustacea of Norway, with short descriptions and figures of all the species*, **Vol. 1**: 141–160. Alb. Cammermeyers, Christiania [= Oslo] & Copenhagen.

Sars, G.O. 1895. Amphipoda. In: *An account of the Crustacea of Norway with short descriptions and figures of all the species*, **Vol. 1**: viii + 711 pp., 240 pls, 8 supplementary pls. Alb. Cammermeyers, Christiania [= Oslo] & Copenhagen.

Scarratt, D.J. 1965. Predation on lobsters (*Homarus americanus*) by *Anonyx* sp. (Crustacea, Amphipoda). *Journal of the Fisheries Research Board of Canada*, **22**: 1103–1104.

Schellenberg, A. 1926. Die Gammariden der Deutschen Sudpolar-Expedition 1901-1903. *Deutsche Sudpolar-Expedition 1901-1903,* **18**: 235–414.

Schellenberg A. 1955. Amphipoda. *Reports of the Swedish Deep-Sea Expedition 1947–1948*, 2: Zoologii, **2**: 181–195.

Scudder, S.H. 1882. Nomenclator Zoologicus. An alphabetical list of all generic names that have been employed by naturalists for recent and fossil animals from the earliest times to the close of the year 1879. 1. Supplemental list. II. Universal index. *Bulletin of the United States National Museum*, **no. 19**: i–xxi, 1–376, 1–340.

Senna, A.R. 2009. The giant deep-sea amphipods (Lysianassoidea: Eurytheneidae) from Brazilian waters. *Nauplius*, **17**: 81–96.

Shi, L., Xiao, W., Liu, Z., Pan, B. & Xu, Y. 2018. Diet change of hadal amphipods revealed by fatty acid profile: A close relationship with surface ocean. *Marine Environmental Research*, **142**: 250–256.

Shi, L., Zhang, X., Xiao, W., Pan, B., Liu, Z. & Xu, Y. 2020. Ontogenetic diet change of hadal amphipods in the New Britain Trench revealed by fatty acid biomarker and stable isotope ratio. *Deep Sea Research Part I: Oceanographic Research Papers*, **160**: 103276.

Shulenberger, E. & Barnard, J. L. 1976. Amphipods from an abyssal trap set in the North Pacific Gyre. *Crustaceana*, **31**: 241–258.

Shulenberger, E. & Hessler, R.R. 1974. Scavenging abyssal benthic amphipods trapped under oligotrophic Central North Pacific Gyre waters. *Marine Biology*, **28**: 185–187.

Smith, K.L. & Baldwin, R.J. 1984. Vertical distribution of the necrophagous amphipods, *Eurythenes gryllus,* in the North Pacific: spatial and temporal variation. *Deep-Sea Research*, **31**: 1179–1196.

Spence Bate, C. 1881. On the Penaeidae. *Annals and Magazine of Natural History*, Series 5, **8**: 169–196.

Stebbing, T.R.R. 1888. Report on the Amphipoda collected by H.M.S. Challenger during the years 1873-1876. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76, Zoology*, **29**: 1–1737.

Stebbing, T.R.R. 1899. Revision of Amphipoda (continued). *Annals and Magazine of Natural History,* Series 7, **4**: 205–211.

Stebbing, T.R.R. 1906. Amphipoda, I: Gammaridea. In: *Das Tierrich*, **Vol. 21**. Friedländer und Sohn, Berlin.

Stoddart, H.E. & Lowry, J.K. 2004. The deep-sea lysianassoid genus *Eurythenes* (Crustacea, Amphipoda, Eurytheneidae n. fam.). *Zoosystema*, **26**: 425–468.

Strauss, E. 1926. Das Gammaridenauge. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899*. **Vol. 20**: 1–84.

Sun, R., Yuan, J., Sonke, J.E., Zhang, Y., Zhang, T., Zheng, W., Chen, S., Meng, M., Chen, J., Liu, Y. & Peng, X. 2020. Methylmercury produced in upper oceans accumulates in deep Mariana Trench fauna. *Nature Communications*, **11**: [https://doi.org/10.1038/s41467-020-17045-3].

Swan, J.A., Jamieson, A.J., Linley, T.L. & Yancey, P.Y. 2021. Distribution of Decapoda (Penaeoidea and Oplophoroidea) across the abyssal-hadal transition zone of eleven subduction trenches and additional deep-sea features. *Journal of Crustacean Biology*, **41**: ruaa102 [https://doi.org/10.1093/jcbiol/ruaa102].

Taira, K., Kitagawa, S., Yamashiro, T. & Yanagimoto, D. 2004. Deep and bottom currents in the Challenger Deep, Mariana Trench, measured with super-deep current meters. *Journal of Oceanography*, **60**: 919–926.

