Gelatinous zooplankton community around a hydrothermally active deep-sea caldera: results from ROV video records

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Abstract: ROV dive surveys were carried out inside and outside the Sumisu Caldera, located in the Izu-Bonin Arc. The caldera is hydrothermally active and nourishes a unique chemosynthetic ecosystem, which includes Bathymodiolus mussel beds and vestimentiferan tubeworms. Sixty-one gelatinous zooplankton morphotaxa were observed (21 ctenophores, 16 siphonophores, 10 hydromedusae, 4 scyphozoans and 10 thaliaceans), and notes on their taxonomy and fine-scale distributional data are presented. The vertical distribution patterns of gelatinous zooplankton clearly differed inside and outside the caldera: three gelatinous zooplankton morphotaxa, the ctenophores Lobata sp. 1, Boli 2 and undescribed Lobata 3auricles 4, and the hydromedusa Earleria bruuni, were highly abundant inside, but not outside, of the caldera. Thaliaceans and Solmissus incisa s.l. (Narcomedusae) were distributed over a wider vertical range inside the caldera than outside. The utility of ROV video records for investigating midwater gelatinous zooplankton taxonomy and ecology is discussed, and the efficacy of ROV investigations for this type of research is shown.

Key words: gelatinous midwater biota, Izu-Bonin Arc, Sumisu Caldera, image-based survey, deep-sea mining

Introduction

Hydrothermal vents, arising from tectonic deformations due, for example, to plate convergence or spreading at ocean spreading centers, emit extremely hot seawater as a plume that contains metals, H₂S, CH₄, etc. The metals, after emission, are precipitated and form seafloor massive sulfide deposits, which are known to provide a higher grade of minerals such as copper, zinc, gold and silver, than land-based volcanogenic massive sulfide deposits (Cherkashov 2017), and they are gathering attention as a future mineral resource alternative to terrestrial ores. On the other hand, some of the other chemical substances emitted from hydrothermal vents sustain chemosynthetic organisms, which are unique to the particular geochemical background. Therefore, hydrothermal vents function simultaneously to provide future mineral resources and also to support rare/unique ecosystems (Tunnicliffe et al. 2003). Because of this, possible minor or major impacts on these ecosystems due to deep-sea mineral mining have been discussed considerably in the scientific literature (reviewed in Van Dover 2014).

Biological assemblages at hydrothermal vents, in particular the chemosynthetic ecosystems, have been actively investigated for over 40 years (e.g., Lonsdale 1977, Tunnicliffe 1988, Van Dover 2000, Rogers et al. 2012). The ecosystems support high productivity in localized areas within an otherwise desolate deep-sea floor, somewhat like oases in a desert. Examples of these thriving benthic or-
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organisms include beds of mussels, lush populations of tube-worms, masses of brachyuran crabs, etc. The influence of the high productivity at hydrothermal vents is not confined only to the benthic organisms around the vent site, because the hydrothermal plumes disperse potential food for mid-water organisms, such as zooplankton, in the form of bacterial flocs, particulate matter and/or the larvae of benthic invertebrates (e.g., Juniper et al. 1995, Mullineaux 1995, Cowen et al. 2001, Yahagi et al. 2017). Some notable previous studies have revealed that hydrothermal vents enhance the abundance and biomass of pelagic zooplankton such as copepods, amphipods and chaetognaths (e.g., Berg & Van Dover 1987, Burd et al. 1992, Burd & Thomson 1994). In addition, Burd & Thomson (2015) demonstrated a correlation between biomass/productivity and physical distance from a hydrothermal vent.

Several scientific reports focusing on the interactions between pelagic zooplankton and hydrothermal vents refer to the occurrence of gelatinous zooplankton, such as medusae, at high abundances around vents (e.g., Berg & Van Dover 1987, Burd & Thomson 1994, Vinogradov et al. 2003). Burd & Thomson (2000) focused on this, investigating the abundance and biomass of medusae based on net sampling data. They concluded that "medusae percent biomass and abundance were greater in the region of deep-water (>1000 m depth) scattering layers at the Endeavour vent field than in the surrounding northeast Pacific, where deep zooplankton scattering layers were not present and total standing stock was lower". This suggests that gelatinous zooplankton is one category of biota that would likely be affected by deep-sea mineral mining if the hydrothermal vent ecosystems were disturbed.

