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ORIGINAL ARTICLE

Hydrozoans, scyphozoans, larvaceans and ctenophores observed *in situ* at hadal depths

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Hydrozoa, Scyphozoa, Larvacea (Appendicularia) and Ctenophora are not typically associated with hadal communities. Here, we report observations of these groups based on 136 benthic camera lander deployments that spanned all five oceans, encompassing 14 deep sites, culminating in > 1000 h of video in the near-bottom waters between 5000 and 10 925 m. Of the Hydrozoa, trachymedusae had a maximum depth of 9066 m in the Mariana Trench, narcomedusae were recorded to a maximum depth of 7220 m in the San Cristobal Trench and a single siphonophore was seen at 7888 m in the Mariana Trench. Scyphozoans were seen as deep as 6898 m in the New Hebrides Trench. The deepest ctenophore was seen at 6037 m in the Kermadec Trench. Larvaceans were seen in the Agulhas Fracture Zone and the Puerto Rico, Kermadec, South Shetland and Java trenches, with the deepest being 7176 m in the Java Trench. None of these groups were seen in the deep Arctic or Antarctic deeper than 6000 m. Narcomedusae, siphonophorae, Scyphozoa and Ctenophora appear very rare at hadal depths, while the larvaceans and trachymedusae appear to be relatively conspicuous in the benthopelagic at hadal depths.

KEYWORDS: jellyfish; trachymedusae; narcomedusae; siphonophorae; Appendicularia; comb jellies; gelatinous zooplankton; deep sea; hadal zone

INTRODUCTION

Gelatinous animals are important components of the marine community typically associated with coastal and surface waters (Boero, 2013; Gibbons and Richardson, 2013) and noted for their effects on carbon cycling in the underlying, deeper, waters (Condon *et al.*, 2011; Sweetman and Chapman, 2011; Lebrato *et al.*, 2012). Cnidarian medusae (jellyfish), Ctenophora (comb jellies) and Appendicularia (larvaceans) are important components of the deep sea community below the euphotic zone (Herring, 2002; Haddock, 2004; Robison *et al.*, 2005). These taxonomic groups are often associated with deep pelagic environments with diverse and often cryptic speciation spanning the bathyal (200–3000 m) and abyssal (3000–6000 m) zones (Haddock and Case, 1999; Collins, 2002; Hopcroft, 2005; Matsumoto *et al.*, 2020). They are not, however, often associated with the hadal environment (6000 to ~11 000 m), in part due to a limited amount of sampling relative to the shallower biozones (Jamieson, 2015, 2018).

The hadal zone, representing the deepest 45% of the total ocean range, provides the opportunity to establish the true depth limits of many major taxa (e.g. Yancey *et al.*, 2014; Jamieson and Vecchione, 2020). However, despite a renaissance in scientific exploration at hadal depths, contemporary work tends to be benthic-focused (Jamieson, 2018). While the hydrography and environmental characteristics of the hadopelagic zone are relatively known (Johnson, 1998; Taira *et al.*, 2004, 2005), biological sampling of the hadopelagic has typically been restricted to microbial studies (Eloe *et al.*, 2011; Nunoura *et al.*, 2015; Tarn *et al.*, 2016). There are only a few examples of vertical plankton hauls from the hadopelagic zone, and these date back to the 1950s and 1960s (Vinogradov 1962).

This dearth of hadopelagic exploration, and limited sampling of the benthopelagic, means that there is very little to currently underpin our understanding of the true vertical distribution of key gelatinous groups such as the trachymedusae, narcomedusae, siphonophorae, scyphozoans, larvaceans and ctenophores, beyond that of the collections of Soviet *Vityaz* and Danish *Galathea* expeditions from the 1950s to 1970s. Furthermore, gelatinous animals are easily damaged and difficult to maintain sample quality during collection and in the preservation process (Hopcroft, 2005). Hi-tech imaging and collection technology for pelagic species (e.g. Robison *et al.*, 2017; Sherlock *et al.*, 2017) have yet to be operated at hadal depths.

On reviewing the *Galathea* and *Vityaz* sample records, Beliaev (Beliaev, 1989) reported on hydroid polyps having been found in several hadal trenches. Among the deepest was *Halisiphonia (galathea) megalotheca* Allman

1888 from 8210 to 8300 m in the Kermadec Trench (SW Pacific; Kramp, 1956), from 8185 to 8400 m in the Kuril-Kamchatka Trench (NW Pacific) and 8950 to 9020 m in the Tonga Trench (SW Pacific). Other polyps found included *Lytocarpia (Aglaophenia) tenuissima* (Bale, 1914) from ~6500 in the Kermadec Trench and *Aglaophenia* sp. from ~7000 m in the Java Trench (Indian Ocean).

What was thought to be very large single hydroid polyps from the genus *Branchiocerianthus* Mark, 1898, was also found from depths between 6000 and 7000 m in the Pacific Ocean. Furthermore, images of giant hydroids, presumed to be *B. imperator* (Allman, 1885), were obtained in the New Hebrides Trench (SW Pacific) from 6758 to 6776 m (Lemche *et al.*, 1976) and the Peru-Chile Trench (SE Pacific) at 6260 m, albeit the latter misidentified at the time by Menzies *et al.* (Menzies *et al.*, 1973). Beliaev (Beliaev, 1989) concluded that hydroid polyps at hadal depths were very rare, low in diversity and are not characteristic of the hadal community. The only other mention of hadal hydroids is an anecdotal observation of potential hydroids on a rock at 7561 m in the Kermadec Trench (Jamieson *et al.*, 2011).

The only recorded sample of a hadal hydromedusae sampled from hadal depths was obtained by a closing plankton net between 6800 and 8700 m in the Kuril-Kamchatka Trench. This specimen was a new species of rhopalonematid trachymedusae, *Pectis (Voragonema) profundicola* (Naumov, 1971).

Historically, there were *in situ* observations made of hydromedusae; Lemche *et al.* (Lemche *et al.*, 1976) reported 17 sightings of trachymedusae out of 4000 images spanning the Palau, New Britain and New Hebrides trenches between 6758 and 8260 m deep. The most common, that were thought to be *Crossota cf. alba* Bigelow, 1913 (Rhopalonematidae), were photographed 12 times in the Palau Trench (NW Pacific) at a depth of 8021–8042 m. Within a single photo, they also reported an individual Anthomedusa (Anthoathecata) and a Leptomedusa (Leptothecata) of unknown species from the New Britain Trench between 8258 and 8260 m. These individuals were just 8 and 5 mm in diameter, respectively.

Within the Scyphozoa, scyphopolyps thought to belong to *Nausithoe (Stephanoscyphus) simplex* Kirkpatrick 1890 (Coronatae incertae sedis) were noted in many trenches during the *Vityaz* expeditions, ‘to as deep as 10 000 m’, with no other details provided except that they were thought to probably represent a number of species (Beliaev, 1989). In addition to these scyphopolyp findings, Lemche *et al.* (Lemche *et al.*, 1976) reported scyphomedusae of the Ulmaridae family from the Bougainville Trench (SW Pacific) between 7847 and 8662 m deep. More recently, nine ulmarid jellyfish,

possibly of the subfamily Poralinae, were observed by submersible in the New Britain Trench between 7984 and 8228 m (Gallo *et al.*, 2015). It is worth noting that the New Britain and Bougainville trenches are a continuous hadal environment without abyssal (<6000 m depth) partitions; thus, the two sightings of ulmarid scyphomedusae and the Anthoathecata and Leptothecata were essentially from the same hadal habitat at similar depths.

