



Maximum depth extensions for Hydrozoa, Tunicata and Ctenophora

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Abstract

The observation of singleton or rare species in the deep sea is extremely valuable for gaining a census of biodiversity. At hadal depths (> 6000 m), these records provide a more complete picture of the vertical distribution of fauna. In this study, we present new in situ video records for Trachymedusae (Hydrozoa), Ascidiacea (Tunicata), and Tentaculata (Ctenophora) taken by submersible and supporting landers in the western Pacific Ocean. Together, these three taxonomic groups are present at depths far deeper than previously known. Observations of the rhopalonematid trachymedusa (*Pectis* cf. *profundicola*) from both lander and submersible dives at 10,063 and 10,040 m in the Philippine Trench (NW Pacific Ocean) extend the maximum depth of the Hydrozoa by a further 997 m and is the first record of Hydrozoa > 10,000 m. The predatory tunicate Octacnemidae sp. was observed nine times at 7799 m in the Mariana Trench and once at 8077 m in the Izu-Ogasawara Trench (NW Pacific Ocean), therefore extending its maximum depth by 1726 m, and 1002 m to historical accounts of what might also be in the Phlebobranchia order of Ascidiacea. Several observations of large, globular ctenophores with long filamentous tentacles and lacking oral lobes from 10,040 m in the Kermadec Trench (SW Pacific Ocean) increase the maximum depth of the Ctenophora by 2823 m and is the first record of Ctenophora > 10,000 m. Benthic ctenophores were also recorded from the Japan Trench at 8001 m, extending their known depth range by a further 2750 m.

Keywords Deep-sea · Hadal zone · Trachymedusae · Ascidiacea · Tentaculata · Submersible

Introduction

In an era where the need to assess and conserve biodiversity and associated habitats is at the forefront of all marine science, there are still large ecosystems that fall significantly behind most other mainstream research efforts. The umbrella term ‘deep-sea’ encapsulates much of that, but more specifically, the mesopelagic and hadal zones where records of

taxa are especially lacking (Webb et al. 2010). Geographically discrete deep-sea benthic habitats also face existential threats that provide a further need for urgency (Santos et al. 2018). Creating a census of biodiversity in these areas can be challenging due to high volume habitats (e.g., mesopelagic; Sutton et al. 2010), sampling over large areas (e.g., polymetallic nodule fields; Briberca-Contreras et al. 2022) and sampling at great depths (e.g., hadal depths; Jamieson 2018). In each case, sampling effort reduces with depth, and so too does population density. In the deep sea, a low population is often coupled with very large habitat sizes that in turn give a false or skewed impression of rarity (McClain 2021). In these environments observation of singleton or doubleton species are potentially extremely valuable (Carney 1997).

Exploration of the hadal zone (depths beyond 6000 m) has lagged behind shallower biozones because of the technical challenges of sampling at great depth and pressure (Weston and Jamieson 2022). Sampling effort has seen a recent uptick as various new technologies emerge (Jamieson 2018). One such technology is the full ocean depth submersible DSV *Limiting Factor*, a privately owned 2-person submersible with supporting landers, that has been in operation

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since 2018 (Jamieson et al. 2019). While the DSV *Limiting Factor* is primarily designed for adventure tourism and marine archaeology, in addition to science, the submersible's descent to the hadal depths provides a critical opportunity for biological exploration. Regardless of a dive's objective new species records are valuable in understanding the ultimate depth limits of taxonomic groups. Due to the complications of low population density over vast geographic areas, the focus of the data resulting from these endeavours is simply species presence rather than species absence.

These new hadal expeditions have, in recent years, extended the depth range of octopus and squid to hadal depths (Jamieson and Vecchione 2020, 2022, respectively), added new hadal records or extended the depth ranges of hydrozoans (Trachymedusae and Siphonophorae), scyphozoans, larvaceans and ctenophores (Jamieson and Linley 2021), and increased the number of fish and decapod families at hadal depths (Jamieson et al. 2021; Swan et al. 2021, respectively). As these new data emerge it is becoming clear that many marine taxa are represented at hadal depths. Although new records and significant depth extensions have been sparse, the increasing presence of technologies at such depths is slowly providing a more complete picture of the vertical distribution of fauna and therefore biodiversity at the deepest parts of the oceans.