Advanced in situ technologies such as Human-Occupied Vehicles (HOVs) and/or Remotely-Operated Vehicles (ROVs) have helped us to understand the abundances and distributions of these animals in the deep-ocean (e.g., reviewed in Robison 2004, Lindsay & Hunt 2005). Other image-based observations can also be effective for obtaining accurate information on the number of gelatinous zooplankton present, albeit there needs to be a match between the imaged volume and the size of the organisms being surveyed (Remsen et al. 2004). Based on the results of Remsen et al. (2004), the difference in abundance between calculations based on net-caught samples vs. images taken by the Shadowed Image Particle Profiling and Evaluation Recorder (SIPPER) for gelatinous zooplankton ranged from just over 50% of the siphonophores that were imaged being caught in the net, to under 10% for the other cnidarians and ctenophores. Based on such observations, Lindsay et al. (2015) supposed that gelatinous zooplankton could be influential consumers at hydrothermal vents. They therefore produced a synopsis of the gelatinous zooplankton fauna at the Hatoma Knoll hydrothermal vent site, based on ROV video footage, and this became the first taxonomic guide to this fauna to be based on characters visible in video images. Following the same concept, the present study provides detailed comparative vertical distribution data, obtained from ROV video footage, and taxonomic treatments of the gelatinous zooplankton above an active vent site and at an off-vent site, inside and outside a deep-sea caldera.

Materials and Methods

Two mid-water dive surveys using the Remotely-Operated Vehicle (ROV) Hyper-Dolphin were carried out during cruise KY02-03 (https://doi.org/10.17596/0000166) of the R/V Kaiyo (from 18 February – 13 March 2002) at the Sumisu Caldera (31°27′N, 140°03′E). This hydrothermally active, semi-closed caldera is located within the Izu-Bonin arc and has a diameter of 10 km, with the deepest point of its rim being at about 490 m depth (Iwabuchi 1999, Japan Coast Guard 2017) (Fig. 1).

Fig. 1. Dive locations of the two ROV Hyper-Dolphin dives carried out inside and outside the Sumisu Caldera, Izu-Bonin Arc.
The first dive (HPD0083) to compare the gelatinous zooplankton community was conducted outside the caldera (launched at 31°29′03″N, 140°09′20″E) from 10:43 AM on 9 March 2002, while the second dive (HPD0084) was conducted inside (launched at 31°28′18″N, 140°04′01″E) from 8:48 AM on 10 March 2002. Video footage, recorded during the descent from the surface to the seafloor, was analyzed quantitatively. The upper 100-m depth stratum was omitted from the analysis because there was too much ambient light to detect translucent gelatinous zooplankton with consistent accuracy. The observation times for each 50-m depth stratum were calculated and are shown in Table 1. The average observation time within each 50-m depth stratum were calculated and are shown in Table 1. The average observation time within each 50-m depth stratum was 8 minutes 45 seconds during dive HPD0083 (range: 3 minutes 18 seconds–20 minutes 30 seconds, total observation time 140 minutes 6 seconds) and 6 minutes 28 seconds during dive HPD0084 (range: 2 minutes 23 seconds–20 minutes 30 seconds, total observation time 109 minutes 22 seconds). The ROV Hyper-Dolphin was equipped with an HDTV (High-Definition TeleVision) camera integrating an ultra-sensitive super HARP (High gain Avalanche Rushing Photo-conductor) tube. Camera sensitivity was F 1.8 at 2 lux, gain was variable at 4–200 times, the signal to noise ratio was 43 dB, and resolution was 800 TV lines. The zoom lens had a minimum focal length of 5.5 mm and a 5× zooming ratio. There were five 400-W SeaArc HMI/MSR metal halide lamps. Two were situated on the port swing arm, and one on the starboard swing arm. These arms were usually opened such that the lights optimized the field of view of the high definition camera when zoomed out and centered in the direction of ROV transit, but were sometimes moved to optimize lighting when making observations (i.e., pan-tilting or zooming the HD camera) of individual organisms in situ. The remaining two lights were forward-pointing and fixed to the frame of the vehicle. Video footage was recorded continuously and simultaneously on BCT-124HDLCAM tapes via a native digital signal at 1080i and 29.97 frames sec⁻¹ and was also down-converted to an analogue composite NTSC signal and recorded with depth/time overlay on Sony BCT-D124L Digital BetaCam tapes. After the cruise, these video tapes were played back on a Sony HDW-M2100 or DVW-A510 video deck and the video was digitized (Apple ProRes 4 : 2 : 2 codec, QuickTime Movie container [.mov]) using an AJA Ki Pro unit. The original timecode embedded in the HDTV files was replaced using qtChange2.26 (videotooshed.com) to match the time shown in the video overlay on the digitized NTSC movie files to frame-level accuracy. The movie files were then analyzed using QuickTime Player Pro 7.6.6 with reference to the embedded time-stamp.