Other cnidarians, such as the hydrozoan siphonophorae (Subclass: Hydroidolina), have never been reported from hadal depths. Of the subclass Trachylinae, no species from the orders Actinuida or Limmomedusae have been reported from hadal depths either (with the latter being primarily a fresh water group), only the single image of Anthoathecata and Leptothecata mentioned above (Lemche *et al.*, 1976). Likewise, no findings or observation of narcomedusae have ever been made at hadal depths.

Within the Appendicularia (larvaceans), there were no reports of any specimens being taken or observed at hadal depths. However, analysis of gut contents taken from hadal amphipods in the Tonga Trench revealed Urochordata DNA including the larvacean *Oikopleura* sp. (Blankenship and Levin, 2007). However, whether the Urochordata sources were from hadal-dwelling salps, larvaceans or tunicates, or as carrion from the overlying waters could not be determined as they are known to sink to much greater depths than their depth ranges in life (Robison *et al.*, 2005).

To date, there has only been one report of the Ctenophora (comb jellies) phylum at hadal depths published in the literature; two tentaculate ctenophores with an affinity to the *Aulacoctena* genus were observed 7217 m in the Ryukyu Trench (NW Pacific; Lindsay and Miyake, 2007). Beliaev (Beliaev, 1989) stated that their apparent absence from depths greater than 6000 m was not unexpected as they are ‘really incapable of penetrating these depths’.

This study capitalizes on 13 years of deep sea baited camera lander deployments, performed in 12 hadal trenches and other deep geomorphological features. While no one expedition has ever produced a solid assessment of Cnidaria, Ctenophora or larvaceans at hadal depths, the combined incidental recordings provide, for the first time, a bathymetric and geographic overview of the true vertical zonation of often overlooked taxonomic groups at these great depths.

METHOD

Observations were made in all of the five ocean basins: The Atlantic, Arctic, Indian, Pacific and Southern (Fig. 1). This study pulls from 455 camera and trap lander deployments between the years 2007 and 2020 from

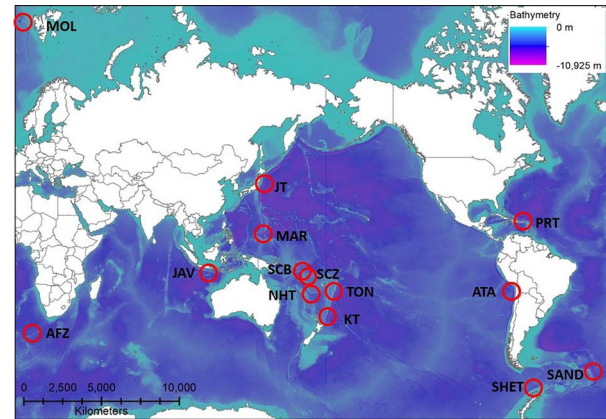


Fig. 1. Sampling locations were AFZ—Agulhas Fracture Zone, ATA—Atacama Trench, JAV—Java Trench, KT—Kermadec Trench, MAR—Mariana Trench, MOL—Molloy Hole, NHT—New Hebrides Trench, PRT—Puerto Rico Trench, SAND—South Sandwich Trench, SCB—San Cristobal Trench, SCZ—Santa Cruz Trench, SHET—South Shetland Trench and TON—Tonga Trench.

depths of 750 to 10 925 m. Of these, 369 included *in situ* filming, either by video or still photography. Of these 369 deployments, 226 were from depths exceeding 5000 m. The shallow depth cutoff of 5000 m was chosen over the true hadal boundary of 6000 m, to provide some contextualization with more common abyssal and bathyal studies. This archive of 226 data sets was assessed for whether gelatinous organisms would be visible. Ninety deployments were discarded on the grounds of awkward orientation on the seafloor (images obscured by facing steep slope, large boulders or obstructions, camera focus issues, or very short bottom time of <60 min). The remaining 136 deployments were assessed for the presence of gelatinous zooplankton within the field of view, and their time after lander touchdown was noted.

Due to the diversity of landers and camera orientations used, this study does not provide quantitative assessments of population density, neither can it provide any insight into seasonal patterns. Therefore, the focus is on the presence of taxonomic groups at depth and not necessarily evidence of absence. To provide some indicative impression of density, the number of individuals per hour of recording is reported for some of the more abundant findings. This should not be taken as absolute density as there are currently no commercially available hadal-rated current meters and therefore the volume of water surveyed in the each deployment is unknown. However, based on tracking drifting animals and resuspended sediment, it can be assumed that the current speeds across these data sets are extremely low. The camera orientation throughout the data sets ranged from horizontal and vertical imaging, 1 and 2 m vertical imaging, time-lapse and

Table I: Summary of deployments within each ocean at each location including depth range, number of deployments and camera orientation where H = Horizontal, V1 = vertical 1 m above bottom and V2 = vertical 2 m above bottom, in parentheses is the number of each

Ocean	Trench	Depth range (m)	No. of lander deployments	Camera orientation
Arctic	Molloy Hole	5547–5591	3	H
Indian	Java Trench	5760–7176	7	H
North Atlantic	Puerto Rico Trench	5046–8380	11	H
South Atlantic	Agulhas Fracture Zone	5493	1	H
North Pacific	Japan Trench	6945–7703	2	V1
	Mariana Trench	5044–10 925	52	V2 (3)/H (49)
South Pacific	Atacama Trench	5329–8074	17	V1 (4)/H (13)
	Kermadec Trench	5046–9005	19	V2 (9)/H (10)
	New Hebrides Trench	5215–6948	6	V2
	San Cristobal Trench	5677–7220	3	V2 (1)/H (2)
	Santa Cruz Trench	5906–7431	2	V2/H
	Tonga Trench	6793–10 823	7	H
Southern	South Sandwich Trench	6044–8266	5	H
	South Shetland Trench	5200	1	H

For more detail, see Supplemental Table S1.

continuous video, and time-lapsed digital still imaging. Details of the camera orientation and settings (including month and year) are given in Supplemental Table S1 but are summarized in Table I. The data set totaled over 1000 h of video and time lapse.

Taxonomic identification was made primarily to order level within the Cnidarian classes of Hydrozoa and Scyphozoa, and the Ctenophora phylum, with some putative identifications to genus level following consultation with experts at the Monterey Bay Aquarium Research Institute (US; S. Haddock, G. Matsumoto, R. Sherlock, personal communication).

In the Arctic Ocean, three deployments were made between 5547 and 5591 m in the Molloy Hole. In the Indian Ocean, seven deployments were made in the Java Trench between 5760 and 7176 m. In the North Atlantic, 13 deployments were included from the Puerto Rico Trench between 5046 and 8380 m, whereas in the South Atlantic one deployment was made at 5493 m in the Agulhas Fracture Zone. The greatest amount of data came from the North and South Pacific. In the North Pacific, there were 2 deployments from the Japan Trench (6945 and 7703 m) and 52 from the Mariana Trench (5044–10 925 m). In the Southeast Pacific, 17 deployments were from the Atacama Trench (5329–8074 m), whereas in the southwest Pacific data were included from the Kermadec (5046–9005 m, $n=20$), New Hebrides (5215–6948 m, $n=10$), San Cristobal (5677–7220 m, $n=4$), Santa Cruz (5906 and 7431 m) and Tonga trenches (6793–10 823 m, $n=7$). In the Southern Ocean, six deployments were included from the South Sandwich Trench (6044–8266 m) and one from the South Shetland Trench (5200 m).