In this study, we report on depth extensions of another three taxonomic groups: Trachymedusae (Hydrozoa), Ascidiacea (Tunicata) and Tentaculata (Ctenophora) following the culmination of the DSV *Limiting Factor*'s 'Ring of Fire' 2021–2022 expeditions in the western Pacific Ocean.

Materials and methods

During the Ring of Fire 2021–2022 expeditions on the DSSV *Pressure Drop*, the manned submersible DSV *Limiting Factor* (Triton 36k/2; Triton Submarines LLC, US; rated for full ocean depth; Jamieson et al. 2019), was deployed numerous times around the Pacific Ocean. Some of these dives were scientifically focused but most were not. Nevertheless, the submersible completed dives to the Philippine Trench (March 2021), Mariana Trench (April 2021), the Kermadec Trench (February 2022), and the Japan and Izu-Ogasawara trenches (August 2022) among others, and in doing so captured various deep-sea species at hadal depths on video.

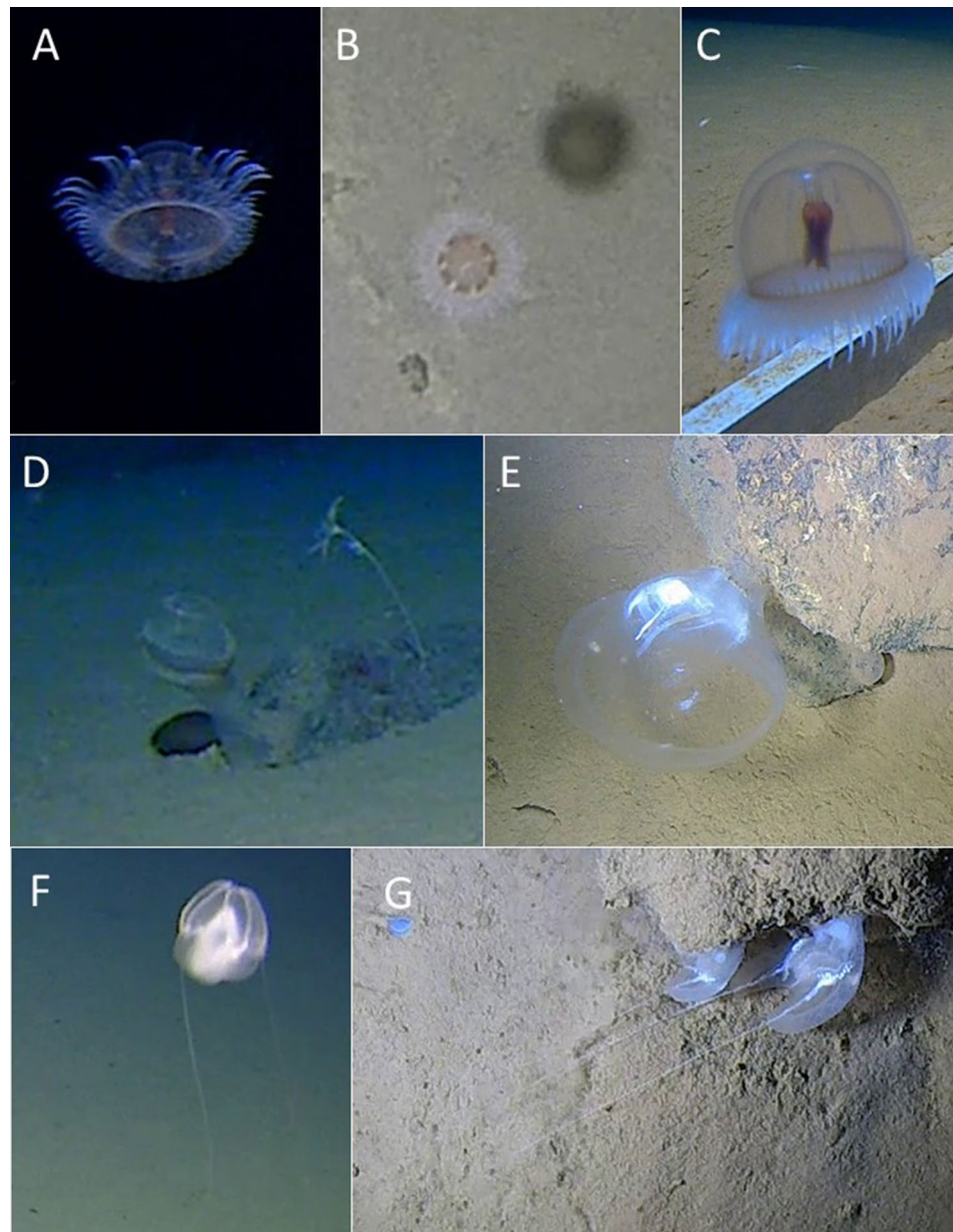
Video data were acquired using two externally mounted High-Definition (HD) video cameras (IP Multi SeaCam 3105; Deep Sea Power and Light, San Diego, CA). Depth was recorded by twin Conductivity, Temperature and Depth (CTD) probes (SBE 49 FastCAT, SeaBird Electronics, Bellevue, WA). Additional footage was captured by static baited camera landers with the same cameras and CTD