Physico-chemical data were collected using a SeaBird SBE19 CTD (Conductivity, Temperature, and Depth profiling system) and an SBE13 dissolved oxygen sensor attached to the vehicle on both dives. The vertical profiles are plotted in Fig. 2. CTD and dissolved oxygen were correlated to the presence of animals by matching the depth information recorded by the CTD to the depth information on the video text overlay. Physico-chemical parameters associated with each morphotaxon occurrence are presented in the following order: temperature, salinity, dissolved oxygen concentration.

Gelatinous zooplankton were identified to the lowest taxonomic level during descent through the water column, although appendicularians were excluded from the analysis because it was hard to distinguish whether living individuals were inside the feeding filters or not, therefore making them unable to be counted quantitatively. For the identifications, the following recent taxonomic works, field guides, and original descriptions were used: Madin & Harbison (1978), Chihara & Murano (1997), Nishikawa (1997), Wrobel & Mills (1998), Pugh (1999, 2003, 2005), Bouillon et al. (2006), Kitamura (2008), Kitamura et al. (2008a, b), Lindsay & Miyake (2009), Horita et al. (2011), Lindsay et al. (2015), Minemizu et al. (2015), Licandro et al. (2017a, b), Licandro & Lindsay (2017). The terminology used in the results is primarily that of Lindsay et al. (2015). Voucher images of each morphotaxon are available as supplementary material at http://www.jamstec.go.jp/datadoi/doi/10.17596/0001982.html. Individual morphotaxon occurrences were binned into 50-m depth strata to investigate the vertical distribution of each morphotaxon. Animal abundances were normalized through dividing by the time spent observing in each stratum after first subtracting time spent with the camera zoomed in or where its field of view was blocked by instruments, etc.

| Depth range (m) | Obs. Time (min.) | Depth range (m) | Obs. Time (min.) |
|----------------|-----------------|----------------|-----------------|
| 100–150        | 3.88            | 100–150        | 2.83            |
| 150–200        | 6.63            | 150–200        | 5.85            |
| 200–250        | 3.47            | 200–250        | 8.20            |
| 250–300        | 6.93            | 250–300        | 8.80            |
| 300–350        | 6.82            | 300–350        | 4.38            |
| 350–400        | 6.80            | 350–400        | 6.57            |
| 400–450        | 3.65            | 400–450        | 5.42            |
| 450–500        | 10.98           | 450–500        | 4.48            |
| 500–550        | 6.23            | 500–550        | 7.30            |
| 550–600        | 14.07           | 550–600        | 14.97           |
| 600–650        | 18.70           | 600–650        | 7.00            |
| 650–700        | 5.42            | 650–700        | 9.28            |
| 700–750        | 20.50           | 700–750        | 5.45            |
| 750–800        | 10.98           | 750–800        | 2.95            |
| 800–850        | 11.73           | 800–850        | 9.27            |
| 850–891        | 3.30            | 850–900        | 4.08            |
| —              | —               | 900–913        | 2.22            |
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Results

1. Environmental profiles

The surface mixed layer was observed to extend throughout the upper 250 m during both dives HPD0083 and HPD0084 (Fig. 2). As depth increased, temperature and salinity decreased fairly rapidly to 600 m depth. Below 600 m depth, extremely different vertical profiles of environmental parameters were observed between the outside

Fig. 2. Vertical profiles of temperature, salinity, oxygen and density vs depth. (A) HPD0083, (B) HPD0084.
A salinity minimum, indicating the presence of North Pacific Intermediate Water (Reid 1965), was observed in the 600–800 m depth strata outside the Sumisu Caldera, while temperature and oxygen levels continued to decrease with increasing depth. On the other hand, the Sumisu Caldera was filled with warmer water with a minimum temperature of around 10°C, relatively high oxygen and no salinity minimum. Below 600 m depth, density values were mostly stable, indicating a high degree of mixing right to the bottom of the caldera.