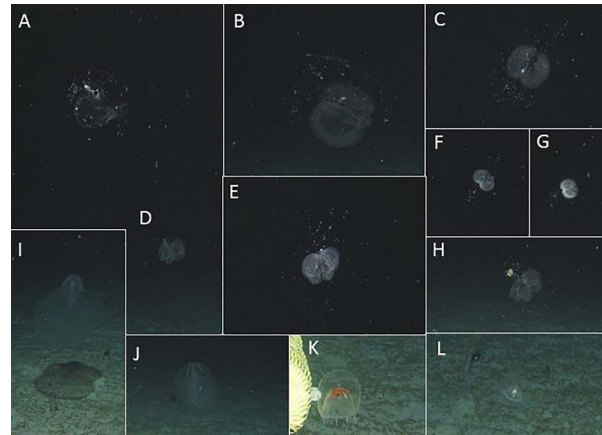


Fig. 2. South Shetland Trench at 5200 m. (A–H) Larvaceans (where B and C are possibly *Oikopleura*), (I and J) ctenophores, (K) Leptothecata and (L) trachymedusae.

RESULTS

Polar regions

In the polar regions, hydrozoans, scyphozoans, larvaceans and ctenophores were not recorded in the Molloy Hole in the Arctic or in the South Sandwich Trench. However, at the 5200 m site in the South Shetland Trench, 485 larvaceans were observed over a period of 24:15 (hh:mm) of 1-min time-lapse still images (24% of 1455 images; Fig. 2A–H). There appeared to be two morphotypes of larvacean and potentially 18 seemingly discarded houses. The encounter frequency of the larvaceans here was 22 Ind.h⁻¹ at 1-min time-lapse interval.

The first type, Morphotype 1, potentially *Fritillaria*, is characterized by a coarse meshed outer filter or ‘house’ with a slightly more opaque two-part bulbous inner filter

that occupies about 50% of the internal volume of the house (Fig. 2B and C). Morphotype 2, resembling *Oikopleura*, has a similar outer filter but has a much smaller and more opaque inner filter, often giving the appearance of being in four segments (Fig. 2D–H).

In addition, two lobate ctenophores were also observed at this site (Fig. 2I and J) as were five individual trachymedusa, four of which were small and probably Rhopalonematidae and the other was of the Leptothecata order, potentially *Chromatonema* sp. (Fig. 2K and L).

Atlantic Ocean

In the Atlantic Ocean at 5493 in the Agulhas Fracture Zone, a similarly high frequency of larvaceans was observed. Over 7:49 (hh.mm), 165 individual larvaceans were observed on a continuous recording horizontal video; 25% encounter of 1 minute sequences. This equates to ~ 21 Ind.h⁻¹. Of these 165 individuals, 46 could have been empty houses. They comprised three putative morphotypes, with the same two morphotypes as in the South Shetland Trench, plus a third, Morphotype 3, that had a much smaller inner filter than in Morphotype 1 and Morphotype 2 and much more opaque (Fig. 3A and B). Also, nine trachymedusae, belonging to the Rhopalonematidae family, were observed (Fig. 3F–H).

In the North Atlantic, in the Puerto Rico Trench, 10 larvaceans were seen during 12:17 (hh.mm) of continuous filming at 5360 m. These larvaceans were much smaller than in the Agulhas Fracture Zone or South Shetland Trench and often too small and/or distant from the camera to accurately assign a morphotype; therefore, the true number may be much higher. The larvacean morphology was very cryptic as this population appeared extremely fragile and very transparent. Despite there being no sightings of larvaceans at the slightly deeper 5880 m site, the next deepest site, 6356 m, recorded 18 larvaceans during 4:50 (hh.mm) of continuous filming. These two sets of observations equate to 0.8 and 4.2 Ind.h⁻¹. Trachymedusae belonging to the Rhopalonematidae family were observed twice at 5360 m and once at 6356 m. No other cnidarians or larvaceans were observed in the eight other deployments deeper than 6356 m in this trench.

Indian Ocean

No cnidarians or ctenophores were observed between the shallowest (5760 m) and the deepest (7176 m) deployments. However, relatively large larvaceans were seen in six of the seven deployments, with the exception of the 6146 m site. However, abundance was low. Only one observation at each deployment from 6439, 6737 and 7168 m, three at 5760 and 7176 m and five at 6957 m;

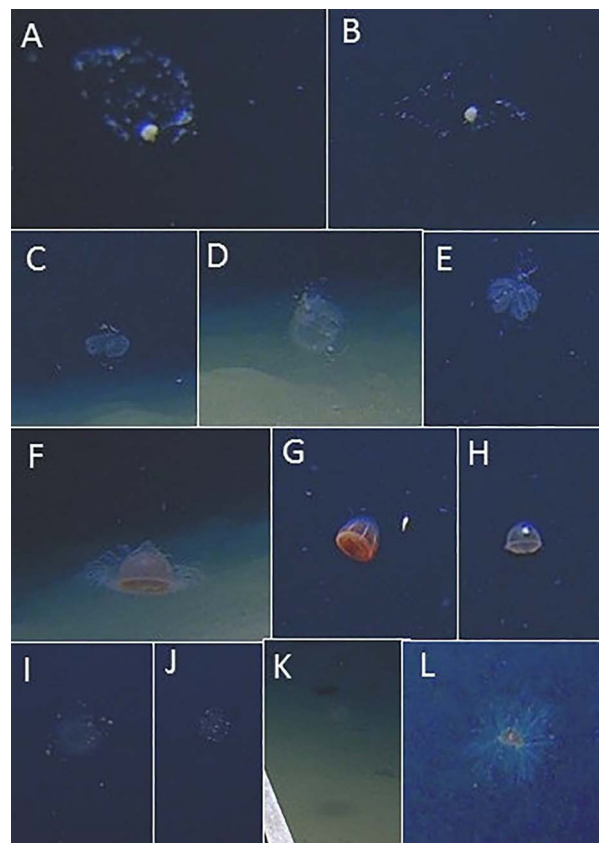


Fig. 3. Agulhas Fracture Zone (South Atlantic) larvaceans at 5493 m (A–E) and trachymedusae (F–H). Puerto Rico Trench larvaceans (I–K) and a rhopalonematid trachymedusa from 6356 m.

therefore, encounter frequencies were 0.1, 0.3, 0.3, 0.4, 0.5 and 1.0 Ind.h⁻¹, respectively. The larvacean comprised the three main morphotypes mentioned above: Morphotype 1 that were likely *Fritillaria* (Fig. 4A and B), Morphotype 2 (Fig. 4C) and Morphotype 3 that were possibly *Oikopleura* (Fig. 4D and E), and occasional instances where the outer filter or house may have been unoccupied (Fig. 4F).

South Pacific Ocean

No larvaceans were recorded in any of the 17 deployments in the Atacama trench; however, single rhopalonematid trachymedusae were seen at 5329, 6520 and 8052 and three at 7204 m (Fig. 5A and B). This equates to a frequency of 0.1, 0.1, 0.1 and 0.2 Ind.h⁻¹. A single lobate ctenophore was also recorded at 5563 m (Fig. 5C).