sensors. The submersible and at least one supporting lander used in this study were deployed in the Philippine Trench (10.221 N/126.140 E, sub depth 10,040 m, lander depth 10,063 m), the Mariana Trench (11.871 N/144.800 E, sub depth 7799 m, lander depth 7396 m), the Kermadec Trench (31.935 S/177.317 W, sub depth 10,040 m), the Japan Trench (36.087 N/142.727 E, sub depth 8001 m) and the Izu-Ogasawara Trench (29.414 N/142.583 E, lander depth 8077 m).

Results and discussion

A solitary rhopalonematid trachymedusa was observed in the *Emden Deep* of the Philippine Trench at 10,063 m passing a baited camera (Fig. 1A). It is identified provisionally here as a *Pectis* species due to the long, red manubrium situated on a distinct peduncle, clear subumbrella with very slight brownish hue and the tentacles being arranged in several rows rather than in a single row. The presence or absence of centripetal canals arising from the ring canal was not able to be determined due to the quality of the imagery so the possibility exists that it is a *Benthocodon* species, though we think this unlikely due to its striking resemblance to an animal closely resembling *Pectis profundicola* Naumov 1971 (Fig. 1C) filmed at 7396 m in the Mariana Trench (see supplemental video). This animal had seven triangular centripetal canals per octant, a transparent subumbrella and peduncle, unpigmented tentacles, and whitish pendant gonads attached by narrow bases at a position about one-quarter along the radial canals from the base of the peduncle. The original description of *P. profundicola* (as *Voragonema profundicola*) contains no mention of gonads in the single 1.5 cm diameter holotype (Naumov 1971), suggesting it may have been immature, but does mention a lack of pigmentation, except for a brown manubrium. Another three morphologically similar rhopalonematid hydromedusae were observed from the submersible in an area 100 km to the North at 10,040 m (Fig. 1B). One of these individuals had white linear gonads but, due to the images being taken looking down apically on the umbrella, it was impossible to determine their position or whether they were partially pendant or not. Prior to this study, the deepest hydrozoan recorded, reported as *Crossota* sp., was from 9066 m in the Mariana Trench (Jamieson and Linley 2021). Reassessment of its taxonomy based on the presence of a gelatinous peduncle attached to the long reddish manubrium, as was also clearly visible on a lander video from the Mariana Trench at 7396 m (Fig. 1C), causes us to withdraw the identification as *Crossota*, all species of which lack a peduncle. It is provisionally re-identified here as *P. profundicola*, although the individual in the video record for which we were able to do unambiguous counts (7396 m depth, Mariana Trench)