2. Gelatinous zooplankton

A total of 61 gelatinous zooplankton morphotaxa were identified during dives HPD0083 and HPD0084: 21 ctenophores, 16 siphonophores, 10 hydromedusae, 4 scyphozoans and 10 thaliacean morphotaxa. The vertical distributions for each taxonomic group per 50-m-thick depth stratum are graphed in Fig. 3, and Figs. 5–7. Details of their distributions, the characters that allowed their identification from video sequences, and interpretive remarks appear below. The number of observed morphotaxa outside and inside the Sumisu Caldera were 39 (n=201) vs. 41 (n=215) while the total time of observation was 140 vs. 109 min, respectively.

2.1 Ctenophora

Twenty-one ctenophore morphotaxa were observed, with 11 morphotaxa identifiable to genus level (described genera) or lower, and with 13 of the 21 morphotaxa definitely belonging to separate, distinct species. Ctenophora were one of the most dominant morphotaxa both outside and inside the Sumisu Caldera (16 morphotaxa and 14 morphotaxa observed, respectively). Lobate ctenophores were abundant in the subsurface layer outside the caldera, but a bimodal distribution was observed inside the caldera, with maximum abundance peaks at 350–400 m and 750–800 m depth. They were observed over a wide depth range, while most “cydippid” ctenophores were distributed below 500 m depth both inside and outside the caldera (Fig. 3).

The genus Bathocyroe and the morphotype “Undescribed Lobata [No auricles]” were abundant inside the caldera.

Undescribed Lobata “No auricles” (Fig. 4 A, B)—A total of 7 individuals of this morphotype were observed only inside the Sumisu Caldera between 826 m–864 m depth (10.0–10.1°C, 34.29–34.31, 2.8 ml L⁻¹). The body shape superficially resembled the genus Bolinopsis but they lacked auricles, which Lobate ctenophores usually have. Substomodeal comb rows did not extend onto the oral lobes. In the present study, only one morphotype was observed, despite several morphotypes of lobate ctenophores lacking auricles having been reported in the lit-
Bathocyroe fosteri Madin & Harbison, 1978—Bathocyroe fosteri occurred both outside and inside the Sumisu Caldera, at 716 m (7.4°C, 34.28, 2.2 ml L⁻¹) and at 687 m and 688 m depths (10.5 & 10.5°C, 34.35 & 34.31, 2.9 & 2.9 ml L⁻¹), respectively. Bathocyroe fosteri possessed extremely short comb rows in comparison with the total body length and fairly large, wide auricles; body with a pair of broad oral lobes slightly compressed in tentacular plane; body colour transparent, except for red-pigmented stomodaeum; eight short comb rows of equal length extending to level of tentacle bulbs; two pairs of white tentacle bulbs facing each other near aboral end of stomodaeum.

Remarks: the extremely short comb rows and broad auricles enable this species to be easily distinguished from its congers.

Bathocyroe longigula Horita, Akiyama & Kubota, 2011 (Fig. 4 C, D)—Bathocyroe longigula was observed inside the Sumisu Caldera at 622 m and at 686 m depth (10.7 & 10.5°C, 34.38 & 34.38, 2.9 & 2.9 ml L⁻¹). Bathocyroe longigula had an extremely long, stomodaeum extending to almost half the length of its oral lobes; stomodaeum clearly observed as long, white line in present video records.

Remarks: Tiny, irregularly-shaped dark-orange spots have been reported to be scattered along the meridional canals, but were unable to be observed in the present video footage due to lighting and resolution constraints. This is only the second record of B. longigula in the literature, although an individual we consider assignable to this species was reported at 428 m depth in Sagami Bay by Kitamura et al. (2008b; see Fig. 25.13). This species was described from southwestern Japan in coastal waters at the surface (14.5°C), so this is the lowest temperature and deepest record for the species.