In the New Hebrides Trench, none of the target groups were observed at either 5215, 5311 or 5344 m; however, at 6082 m, 6397 and 6898 m, 1, 3 and 22 cnidarians were seen, respectively. The trachymedusae *Crossota* sp. was seen once at 6082 m, three times at 6397 m and five times

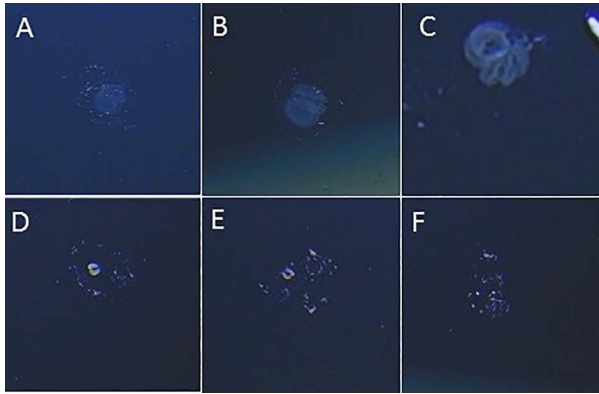


Fig. 4. Larvaceans of the Java Trench, East Indian Ocean between 5760 and 7176 m. (A, B) Morphotype 1 (*Fritillaria?*), (C) Morphotype 2 and (D, E) (and possibly F) Morphotype 3 (*Oikopleura?*).

at 6898 m (Fig. 5D), and the remaining 17 cnidarians at 6989 m were trachymedusae, but unidentified due to being between 2 and 3 cm in diameter and very close to the seafloor. Two individual scyphozoans, tentatively identified as *Poralia* sp. (Family: Ulmaridae), were seen at 6898 m (Fig. 5E), as was the narcomedusa cf. *Sigiweddellia* sp. (Fig. 5F).

In the San Cristobal Trench, 4 rhopalonematid trachymedusae, cf. *Crossota* sp. (Fig. 5G) and 4 narcomedusae were seen at 6515 m (Fig. 5H). Another six medusae, too small to confidently identify, were also observed but appeared closer to trachymedusae than narcomedusae. This conclusion was based on swimming behavior as all trachymedusae observed in this study held a constant altitude above the seafloor and a stable, upright body orientation, whereas the narcomedusae often tumble rather than glide through the water. At 7220 m, there was one rhopalonematid trachymedusa and two narcomedusae (Fig. 5I). None of the target groups were seen at the shallowest deployment at 6013 m.

No cnidarians, ctenophores or larvaceans were seen at either 5906 or 7431 m in the neighboring Santa Cruz Trench. Similarly, in the Tonga Trench, no representatives of these groups were seen in any of the seven deployments between 6793 and 10 823 m, which collectively totaled 43 h of footage.

The Kermadec Trench comprised the second largest dataset with 19 deployments totaling over 176 h of observations. The most numerous group was the larvaceans assigned to Morphotype 1. At 5046 m, 27 individuals were seen over 11:43 (hh.mm) or 2.3 Ind.h⁻¹, with another one seen at 5075 m (0.1 Ind.h⁻¹). While none were seen in the next five deeper deployments (5100–5295 m), they were observed in five of the next six deepest deployments (5460–6068 m). Two individuals were seen at 5460, 5880 and 6068 m (0.1 Ind.h⁻¹ each), 10 were

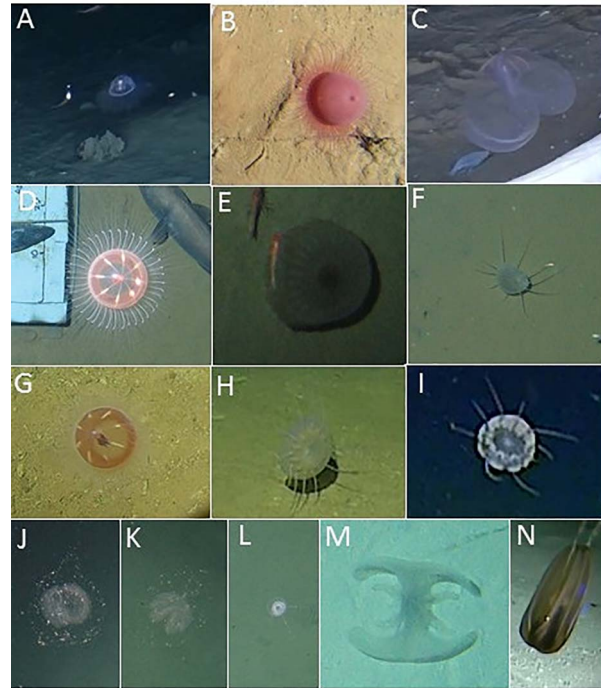


Fig. 5. Cnidarians, ctenophores and larvaceans from the South Pacific. (A, B) Trachymedusae, (C) Ctenophore from the Atacama Trench, (D) trachymedusae, (E) Scyphozoa (*Poralia* sp.), (F) narcomedusae from the New Hebrides Trench, (G) trachymedusa and (H, I) narcomedusae from the San Cristobal Trench, (J–L) two larvaceans, one narcomedusae and two ctenophores from the Kermadec Trench (6037 and 5153 m, respectively).

seen at 5646 m (1.0 Ind.h⁻¹) and 7 were seen at 6037 m (0.4 Ind.h⁻¹) (Fig. 5J–L).

Sightings of trachymedusae and narcomedusae in the Kermadec Trench were infrequent and sporadic with just two trachymedusae seen at 5100 and four at 6037 m (0.1 and 0.2 Ind.h⁻¹, respectively); all were red in color and small in size, <50 mm diameter. A single narcomedusa was seen at 5100 m (Fig. 5L). No scyphozoans were seen throughout. Two ctenophores were seen, one unidentified ctenophore at 5135 m (Fig. 5N) and a lobate ctenophore at 6037 m (Fig. 5M).

North Pacific Ocean

Of the two deployments in the Japan Trench, one single Trachymedusa, a small deep red species, drifted past the camera approximately 10 cm above the seafloor at 6945 m deep.

Of the 52 deployments in the Mariana Trench, covering over 300 h of observations, only two narcomedusae were seen, both at 6777 m (Fig. 6A and B). At 7888 m, what is thought to be the lower half of a siphonophore, possibly Calycophorae, was observed drifting past the

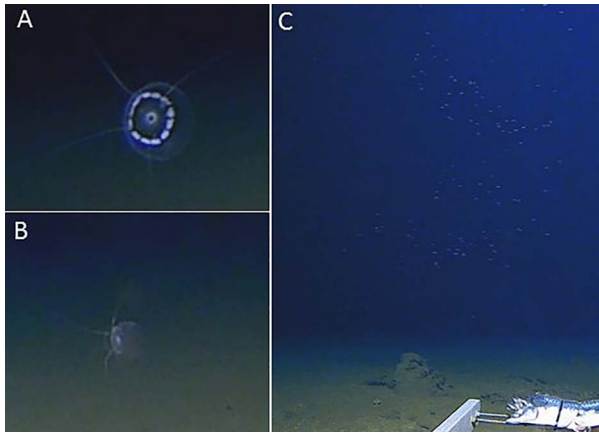


Fig. 6. (A, B) Narcomedusae at 6777 m in the Mariana Trench and (C) the near-helical formation of the trailing siphosome of siphonophore.

camera. It appeared to be a siphonophore with fully deployed ‘fishing net’ (Fig. 6C). Approximately 115 zooids on the siphosome were recorded drifting past the camera in unison in a near helical formation with the extremely fragile tentacles and tentilla trailing. The nectosome was not visible in the field of view, therefore making identification beyond a siphonophorae difficult to speculate.