Fig. 1 **A** Lateral view of the rhopalonematid trachymedusa (*Pectis* cf. *profundicola*) at 10,063 m taken by lander and **B** top view by submersible at 10,040 m in the Philippine Trench. **C** A more detailed image of *Pectis* cf. *profundicola* from 7396 m in the Mariana Trench. **D** The tunicate Octacnemidae sp. at 8077 m in the Izu-Ogasawara Trench and **E** 7799 m in the Mariana Trench. **F** Large tentaculate ctenophore from 10,040 m in the Kermadec Trench, and **G** the benthic ctenophore Lyroctenidae sp. from 8001 m in the Japan Trench. See also Supplemental Video



had seven centripetal canals per octant, rather than the eight per octant reported for the holotype (Naumov 1971). In any case, the present new record from 10,063 m in the *Emden Deep*, therefore, adds a further 997 m to the depth range of the Trachymedusae order of Hydrozoa. It is also the first record of any hydrozoan greater than 10,000 m. The present observations would appear to be the first records of *P. profundicola* from outside the Kurile-Kamchatka Trench. Although Matsumoto et al. (2020) reported the species' occurrence in Monterey Bay and off Oregon, their photographed specimens had reddish-brown pigmentation on the subumbrella and tentacles, radial canals that were wider in their distal halves, and the deepest of their specimens was captured at only 1384 m depth. Our in situ images clearly

show specimens with very minimal pigmentation on either the subumbrella or tentacles, as well as the radial canals being narrow along their entire length, just as explicitly stated in the original description by Naumov (1971). The only pigmentation Naumov (1971) reported in *P. profundicola* was that the manubrium was brown, implying that the peduncle was non-pigmented as in our images and in contrast to those of Matsumoto et al. (2020). Matsumoto et al. (2020) also mentioned that the species they referred to as *P. profundicola* sometimes has more tentacles (1000–2000 versus around 500 in the original description) and a varying number of centripetal canals (7–9 versus 8 in the original description). It is not possible to assess whether the material of Matsumoto et al. (2020) contained cryptic species

because no photographs of these aberrant individuals were provided and none were sequenced, but it can be assumed that the pigmentation of the subumbrella resembled the photographically documented individuals. The specific identity of our material, therefore, rests on whether the number of centripetal canals per octant can vary between individuals of the same species or not. If this number can be variable then the specimens in our observations can safely be referred to as *P. profundicola*, but if the exact number is diagnostic then it may be an undescribed species and the material of Matsumoto et al. (2020) would also contain several undescribed species. Unfortunately, the specimens that were sequenced by Matsumoto et al. (2020) were not the same individuals for which photographs were provided and no specimen-level descriptions were attempted of either the sequenced or non-sequenced material. What does seem certain though is that the material they refer to as *P. profundicola* is actually an undescribed, or several undescribed, species. The collection of new material from the type locality of the Kurile-Kamchatka Trench will be necessary to solve this taxonomic quagmire. Present records for other hydrozoan orders are 7888 m for an unidentifiable siphonophore, 7220 m for a narcomedusa with ten perradial tentacles and the same number of stomach pouches, 5200 m for a leptothecate medusa (Figs. 6C, 5I, 2K, respectively, in Jamieson & Linley 2021) and 6758–6776 m for an Anthomedusa (Lemche et al. 1976).

At 8077 m in the Izu-Ogasawara Trench, a baited lander recorded a predatory tunicate (Octacnemidae) attached to rock several meters from the landing site (Fig. 1D). Clearer, albeit slightly shallower images were acquired from 7799 m in the Mariana Trench where Octacnemidae sp. was observed nine times, attached to boulders at the base of an unnamed seamount on the southern slope adjacent to *Sirena Deep* (Fig. 1E). The deepest records prior to this study were of a morphologically similar species, recorded as '*Ascidia- cea* sp. 1' from 6351 m in the Yap Trench (Zhang et al. 2021) and unidentified solitary ascidians from 7057–7075 m in the New Britain Trench and 6758–6776 m in the New Hebrides Trench (Lemche et al. 1976), although the latter records had more slender bodies and elongated stalks. With so few records at hadal depths, these new observations add a further 1726 m to the depth range of the similar morph in Zhang et al. (2021) and 1002 m to the Lemche et al. (1976) records of what may also be in the Phlebobranchia order of Ascidiacea. The only other record from hadal depths is of a stalked ascidian tunicate, aff. *Culeolus* sp., (Order Solidobranchia) drifted passed the same hadal-lander used in this study at 6430 m in the Java Trench (Jamieson et al. 2022).