Tamburri, M.N. & Barry, J.P. 1999. Adaptations for scavenging by three diverse bathyal species, *Eptatretus stouti, Neptunea amianta* and *Orchomebe obtusus*. *Deep Sea Research Part I: Oceanographic Research Papers*, **46**: 2079–2093.

Taylor, M.L., Gwinnett, C., Robinson, L.F. & Woodall, L.C. 2016. Plastic microfibre ingestion by deep-sea organisms. *Scientific Reports*, **6**: [https://doi.org/10.1038/srep33997].

Thoen, H.H., Johnsen, G. & Berge, J. 2011. Pigmentation and spectral absorbance in the deep-sea arctic amphipods *Eurythenes gryllus* and *Anonyx* sp. *Polar Biology*, **34**: 83–93.

Thurston, M.H. 1979. Scavenging abyssal amphipods from the North-east Atlantic Ocean. *Marine Biology*, **51**: 55–68.

Thurston, M.H., Petrillo, M. & Della Croce, N. 2002. Population structure of the necrophagous amphipod *Eurythenes gryllus* (Amphipoda: Gammaridea) from the Atacama Trench (south-east Pacific Ocean).

Journal of the Marine Biological Association of the United Kingdom, **82**: 205–211.

Tokuda, A.K., Drazen, J.C., Gerringer, M.E., Popp, B.N., Grammatopoulou, E. & Mayor, D.J. 2020. Trophic interactions of megafauna in the Mariana and Kermadec trenches inferred from stable isotope analysis. *Deep Sea Research Part I: Oceanographic Research Papers*, **164**: 103360 [https://doi.org/10.1016/j.dsr.2020.103360].

Van Cauwenberghe, L., Vanreusel, A., Mees, J. & Janssen, C.R. 2013. Microplastic pollution in deep-sea sediments. *Environmental Pollution*, **182**: 495–499.

Vinogradov, M.E. 1956. Giperiidy (Amphipoda - Hyperiidea) zapadnykh rajonov Beringova morja [Hyperiids (Amphipoda - Hyperiidea) of western regions of the Bering Sea]. *Zoologicheskij Zhurnal,* **35**: 194–218 [in Russian].

Vinogradov, M.E. 1957. Giperiidy (Amphipoda - Hyperiidea) severozapadnoj chasti Tikhogo okeana. 1. Triba Hyperiidea Physosomata [Hyperiids of the north-western Pacific Ocean. 1. Tribe Hyperiidea Physosomata]. *Akademija Nauk S.S.S.R., Trudy Instituta Okeanologii*, **20**: 186–227 [in Russian].

Vinogradov, M.E. 1970. New data on Amphipoda Hyperiidea Physosomata of the northwestern Pacific. *Trudy Instituta Okeanologii,* **86**: 382–400 [in Russian].

Vinogradov, M.E. & Vinogradov, G.M. 1993 [Notes about pelagic and benthopelagic gammarids in the Orkney Trench]. *Akademiya Nauk S.S.S.R., Trudy Instituta Okeanologii,* **127**: 129–133 [in Russian].

Wagner, H.J., Kemp, K., Mattheus, U. & Priede, I.G. 2007. Rhythms at the bottom of the deep sea: Cyclic current flow changes and melatonin patterns in two species of demersal fish. *Deep Sea Research Part I: Oceanographic Research Papers*, **54**: 1944–1956.

Wang, N., Shen, C., Sun, W., Ding, P., Zhu, S., Yi, W., Yu, Z., Sha, Z., Mi, M., He, L. & Fang, J. 2019. Penetration of bomb 14C into the deepest ocean trench. *Geophysical Research Letters*, **46**: 5413–5419.

Weston, J.N.J. & Jamieson, A.J. 2022. The multi-oceanic distribution of the hadal amphipod, *Hirondellea dubia* Dahl, 1959 (Crustacea, Amphipoda). *Frontiers in Marine Science*. **9**: 824640 [https://doi.org/10.3389/fmars.2022.824640].

Weston, J.N.J., Carrillo-Barragan, P., Linley, T.D., Reid, W.D. & Jamieson, A.J. 2020. New species of *Eurythenes* from hadal depths of the Mariana Trench, Pacific Ocean (Crustacea: Amphipoda). *Zootaxa*, **4748**: 163–181.