The most abundant of the target groups observed in the Mariana Trench was the rhopalonematid trachymedusa *Crossota* sp. (Fig. 7). It had a depth range of 6495–9066 m. There were 37 deployments between these two depths of which they were observed in 13 (35%). Single individuals were seen in five of these sites (6495, 7012, 7440, 7654 and 8143 m), two in two sites (7037 and 8007 m), three in three sites (7888, 8078 and 8232 m), four in one site (6777 m), six in one site (8186 m) and nine at the deepest depth they were observed, 9066 m. Therefore, encounter frequencies ranged from $<0.1 \text{ Ind.h}^{-1}$ at $<8186 \text{ m}$, to 1.2 and 1.5 Ind.h^{-1} at 8186 and 9066 m, respectively. No *Crossota* sp. was seen in the shallowest 13 deployments (5044–6469 m) nor in the deepest 8 (10 545–10 925 m) (Fig. 8).

The *Crossota* sp. was typically observed drifting motionless in the current at an altitude of $<50 \text{ cm}$, on occasional up to 1 m. As they traversed the seafloor, they did so with all tentacles pointed upward and outward (e.g. Fig. 7F and G). On one occasion, at 8186 m, an individual descended close to the seafloor, repositioning its tentacles to point down and briefly making contact with the seafloor before rapidly ascending back into the overlying water at $\sim 50 \text{ cm}$ altitude (Fig. 7H).

DISCUSSION

The objective of this study was to revisit a large *in situ* observational dataset, derived from autonomous landers

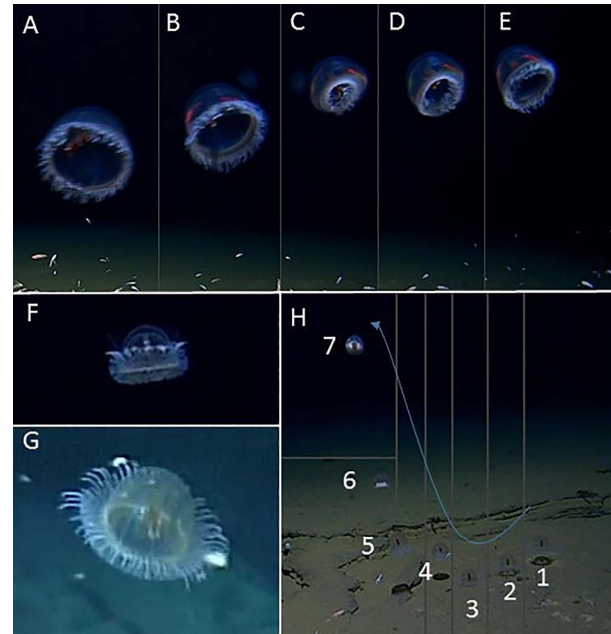


Fig. 7. The trachymedusa *Crossota* sp. from the Mariana Trench. (A–E) Close-up series of images of individual swimming passed the camera at 9066 m, each image is $\sim 1.5 \text{ s}$ apart. (F, G) The typical swimming position with tentacles pointed up and out. (H) A potential feeding event illustrated as a collage of the same event with image 1–7 being $\sim 1 \text{ s}$ apart, where 1–2 are descending to seafloor and repositioning tentacles down to make contact at 3, before ascending again in 4–7. Blue arrow indicates travel direction.

at hadal depths, to focus on the maximum depths of several free-swimming gelatinous deep sea taxa. An important point is that the absence of any of these groups from this study at any depth does not unequivocally represent the absence from hadal depths as the data explored here are incidental encounters confined to within 1–2 m of the seafloor and lack seasonality in observations at each site. What it does do, however, is put various taxa at depths and locations often not previously known and therefore can be used to infer, in the case of the more abundant taxa, the true maximum depth limits of some of these important faunal groups, and whether they are likely to be significant members of the hadal community. This study adds 31 new records from $>5000 \text{ m}$ to the existing 17 records at hadal depths, an increase of 282% (Table II).

Of the six main target taxa, ctenophores were only seen once at hadal depths and at just 6037 m in the Kermadec Trench (SW Pacific). This suggests, as Beliaev (Beliaev, 1989) commented, that the ctenophores are somewhat rare in the hadal zone (e.g. Lindsay and Miyake, 2007). Likewise, the siphonophorae were also very rare, with just one individual observed, albeit tentatively identified as a calycophoran siphonophore. This does however place the siphonophorae to at least 7888 m. Their rarity in this study is likely due to a lack of observation in the

Table II: All known records of hydrozoans, scyphozoans, larvaceans and ctenophores at hadal depths from previous studies and from >5000 m in this study

Phylum	Class	Order	Family	Species	Location	Depth (m)	Reference
Cnidaria	Hydrozoa	Anthoathecata	Corymorphidae	<i>Branchiocerianthus imperator</i> ^a	New Hebrides	6758-6776	Lemche et al. (1976)
				Unidentified sp.	Peru-Chile	6260	Menzies et al. (1973)
				<i>Halisiphonia megalotheca</i> ^a	New Britain Kermadec	8258-8260 8210-8300	Lemche et al. (1976) Bellaev (1989)
				<i>Aglaophenia</i> sp.	Kuril-Kamchatka	8185-8400	Bellaev (1989)
				<i>Lytocarpia tenuissima</i> ^a	Tonga	8950-9020	Bellaev (1989)
					Java	~7000	Bellaev (1989)
					Kermadec	~6500	Bellaev (1989)
					South Shetland	5200	This Study
					New Britain	8258-8260	Lemche et al. (1976)
					Mariana	7888	This Study
					New Hebrides	6898	This Study
					Kermadec	5100	This Study
					Mariana	6777	This Study
					San Cristobal	7220	This Study
				Scyphozoa	Scyphozoa	Semaostomeae	Unknown
<i>Crossota</i> sp.	Palau	8021-8042	Lemche et al. (1976)				
	Mariana	6495-9066	This Study				
	New Hebrides	6082-6898	This Study				
	San Cristobal	6515	This Study				
	Kuril-Kamchatka	6800-8700	Naumov (1971)				
	Agulhas FZ	5493	This Study				
	Atacama	5329-7204	This Study				
	Japan	6945	This Study				
	Kermadec	5100-6037	This Study				
	New Hebrides	6989	This Study				
	Puerto Rico	5360-6356	This Study				
	San Cristobal	6515-7220	This Study				
	South Shetland	5200	This Study				
Ctenophora	Tentaculata	Lobata	Unknown				
				Unidentified sp. ^a	Kermadec	7561	Jamieson et al. (2011)
				<i>Nausithoe simplex</i>	Unspecified	≤10 000	Bellaev (1989)
				Unidentified sp.	Bougainville	7848-8662	Lemche et al. (1976)
					New Britain	7984-8228	Gallo et al. (2015)
					New Hebrides	6898	This Study
					Atacama	5563	This Study
					Kermadec	6037	This Study
					Ryukyu	7217	Lindsay and Miyake (2007)
					Kermadec	5135	This Study

Continued

Table II: Continued

Phylum	Class	Order	Family	Species	Location	Depth (m)	Reference			
Chordata	Appendicularia	Copeolata	Morphotype 1		Agulhas FZ	5493	This Study			
					Java	5760–7176	This Study			
					Kermadec	5100–6037	This Study			
					South Shetland	5200	This Study			
					Agulhas FZ	5493	This Study			
					Java	5760–7176	This Study			
			Morphotype 2		South Shetland	5200	This Study			
					Agulhas FZ	5493	This Study			
					Java	5760–7176	This Study			
			Morphotype 3		Java	5493	This Study			
					Puerto Rico	5360–6356	This Study			
						Unknown				

^aPolyp only.
^b'LRJ' refers to the 'Little Red jelly' complex (Matsumoto *et al.*, 2020).