At 10,040 m in the *Scholl Deep* of the Kermadec Trench, two large, globular ctenophores with long filamentous tentacles and lacking oral lobes were observed during a submersible dive (Fig. 1F). Curiously, the adradial canals appear to connect to the meridional canals under the comb rows

near their oral end, while both the tentacle bulbs and their exit point from the body are also near the oral ends of the comb rows. This combination of characters has only been reported in the miniscule mertensid ctenophore *Charistephane fugiens* Chun, 1880, which is highly laterally compressed and is likely to warrant the erection of new higher taxa were it to ever be recovered and/or imaged in high resolution with an accompanying DNA barcode and so that the internal canal structure could be properly assessed. The deepest ctenophore recorded by Jamieson and Linley (2021) was a lobate ctenophore at 6037 m, also in the Kermadec Trench, whereas the deepest known ctenophore prior to this study was a novel tentaculate ctenophore from 7217 m in the Ryukyu Trench (Lindsay and Miyake 2007). This new record of a cydippid from the Kermadec Trench adds another 2823 m to the known depth distribution of Ctenophora and a further 4887 m to the deepest reported "cydippid" (Fig. 5N in Jamieson and Linley 2021), which appears to be an undescribed species.

Within the Tentaculata is the order Playctenida which includes benthic ctenophores. Lyroctenidae sp. was observed frequently on a submersible dive to 8001 m in the Japan Trench (Fig. 1G). These observations add another 2750 m to the next deepest record of a benthic ctenophore, which was reported as *Lyrocteis*, from 4855–5251 m in the eastern Pacific Ocean (Durden et al. 2021), though it actually appears to belong to an undescribed higher taxon of benthic ctenophores.

These new records, combined with Jamieson and Linley (2021), have so far revealed hadal Rhopalonematid medusae (e.g., *Pectis*) to be prevalent in trenches around the central western Pacific Ocean. Similarly, the Octacnemidae sp. are from adjoining trenches (Mariana and Yap trenches), physically partitioned by a 95 km wide topographic high of 5330 m water depth (Jamieson and Stewart 2021). Given the proximity to one another, it is perhaps not surprising this new record is morphologically similar to that of the Yap Trench record (Zhang et al. 2021). The other records of tunicates by Lemche et al. (1976) are from trenches also in the central western Pacific Ocean. Conversely, the ctenophore records are from the Kermadec Trench (this study and Jamieson and Linley 2021) and the Ryukyu Trench (Lindsay and Miyake 2007), which are at opposing higher latitudes in the western Pacific (31° S and 25° N, respectively). At this stage, drawing conclusions on geographical distribution is premature given the number of observations is so low. Furthermore, the concentration of records in the Western Pacific is likely a result of there being more trenches in this region than anywhere else, and also reflects a greater sampling effort (Jamieson 2018).

These observations provide further new insight into the true depth range of major taxonomic groups, which have only been realised through repeatedly diving to hadal depths.

Table 1 All known records of Trachymedusae, Tentaculata and Ascidiacea at hadal depths from previous studies and this study