Weston, J.N.J., Espinosa-Leal, L., Wainwright, J.A., Stewart, E.C., González, C.E., Linley, T.D., Reid, W.D., Hidalgo, P., Oliva, M.E., Ulloa, O. & Wenzhöfer, F. 2021a. *Eurythenes atacamensis* sp. nov. (Crustacea: Amphipoda) exhibits ontogenetic vertical stratification across abyssal and hadal depths in the Atacama Trench, eastern South Pacific Ocean. *Marine Biodiversity*, **51** [https:// doi.org/10.1007/s12526-021-01182-z].

Weston, J.N.J., Jensen, E.L., Hasoon, M.S.R., Kitson, J.J.N., Stewart, H.A. & Jamieson, A.J. 2022. Barriers to gene flow in the deepest ocean ecosystem: Evidence from global population genomics of a cosmopolitan amphipod. *Science Advances*, **8**: eabo6672 [https:// doi.org/10.1126/sciadv.abo6672].

Weston, J.N.J., Peart, R.A., Stewart, H.A., Ritchie, H., Piertney, S.B., Linley, T.D. & Jamieson, A.J. 2021b. Scavenging amphipods from the Wallaby-Zenith Fracture Zone: Extending the hadal paradigm beyond subduction trenches. *Marine Biology*, **168**: [https://doi.org/10.1007/s00227-020-03798-4].

Wilson, J.P., Schnabel, K.E., Rowden, A.A., Peart, R.A., Kitazato, H. & Ryan, K.G. 2018. Bait-attending amphipods of the Tonga Trench and depth-stratified population structure in the scavenging amphipod *Hirondellea dubia* Dahl, 1959. *PeerJ*, **6**: e5994 [https://doi.org/10.7717/peerj.5994].

Wolff, T. 1960. The hadal community, an introduction. *Deep Sea Research,* **6**: 95–124.

Wolff, T. 1970. The concept of the hadal or ultra-abyssal fauna. *Deep Sea Research*, **17**: 983–1003.

World Register of Marine Species (WoRMS Editorial Board). 2023. [https://www.marinespecies.org].

Yancey, P.H. 2020. Cellular responses in marine animals to hydrostatic pressure. *Journal of Experimental Zoology Part A*, **333**: 398–420.

Yancey, P.H., Fyfe-Johnson, A.L., Kelly, R.H., Walker, V.P. & Auñón, M.T. 2001. Trimethylamine oxide counteracts effects of hydrostatic pressure on proteins of deep-sea teleosts. *Journal of Experimental Zoology*, **289**: 172–176.

Yancey, P.H., Gerringer, M.E., Drazen, J.C., Rowden, A.A. & Jamieson, A.J. 2014. Marine fish may be biochemically constrained from inhabiting the deepest ocean depths. *Proceedings of the National Academy of Sciences of the United States of America*, **111**: 4461–4465.

Yayanos, A.A. 1978. Recovery and maintenance of live amphipods at a pressure of 508 bars from an ocean depth of 5700 metres. *Science*, **200**: 1056–1059.

Yayanos, A.A. 1981. Reversible inactivation of deep-sea amphipods (*Paralicella caperesa*) by a decompression from 601 bars to atmospheric pressure. *Comparative Biochemistry and Physiology Part A*, **69**: 563–565.

Yayanos, A.A. 1986. Evolutional and ecological implications of the properties of deep-sea barophilic bacteria. *Proceedings of the National Academy of Sciences of the United States of America*, **83**: 9542–9546.

Yayanos, A.A. 2009. Recovery of live amphipods at over 102 mpa from the Challenger Deep. *Marine Technology Society Journal*, **43**: 132–136.

Yayanos, A.A. & Nevenzel, J.C. 1978. Rising-particle hypothesis: Rapid ascent of matter from the deep ocean. *Naturwissenschaften*, **65**: 255–256.

Yayanos, A.A., Dietz, A.S. & Van Boxtel, R. 1981. Obligately barophilic bacterium from the Mariana Trench. *Proceedings of the National Academy of Sciences of the United States of America*, **78**: 5212–5215.

Zhang, W., Tian, R.M., Sun, J., Bougouffa, S., Ding, W., Cai, L., Lan, Y., Tong, H., Li, Y., Jamieson, A.J. & Bajic, V.B. 2018. Genome reduction in *Psychromonas* species within the gut of an amphipod from the ocean's deepest point. *Msystems*, **3**: e00009–18 [https:// doi.org/10.1128/mSystems.00009-18].

Zhang, W., Watanabe, H.K., Ding, W., Lan, Y., Tian, R.M., Sun, J., Chen, C., Cai, L., Li, Y., Oguri, K. & Toyofuku, T. 2019. Gut microbial divergence between two populations of the hadal amphipod *Hirondellea gigas*. *Applied and Environmental Microbiology*, **85**: e02032–18 [https://doi.org/10.1128/AEM.02032-18].