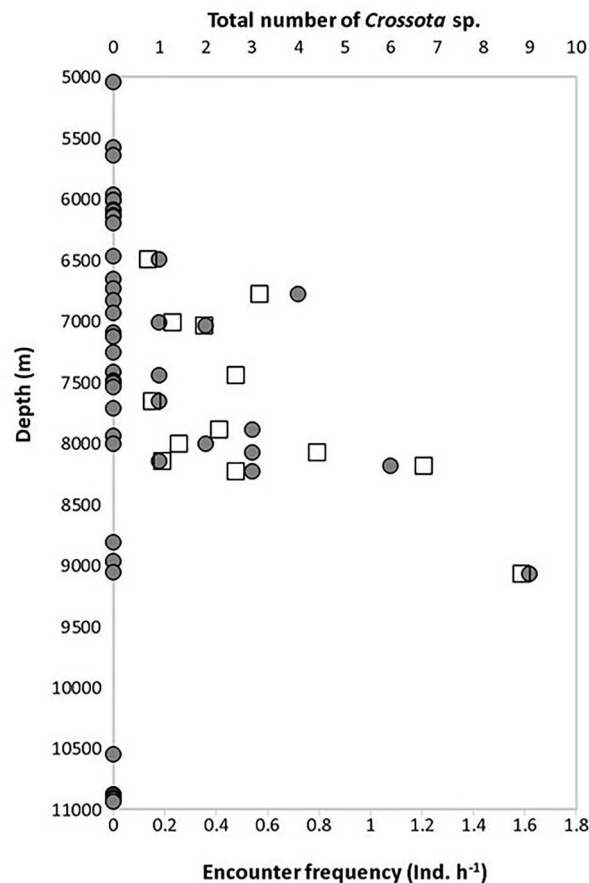


Fig. 8. The total number of the trachymedusae *Crossota* sp. observed during the 37 lander deployments between 5044 and 10 925 m in the Mariana Trench (solid circles). The open squares show the encounter frequency (individuals per hour of observation) at the sites where *Crossota* sp. was recorded.

true hadopelagic. If future studies focus on much greater altitudes from the seafloor, more may be found.

Although the Scyphozoa, of the Ulmaridae family, were also rare in this study (one individual at 6989 m, New Hebrides Trench), it is in keeping with the reports of Lemche *et al.* (Lemche *et al.*, 1976) from the Bougainville Trench at 7847–8662 m and Gallo *et al.* (Gallo *et al.*, 2015) from the New Britain Trench (7984–8228 m). These three trenches are all located in the same Indo-Pacific region and biochemical province (Western Pacific Archipelagic Deep Basins, ARCH; Longhurst, 2007). The combined depth range of 6898–8662 m suggests that they are a significant component to the hadal community of this region, although they may be limited to this geographical region, albeit unlikely.

The deepest narcomedusae were observed in the San Cristobal Trench (SW Pacific) at 6515 and 7220 m, while others were observed in the Kermadec Trench (5100 m), the Mariana Trench (6777 m) and the New

Hebrides Trench (6898 m). These observations place the narcomedusae within the upper hadal zone of the western Pacific trenches; however, their occurrence is somewhat patchy and unpredictable. For example, although they were recorded in two of three deployments in the San Cristobal Trench, none were seen just 300 km away at the equivalent depths in the neighboring Santa Cruz Trench in the same week. Furthermore, only one individual was seen in 19 deployments in the Kermadec Trench that collectively spanned over 176 h of observations. Similarly, in the Mariana Trench, two individuals were seen at the same site out of 52 deployments spanning >300 h of observations. These confirmed sightings in four trenches suggest that they are relatively widespread throughout the west Pacific trenches, albeit rare in the benthopelagic at least. These are, however, the first records of narcomedusae at hadal depths.

The two most numerous groups were the larvaceans and the trachymedusae. Both groups are particularly difficult to identify from *in situ* images (Hopcroft, 2005; Matsumoto *et al.*, 2020).

The larvaceans were seen in relative abundance between 5000 and 6500 m in the Agulhas Fracture Zone (SE Atlantic), and the Puerto Rico (NW Atlantic), Kermadec (SW Pacific), South Shetland (Southern Ocean) and Java (NE Indian Ocean) trenches, placing them in every ocean except the Arctic, although they are known from shallower Arctic waters (Raskoff *et al.*, 2005).

The records of larvaceans in this study represent the first from hadal depths. They were perhaps most consistently observed at depths from 5760 to 7176 m in the Java Trench with the latter being the deepest. They were most abundant in the Puerto Rico Trench at 5360 and 6356 m; the Agulhas Fracture Zone at 5493 m; the Kermadec Trench at 5100, 5456 and 6037 m; and the South Shetland Trench at 5200 m. This suggests that they are found to be most abundant in the benthopelagic zones of the lower abyssal zone, rather than being a characteristically hadal group. Their bathymetric distribution was, however, very patchy. For example, in the Puerto Rico Trench, 10 and 19 individuals were seen at 5360 and 6356 m, but none were seen in the intermediate depth of 5880 m despite all deployments being within a week of each other. Likewise, in the Kermadec Trench, they were observed at deployments at 5046 and 5075 m; then, none were seen in the next five deeper deployments (5100–5295 m) but then relatively consistently between 5460 and 6068 m. Observations within these three depth strata were made in both January 2013 and April 2014, and the time of year did not correlate with the presence or absence at each depth.

The two most abundant sites for larvaceans were the Agulhas Fracture Zone with 165 sightings in 7 h and

49 min (21.1 Ind.h⁻¹) and the South Shetland Trench with 531 sightings in 24 h and 15 min (21.9 Ind.h⁻¹). Unfortunately, the Agulhas Fracture Zone deployment was the only one from the area, and therefore, there is little to contextualize it in terms of area or depth. However, the high abundance at 5200 m in the South Shetland Trench is surprising, given not a single larvacean was seen in the South Sandwich Trench approximately 2000 km to the east within the Antarctic convergence zone. The times of year were also similar: December and February, respectively, both in the austral summer. This may be explained by differences in biochemical provinces with South Sandwich being in the Antarctic (ANTA) province and South Shetland Trench being in the Austral Polar (APLR) province, where the APLR has a higher primary production rate of 398 g C m⁻¹ year⁻¹ than ANTA with 165 g C m⁻¹ day⁻¹ (Longhurst, 2007). However, this seems contrary to the Agulhas Fracture Zone results, which lies 2800 km east of South Sandwich Trench in the South Atlantic Tropical Gyre (SATL) province that receives just 75 g C m⁻¹ day⁻¹ (Longhurst, 2007). Alternatively, their abundance may be affected by proximity to the Antarctic land mass and more local conditions, or very acute seasonality.

In terms of biodiversity, larvaceans are already known to be a difficult group (Hopcroft, 2005). This is in part due to the technical difficulties in maintaining sample quality when collected by towed nets, degradation of samples in the preservation process and the low number of mid-water optimized remotely operated vehicles with suitably high-resolution cameras to record morphological detail sufficient for taxonomy (Robison *et al.*, 2017; Sherlock *et al.*, 2017). The diversity of the larvaceans is likely to be much higher than current species counts and little is known about larvacean diversity deeper than 1500 m (Hopcroft, 2005). Given there are no records of any larvaceans at the depths included in this study, there is a high likelihood of new species within these images. However, as the cameras used in this study were not optimized for this type of organism, nor was it possible to target individuals using high definition optical zoom to image delicate and fragile morphological structures, it is perhaps not useful to speculate what species they might be, but based on filter morphology probably include *Oikopleura* and *Fritillaria*. As such, three broad morphotypes were identified (Morphotypes 1–3; Fig. 9).