Class	Order	Family	Species	Trench	Depth (m)	References
Hydrozoa	Trachymedusae	Rhopalonematidae	<i>Benthocodon pedunculatus?</i> etc.	Atacama	5329–7204	Figure 5B etc. in Jamieson and Linley (2021)
			<i>Crossota alba</i> (<i>Pectis?</i>)	New Hebrides	6758–6776	Lemche et al. (1976)
			<i>Crossota</i> cf. <i>millsae</i> ***	Puerto Rico*	6356	Figure 3L in Jamieson and Linley (2021)
			Misc. spp.	San Cristobal	6515–7220	Jamieson and Linley (2021)
			<i>Pectis profundicola</i>	Kuril-Kamchatka	6800–8700	Naumov (1971)
			<i>Pectis</i> cf. <i>profundicola</i>	Mariana	7396	This study
			<i>Pectis</i> cf. <i>profundicola</i> ***	Palau	8021–8042	Lemche et al. (1976)
			<i>Pectis</i> cf. <i>profundicola</i> ***	Mariana	9066	Figure 7 in Jamieson and Linley (2021)
			<i>Pectis</i> cf. <i>profundicola</i>	Philippine	10,040–10,063	This study
			<i>Pectis</i> cf. <i>tatsunoko</i> ***	San Cristobal	6515	Jamieson and Linley (2021)
			<i>Pectis</i> cf. <i>tatsunoko</i> ***	New Hebrides	6898	Jamieson and Linley (2021)
			Rhopalonematidae***	Kermadec	5100–6037	Jamieson and Linley (2021)
			Rhopalonematidae	Japan	6945	Jamieson and Linley (2021)
			Unidentified sp.	New Britain	7057–7075	Lemche et al. (1976)
			Tentaculata	<i>Cydrippida</i>	<i>incertae sedis</i>	<i>incertae sedis</i> sp. 1
<i>incertae sedis</i> sp. 2	Kermadec	10,040				This study
Lobata	Unknown	<i>Lobata</i> sp. indet		Kermadec	6037	Figure 5M in Jamieson and Linley (2021)
Platyctenida	Lyroctenidae	Lyroctenidae sp.		Japan	8001	This study
Ascidiacea	Phlebobranchia	Octacnemidae		Ascidiacea sp. 1	Yap	6351
			Octacnemidae sp.	Mariana	7799	This study
				Izu-Ogasawara	8077	This study
			‘Solitary ascidian’	New Hebrides	6758–6776	Lemche et al. (1976)
			‘Solitary ascidian’	New Britain	7057–7075	Lemche et al. (1976)
Solidobranchia	Pyuridae	<i>Culeolus</i> sp.	Java**	6430	Jamieson et al. (2022)	

All trenches are in the Pacific Ocean except for *Atlantic Ocean and **Indian Ocean, *** indicate tentative new species identification corrections

Such an increase in observational effort, over as many hadal features as possible, will be essential in establishing how far each taxon has vertically penetrated the ocean, as clearly population density is very low relative to the observed area of a submersible transect. Higher resolution imaging systems at full ocean depth will enhance the taxonomic resolution of these observational data and developing sampling tools that are common in 6000 m-rated vehicles for 11,000 m operations would permit species descriptions, morphologically and genetically. Until the technical and financial challenges in these developments are overcome, a multi-hadal feature and/or multi-ocean diving campaign is required to resolve how many of these observations are global or restricted to specific locations. Utilising commercial ‘non-scientific’ submersible dives in aiding scientific discovery will also be highly valuable, as shown in this study Table 1.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-023-04177-5>.

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Author contributions Conceptualization, methodology and data collection: AJJ, formal analysis and investigation: AJJ, writing of original draft preparation, review and editing: AJJ, DJL, HK.

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Data availability The data that support the findings of this study are copyright of Caladan Oceanic LLC and restrictions apply to the availability of these data, which were used under licence for the current study, and so are not publicly available. Data are, however, available from the authors upon reasonable request and with permission of Caladan Oceanic LLC.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for sampling, care and experimental use of organisms for the study have been followed.