Bathocyroe sp. Not B. fosteri—Two individuals of this ctenophore morphotype were observed inside the Sumisu Caldera at 662 m and 686 m depth (10.6 & 10.5°C, 34.31 &

Fig. 4. Frame grabs of two lobate ctenophores Undescribed Lobata “No auricles” (A, B) and Bathocyroe longigula (C, D). Au: auricle, Cr: comb row, Sto: stomodaeum, Tb: tentacle bulb.
34.36, 2.9 & 2.9 ml L⁻¹), Bathocyroe sp. Not B. fosteri were clearly distinguishable from B. fosteri by having comb rows extending to the level of the base of the oral lobes.

Remarks: The ctenophores are possibly B. longigula but the comparative length of the stomodaeeum could not be ascertained.

**Bathocyroe spp.**—Three individuals were observed between 585–756 m depth (6.5–10.9°C, 34.27–34.32, 2.0–3.0 ml L⁻¹) outside the Sumisu Caldera, five individuals were observed between 577–753 m depth (10.4–11.4°C, 34.32–34.36, 2.8–3.1 ml L⁻¹) inside. Most of the individuals were identified by the position of the tentacle bulbs at the aboral end of the stomodaeeum and/or by the “frog kick” lobe-flapping behavior, the undulating form of which is particular to the genus Bathocyroe.

Remarks: Bathocyroe sp. includes several indeterminable species of Bathocyroe.

**Lobata sp. “Boli”**—Three individuals of Lobata sp. “Boli” were observed between 231–338 m depth (17.1–18.7°C, 34.71–34.80, 3.6–4.1 ml L⁻¹) above the outside of the caldera, eleven individuals between 577–753 m depth (15.6–16.6°C, 34.59–34.64, 3.5–3.6 ml L⁻¹) above the inside of the caldera. Lobata sp. “Boli” is a proxy name for one morphotype of lobate ctenophore. Lobata sp. “Boli” possessed an elliptical body shape; oral lobes were as large as half body length; body color transparent; comb row lengths superficially equal, but substomodaeal comb rows slightly longer than subtentacular comb rows; mouth placed halfway along length of oral lobes, with tentacle bulbs present. Video quality did not allow observations of the auricles or canal structures. Video quality did not allow observations of the auricles or canal structures.

Remarks: They might be immature Bolinopsis.

**Bolinopsis sp.**—Only one individual of Bolinopsis sp. was observed at 284 m (18.3°C, 34.77, 3.8 ml L⁻¹) above the outside of the caldera. The ctenophore possessed an ovoid body shape; statocyst deeply sunken; substomodaeal comb rows extending to end of oral lobes, auricles extending to almost same level as tip of mouth; subtentacular comb rows ratio 4:7 to total body length.

Remarks: Three congeners are known from Japanese waters, Bolinopsis infundibulum (O.F. Müller, 1776), Bolinopsis mikado (Moser, 1907) and Bolinopsis rubripunctata Tokioka, 1964. The observed individual was obviously distinguishable from B. infundibulum because of the differences in the length of the comb rows, but was difficult to attribute to, or distinguish from, B. mikado or B. rubripunctata. Furthermore, Bolinopsis mikado sensu Komai, 1918 resembles Bolinopsis vitrea (L. Agassiz, 1860) in the extreme (e.g., see illustrations from the São Sebastião Channel (Brazil) in Oliveira & Migotto 2006), not only in the general body structure but also with regard to the colour of the canals. These two species are possibly synonymous (personal observations), so it is also possible that B. vitrea occurs in Japanese waters.

**Eurhamphaea vexilligera** Gegenbaur, 1856—Three individuals of E. vexilligera were observed between 218–604 m depth (18.7–10.0°C, 34.80–34.31, 4.1–2.8 ml L⁻¹) outside the caldera. Eurhamphaea vexilligera possessed a fairly flattened body shape in the tentacular axis, aboral ends pointed and projected with two flexible filaments; round oral lobes arising at level of mouth, being small and only around 1/3 of total body length; auricles relatively short, their widths entirely equal, changing position only slowly; aboral sense organ extremely deeply sunken between the two pointy aboral projections.