While there were instances where the occupancy of the house could not be determined, but appeared unoccupied, there was nothing about the behavior of these, compared with clearly occupied houses, to suggest they were discards. Not a single house was seen to be disintegrating, or in contact with the seafloor, in fact the potentially unoccupied houses drifted in the same manner as

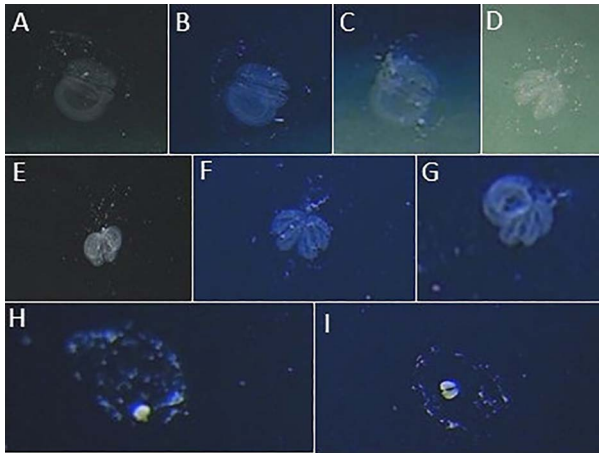


Fig. 9. Summary of the three larvacean morphotypes. Morphotype 1 from South Shetland Trench (A), Java Trench (B), Agulhas Fracture Zone (C) and Kermadec Trench (D). Morphotype 2 from South Shetland Trench (E), Agulhas Fracture Zone (F) and Java Trench (G). Morphotype 3 from Agulhas Fracture Zone (H) and Java Trench (I).

those clearly occupied. As the vast majority of larvaceans were represented by occupied houses, and again, none appeared to indicate the rapid sinking of these structure from overlying waters, such as that described by Robison *et al.* (Robison *et al.*, 2005). Therefore, based on these observations, these populations are indeed hadal.

The trachymedusae were also observed all the study areas except the Molloy Hole and the Java, Santa Cruz, Tonga and South Sandwich trenches. Taxonomic identification of trachymedusae is notoriously difficult in the absence of physical specimens or very high-resolution imaging systems. Subsequently, this study can loosely categorize the trachymedusae into two broad groups. The first is the relatively confident identification of the *Crossota* genus. This genus was generally larger than the other observed trachymedusae and tended to drift slowly at a constant altitude above the seafloor, giving a much clearer view of key features. *Crossota* sp. was seen in the San Cristobal and New Hebrides trenches and, particularly, in the Mariana Trench, and all at hadal depths. These observations, combined with the sighting of *Crossota* sp. in the Palau Trench by Lemche *et al.* (Lemche *et al.*, 1976) between 8021 and 8042 m, suggest that this trachymedusae genus is perhaps a common component of the hadal trench communities of the western Pacific at tropical latitudes.

The true maximum depth of the Mariana *Crossota* sp. could potentially be deeper, in which no deployments were done between 9066 and 10 545 m. Furthermore, there is an anecdotal mention in Gallo *et al.* (Gallo *et al.*, 2015) of a single rhopalonematid jellyfish being sighted by National Geographic at 9970 m near Challenger Deep. Their apparent absence in the combined

>37 h of footage from depths > 10 500 m could mean that they are absent > 10 000 m, or that the current speeds at the very deepest depths are so low (Taira *et al.*, 2004), and they are unlikely to be detected by this method of filming.

Of all the other sightings of trachymedusae, the majority tended to be <6500 m depth, although the deepest was a small red species in the Atacama Trench at 8052 m deep. Morphologically, many of those recorded were too small to identify with confidence. Others were simply too far from the camera to speculate taxonomically. However, they do all fall under the common umbrella term of ‘little red jellies’, which likely comprise a mixture of genera including *Benthocodon*, *Pectis* and other *Crossota* species (Matsumoto *et al.*, 2020).

The next step in establishing the diversity, maximum depth limits and abundance of the gelatinous zooplankton at hadal depths lies within technology. Ideally, remotely operated vehicles optimized for midwater research, such as those detailed by Robison *et al.* (Robison *et al.*, 2017), with sophisticated imaging systems and sampling methods such as that described by Sherlock *et al.* (Sherlock *et al.*, 2016) should be adopted. This would provide a much needed specimen collection for morphological and genetic taxonomic work. However, at hadal depths, such technology to provide a multitude of specimens is not commonplace and likely extraordinarily expensive given the depth rating required. An alternative, albeit compromise between sample collection and nothing at all, would be to continue using static imaging platforms, but with very high resolution still imaging with more powerful illumination, and perhaps motion sensors triggering burst imaging to optimize the amount of data collected but providing a sufficiently high enough resolution images to identify key morphological features. It will only be with the integration of hadal-rated current meters, longer term deployments and the potential for moored systems higher up into the hadopelagic that the true density, diversity and dynamics of these groups of animals could be truly resolved.

CONCLUSION

Within the gelatinous zooplankton, the benthopelagic Hydrozoa (trachymedusae, narcomedusae and siphonophorae), Scyphozoa, Larvacea and Ctenophora were all observed at hadal depths within an autonomous lander dataset spanning 136 deployments, totaling over 1000 h of *in situ* surveillance. These data also spanned 12 subduction trenches, plus a fracture zone, and a hole, and included all five oceans.

The Ctenophora do not appear characteristically hadal as the deepest sighting was at 6037 m, in the Kermadec

Trench (SW Pacific). The deepest Scyphozoan, of the Ulmaridae family, was 6898 m in the New Hebrides Trench (SW Pacific). While the siphonophorae sightings amounted to just one, a single calycophoran recorded at 7888 m in the Mariana Trench. Narcomedusae were recorded to a maximum depth of 7220 m in the San Cristobal Trench (SW Pacific). Of the Hydrozoa, trachymedusae, *Crossota* sp., were recorded to a maximum depth of 9066 m in the Mariana Trench (NW Pacific), while many other sightings were made <6500 m that likely encompass multiple species of the ‘little red jellies’—*Benthocodon*, *Pectis* and other *Crossota* species (Matsumoto *et al.*, 2020). Larvaceans appear relatively abundant between 5000 and 6500 m in several areas, while being quite conspicuous at hadal depths in the Java Trench (NE Indian Ocean), from 5760 to 7176 m with the latter being the deepest recorded. None of these groups were seen in the deep Arctic or in the Antarctic deeper than 6000 m in this study. Despite the conclusion that the narcomedusae, siphonophorae, Scyphozoa and Ctenophora appear rare in the hadal benthopelagic, the larvaceans and trachymedusae appear to be relatively conspicuous component of the benthopelagic fauna at the lower abyssal to hadal depths, at least at temperate and tropical latitudes.

SUPPLEMENTARY DATA

Supplementary data can be found at *Journal of Plankton Research* online.