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References

- Bribiesca-Contreras G, Dahlgren TG, Amon DJ, Cairns S, Drennan R, Durden JM, Eléaume MP, Hosie AM, Kremenetskaia A, McQuaid K, O'Hara TD, Rabone M, Simon-Lledó E, Smith CR, Watling L, Wiklund H, Glover AG (2022) Benthic megafauna of the western Clarion-Clipperton Zone, Pacific Ocean. *Zookeys* 1113:1–110
- Carney RS (1997) Basing conservation policies for the deep-sea floor on current-diversity concepts: a consideration of rarity. *Biodivers Conserv* 6(11):1463–1485
- Durden JM, Putts M, Bingo S, Leitner AB, Drazen JC, Gooday AJ, Jones DOB, Sweetman AK, Washburn TW, Smith CR (2021) Megafaunal ecology of the western Clarion Clipperton Zone. *Front Mar Sci* 8:671062
- Jamieson AJ (2018) A contemporary perspective on hadal science. *Deep Sea Res II* 155:4–10
- Jamieson AJ, Linley TL (2021) Hydrozoans, scyphozoans, larvaceans and ctenophores observed *in situ* at hadal depths. *J Plankt Res* 43(1):20–32
- Jamieson AJ, Vecchione M (2020) First in situ observation of Cephalopoda at hadal depths (Octopoda: Opisthoteuthidae: *Grimptoteuthis* sp.). *Mar Biol* 167:82
- Jamieson AJ, Vecchione M (2022) Hadal cephalopods: First squid observation (Oegopsida, Magnapinnidae, *Magnapinna* sp.) and new records of finned octopods (Cirrata) at depths >6000 m in the Philippine Trench. *Mar Biol* 168:11
- Jamieson AJ, Ramsey J, Lahey P (2019) Hadal manned submersible. *Sea Technol* 60(9):22–24
- Jamieson AJ, Linley TD, Eigler SJ, Macdonald T (2021) A global assessment of fishes at lower abyssal and upper hadal depths (5000 to 8000 m). *Deep Sea Res I* 178:103642
- Jamieson AJ, Stewart HA, Weston JNJ, Lahey P, Vecchione VL (2022) Hadal biodiversity and potential chemosynthesis in the Java Trench. *Eastern Indian Ocean Front Mar Sci* 9:856992
- Jamieson AJ, Stewart HA (2021) Hadal zones of the Northwest Pacific Ocean. *Prog Oceanogr* 102477
- Lemche H, Hansen B, Madsen FJ, Tendal OS, Wolff T (1976) Hadal life as analysed from photographs. *Vidensk Meddr Dansk Naturh Foren* 139:263–336
- Lindsay DJ, Miyake H (2007) A novel benthopelagic ctenophore from 7,217 m depth in the Ryukyu Trench, Japan, with notes on the taxonomy of deep-sea cydippids. *Plankt Benth Res* 2(2):98–102
- Matsumoto GI, Bentlage B, Sherlock R, Walz K, Robison BH (2020) “Little Red Jellies” in Monterey Bay, California (Cnidaria: Hydrozoa: Trachymedusae: Rhopalonematidae). *Front Mar Sci* 6:798
- McClain CR (2021) The commonness of rarity in a deep-sea taxon. *Oikos* 130(6):863–878
- Naumov DV (1971) Gydroidnye i stsfoidnye medusy iz Kurilo-Kamchatskogo zhelova. Hydromedusae and Scyphomedusae from the Kurile-Kamchatka trench. *Trudy Instituta Okeanologii* 92:9–17
- Santos MM, Jorge PAS, Coimbra J, Vale C, Caetano M, Bastos L, Iglesias I, Guimarães L, Reis-Henriques MA, Teles LO, Vieira MN (2018) The last frontier: coupling technological developments with scientific challenges to improve hazard assessment of deep-sea mining. *Sci Total Environ* 627:1505–1514
- Sutton TT, Wiebe PH, Madin L, Bucklin A (2010) Diversity and community structure of pelagic fishes to 5000 m depth in the Sargasso Sea. *Deep Sea Res II* 57(24–26):2220–2233
- Swan JA, Jamieson AJ, Linley TL, Yancey PY (2021) Worldwide distribution and depth limits of decapod crustaceans (Penaeoidea, Oplophoroidea) across the abyssal-hadal transition zone of eleven subduction trenches and five additional deep-sea features. *J Crust Biol* 41(1):p.ruaa102
- Webb TJ, Vanden Berghe E, O'Dor R (2010) Biodiversity's big wet secret: the global distribution of marine biological records reveals chronic under-exploration of the deep pelagic ocean. *PLoS one* 5(8):e10223
- Weston JN, Jamieson AJ (2022) Exponential growth of hadal science: perspectives and future directions identified using topic modeling. *ICES J Mar Sci* 79(4):1048–1062
- Zhang D, Zhou Y, Yang J, Linley T, Zhang R, Lu B, Xu P, Shen C, Lin S, Wang Y, Sun D (2021) Megafaunal community structure from the abyssal to hadal zone in the Yap Trench. *Front Mar Sci* 8:617820

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