Remarks: although reddish-pigmented spots along the meridional canals are an important character to identify this species, the present video did not allow visualization of the pigmentation. All individuals were identified by the body shape and presence of aboral filaments. To this date, although four other congeners have been described, they are all thought to be synonyms or to be species inquirenda (Mills 2017, and personal observations).

**Kiyohimea sp.**—Only one Kiyohimea sp. was observed, at 572 m depth (11.5°C, 34.35, 3.1 ml L⁻¹) inside the Sumisu Caldera. Kiyohimea sp. possessed a strongly compressed body in the tentacular axis, as with E. vexilligera, and also possessed two triangular aboral processes, but lacked aboral filaments; the aboral sense organ was situated at the bottom of the depression between the aboral projections; subtentacular comb rows began at top of aboral projections and continued onto auricles, substomodaeal comb rows began slightly above level of statocyst and extended aborally beyond level of mouth.

Remarks: The genus Kiyohimea includes two species, Kiyohimea usagi Matsumoto & Robison, 1992 and Kiyohimea aurita Komai & Tokioka, 1940. At this time, these two congeners are distinguished by the presence or absence of oral tentacles; K. usagi possesses tentacles but K. aurita only possesses a vestigium. However, except for this character, these two species are extremely similar. It is possible that these species were described as two different species but in reality they are the same species at a different state of development. The life history of this species should be investigated in the future, paying close attention to its development.

**Ocyropsis sp.**—Three individuals of Ocyropsis sp. were observed between 241–295 m depth (18.6–18.2°C, 34.79–34.73, 4.1–3.8 ml L⁻¹) above the outside of the caldera. Ocyropsis sp. possessed a laterally compressed body in the tentacular axis with a rounded aboral end, with the body shape looking like a rounded rectangle when viewed from the stomodaeal plane, since it had a slightly flattened aboral end; stout body structure and large lobes produced a vigorous flapping motion; auricles were long; four of the eight comb rows ran nearly parallel and almost faced the other four comb rows across the tentacular axis; substomodaeal comb rows were longer than subtentacular comb rows.

**Lobata spp.**—Three other individuals of Lobata spp. were observed above the outside of the caldera between 112–352 m depth (18.8–16.7°C, 34.81–34.69, 4.1–3.6 ml L⁻¹), six individuals of Lobata spp. were observed
inside the caldera between 634–871 m depth (10.7–10.0°C, 34.31–34.34, 2.9–2.8 ml L⁻¹). Apart from possessing two oral lobes, nothing more was able to be ascertained about their morphology due to the quality of the video. Lobata spp. obviously included more than one species.

**Cestum veneris Lesueur, 1813**—One individual of *C. veneris* was observed at 167 m depth (18.7°C, 34.81, 4.1 ml L⁻¹) above the outside of the caldera. *Cestum veneris* possessed a fairly flattened, ribbon-like body shape, without any lobes and/or auricles, that was strongly compressed in the tentacular plane and extended in the stomodaeal plane; four subtentacular meridional canals arose from the stomodaeum, then curved immediately outward and ran along the mid-line of the body.

Remarks: Family Cestidae includes only two species, belonging to two different genera: *C. veneris* and *Velemen parallelum* (Fol, 1869). These two species are distinguished by characteristics of the comb rows, meridional canal structure, form of the gonads, and body size. *Velemen parallelum* possesses four subtentacular meridional canals that arise directly, without curving, at the midpoint of the body to run parallel to the body edge.

**Cestidae sp.**—Four individuals of *Cestidae* sp. were observed between 161–326 m depth (18.7–17.4°C, 34.80–34.71, 4.1–3.7 ml L⁻¹) above the outside of the caldera, and one individual was observed at 312 m (17.0°C, 34.69, 3.7 ml L⁻¹) above the inside of the caldera. The most representative character of the family is a ribbon-like, long and flat body shape without lobes and/or auricles with a basically transparent body colour.

Remarks: Occasionally, cestid ctenophores superficially seem like the leptocephalus larva stage of Anguilliformes (i.e. eels), especially when they curl themselves up. When ribbon-like, transparent, gelatinous animals are observed, one should carefully investigate whether or not they have a head, or whether there are gastrovascular structures in the midline of the body.