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REFERENCES

- Beliaev, G. M. (1989) *Deep Sea Ocean Trenches and Their Fauna*, Nauka Publishing House, Moscow, p. 385.
- Blankenship, L. E. and Levin, L. A. (2007) Extreme food webs: foraging strategies and diets of scavenging amphipods from the ocean’s deepest 5 kilometers. *Limnol Oceanogr*, **52**, 1685–1697.
- Boero, F. (2013) Review of jellyfish blooms in the Mediterranean and Black Sea. In *General Fisheries Commission for the Mediterranean. Studies and Reviews*, Rome, FAO, p. 92, 53.
- Collins, A. G. (2002) Phylogeny of Medusozoa and the evolution of cnidarian life cycles. *J Evol Biol*, **15**, 418–432.
- Condon, R. H., Steinberg, D. K., Del Giorgio, P. A., Bouvier, T. C., Bronk, D. A., Graham, W. M. and Ducklow, H. W. (2011) Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. *Proc Natl Acad Sci*, **108**, 10225–10230.
- Eloe, E. A., Shulse, C. N., Fadrosch, D. W., Williamson, S. J., Allen, E. E. and Bartlett, D. H. (2011) Compositional differences in particle-associated and free-living microbial assemblages from an extreme deep-ocean environment. *Environ Microbiol Rep*, **3**, 449–458.
- Gallo, N. D., Cameron, J., Hardy, K., Fryer, P., Bartlett, D. H. and Levin, L. A. (2015) Submersible- and lander-observed community patterns in the Mariana and New Britain trenches: influence of productivity and depth on epibenthic and scavenging communities. *Deep Sea Res, PT I*, **99**, 119–133.
- Gibbons, M. J. and Richardson, A. J. (2013) Beyond the jellyfish joyride and global oscillations: advancing jellyfish research. *J Plankton Res*, **35**, 929–938.
- Haddock, S. H. (2004) A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. *Hydrobiologia*, **530**, 549–556.
- Haddock, S. H. and Case, J. F. (1999) Bioluminescence spectra of shallow and deep-sea gelatinous zooplankton: ctenophores, medusae and siphonophores. *Mar Biol*, **133**, 571–582.
- Herring, P. (2002) *The Biology of the Deep Ocean*, Oxford University Press, Oxford, UK.
- Hopcroft, R. R. (2005) *Diversity in Larvaceans: How Many Species. Response of Marine Ecosystems to Global Change: Ecological Impact of Appendicularians*, Contemporary Publishing International, Paris, pp. 45–57.
- Jamieson, A. (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 Res PT II*, **155**, 4–10.

- Jamieson, A. J. and Vecchione, M. (2020) First in situ observation of Cephalopoda at hadal depths (Octopoda: Opisthoteuthidae: *Grimptoteuthis* sp.). *Mar Biol*, **167**, 1–5.
- Jamieson, A. J., Kilgallen, N. M., Rowden, A. A., Fujii, T., Horton, T., Lörz, A. N., Kitazawa, K. and 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 Res PT I*, **58**, 49–62.
- Johnson, G. C. (1998) Deep water properties, velocities, and dynamics over ocean trenches. *J Mar Res*, **56**, 329–347.
- Kramp, P. L. (1956) Hydroids from depths exceeding 6000 meters. *Galathea Rep*, **2**, 17–20.
- Lebrato, M., Pitt, K. A., Sweetman, A. K., Jones, D. O., Cartes, J. E., Oschlies, A., Condon, R. H., Molinero, J. C. *et al.* (2012) Jelly-falls historic and recent observations: a review to drive future research directions. *Hydrobiologia*, **690**, 227–245.
- Lemche, H., Hansen, B., Madsen, F.J., Tendal, O. S. and Wolff, T. (1976) Hadal life as analysed from photographs. *Vidensk Meddr Dansk Naturh Foren*, **139**, 263–336.
- Lindsay, D. J. and Miyake, H. (2007) A novel benthopelagic ctenophore from 7,217 m depth in the Ryukyu trench, Japan, with notes on the taxonomy of deepsea cydippids. *Plankton Benthos Res*, **2**, 98–102.
- Longhurst, A. (2007) *Ecological Geography of the Sea*, 2nd edn, Academic Press, San Diego.
- Matsumoto, G. I., Bentlage, B., Sherlock, R., Walz, K. and Robison, B. H. (2020) “Little red jellies” in Monterey Bay, California (Cnidaria: Hydrozoa: Trachymedusae: Rhopalonematidae). *Front Mar Sci*, **6**, 798.
- Mark, E. L. (1898) Preliminary report on *Branchiocerianthus urceolus*, a new type of Actinian. Report on the dredging operations off the west coast of central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U. S. Fish commission steamer “albatross”, during 1891. *Bull Mus Comp Zool*, **32**, 147–154.
- Menzies, R. J., George, R. Y. and Rowe, G. T. (1973) *Abyssal Environment and Ecology of the World Oceans*, John Wiley and Sons, New York, pp. 323–327.
- Naumov, D. V. (1971) Gydroidnye i stisfoidnye medusy iz Kurilo-Kamchatskogo zhelova. Hydromedusae and Scyphomedusae from the Kurile-Kamchatka trench. *Trudy Instituta Okeanologii*, **92**, 9–17.
- Nunoura, T., Takaki, Y., Hirai, M., Shimamura, S., Makabe, A., Koide, O., Kikuchi, T., Miyazaki, J. *et al.* (2015) Hadal biosphere: insight into the microbial ecosystem in the deepest ocean on earth. *Proc Natl Acad Sci*, **112**, E1230–E1236.
- Raskoff, K. A., Purcell, J. E. and Hopcroft, R. R. (2005) Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice. *Polar Biol*, **28**, 207–217.
- Robison, B. H., Reisenbichler, K. R. and Sherlock, R. E. (2005) Giant larvacean houses: rapid carbon transport to the deep sea floor. *Science*, **308**, 1609–1611.
- Robison, B. H., Reisenbichler, K. R. and Sherlock, R. E. (2017) The evolution of midwater research and ROV technology at MBARI. *Oceanography*, **30**, 26–37.
- Sherlock, R. E., Walz, K. R. and Robison, B. H. (2016) The first definitive record of the giant larvacean, *Bathochordaeus charon*, since its original description in 1900 and a range extension to the Northeast Pacific Ocean. *Mar Biodivers Rec*, **9**, 79.
- Sherlock, R. E., Walz, K. R., Schlining, K. L. and Robison, B. H. (2017) Morphology, ecology, and molecular biology of a new species of giant larvacean in the eastern North Pacific: *Bathochordaeus mcnutti* sp. nov. *Mar Biol*, **164**, 20.
- Sweetman, A. K. and Chapman, A. (2011) First observations of jelly-falls at the seafloor in a deep-sea fjord. *Deep Sea Res PT I*, **58**, 1206–1211.
- Taira, K., Kitagawa, S., Yamashiro, T. and Yanagimoto, D. (2004) Deep and bottom currents in the challenger deep, Mariana trench, measured with super-deep current meters. *J Oceanogr*, **60**, 919–926.
- Taira, K., Yanagimoto, D. and Kitagawa, S. (2005) Deep CTD casts in the challenger deep, Mariana trench. *J Oceanogr*, **61**, 447–454.
- Tarn, J., Peoples, L. M., Hardy, K., Cameron, J. and Bartlett, D. H. (2016) Identification of free-living and particle-associated microbial communities present in hadal regions of the Mariana trench. *Front Microbiol*, **7**, 665.
- Vinogradov, M. E. (1962) Quantitative distribution of deep-sea plankton in the northern section of the Indian Ocean. *Okeanologiya SSSR*, **2**, 577–592.
- Yancey, P. H., Geringer, M. E., Drazen, J. C., Rowden, A. A. and Jamieson, A. J. (2014) Marine fish may be biochemically constrained from inhabiting the deepest ocean depths. *Proc Natl Acad Sci*, **111**, 4461–4465.