**Cydippid larvae**—“Cydippid larvae” occurred both inside and outside the Sumisu Caldera at 613 m (9.6°C, 34.32, 2.7 ml L⁻¹) outside the caldera and at 548 m (12.1°C, 34.39, 3.2 ml L⁻¹) inside the caldera. “Cydippid larvae” possessed a transparent ovoid body, with eight short comb rows and two tentacles that were positioned at the midpoint of the stomodaeum and near the external surface of the body.

Remarks: presumable the larval stage of lobate, cestid or thalassocalycid ctenophores.

**Cydippida sp. “Little ruby”**—One individual of *Cydippida* sp. “Little ruby” was observed at 756 m (6.48°C, 34.28, 2.0 ml L⁻¹) outside the Sumisu Caldera. *Cydippida* sp. “Little ruby” was ovoid in body shape, being slightly compressed in the substomodaeal plane; cardinal red-colored body and dark red-pigmented stomodaeum; tentacle bulbs long; fine tentacles with numerous simple side branches, superficially emerging from the aboral end, however the opening of the tentacle sheath was wide and extensive, so the tentacles can seem to emerge at any level; eight comb rows extended nearly the entire body length.

Remarks: *Cydippida* sp. “Little ruby” is clearly an undescribed species. The canal structure has yet to be observed in detail (Fig. 25.9 in Kitamura et al. 2008b).

**Bathyctena sp. “Sagami”**—One individual of *Bathyctena* sp. “Sagami” was observed at 707 m depth (10.40°C, 34.37, 2.9 ml L⁻¹) inside the Sumisu Caldera. *Bathyctena* sp. “Sagami” possessed a spherical body shape; body colour transparent, dark reddish-brown pigmented stomodaeum with side branches called diverticula arising from the paragastric canals and extending onto the stomodaeum; short, white tentacle bulbs were large and angled in an “L” shape, placed mid-length along the body; comb row lengths equal, extending 70–80% of total body length.

Remarks: *Bathyctena* sp. “Sagami” is often observed with its tentacles retracted (Hidaka, unpublished data). When sighted in situ during ROV dives, the two large tentacle bulbs are very reflective and appear as two bright white, round spots, leading to its other nickname “two spots”. The first report of *Bathyctena* sp. “Sagami” was between 500 to 1000 m in depth in Sagami Bay, which is located halfway along the Pacific coast of Japan (Lindsay & Hunt 2005). Lindsay & Miyake (2007) gave a preliminary morphological description, with more detailed descriptions of the species given in Japanese in 2009 (Lindsay & Miyake 2009), under the Japanese common name “Sagamishinkai-fusenkurage” meaning “bathycetenid cydippid from Sagami”, and by Lindsay in 2015 (Minemizu et al. 2015).

**Mertensiidae sp. “Wadako”**—One individual of *Mertensiidae* sp. “Wadako” was observed at 533 m (12.19°C, 34.43, 3.2 ml L⁻¹) outside the Sumisu Caldera. *Mertensiidae* sp. “Wadako” possessed an extremely compressed body in the substomodaeal plane with two keel-like projections at the aboral end, and a slightly extended mouth; transparent body; statocyst not sunken; substomodaeal comb rows extended from tip of aboral end of keels to edge of mouth; substentacular comb rows extended from aboral end near statocyst to edge of mouth; two tentacle bulbs of boomerang shape, curved concavely towards mouth; tentacle sheath opening at same level as base of keels; tentacles arose from stomodaeal side of tentacle bulbs, emerging aborally with sausage-shaped, coiled tentilla.

Remarks: Kitamura et al. (2008b) gave a short description of the morphotype Mertensiidae sp. “Wadako”, as “*Mertensia* sp.” (Fig. 25.6 in Kitamura et al. 2008b). Since then, Lindsay & Miyake (2009) gave a slightly more detailed description in Japanese as “*Mertensiidae* sp. B”, based on two collected specimens. In the article, they also gave it the Japanese common name “Wadako-kurage” meaning “Japanese traditional kite-shaped jellyfish”. This morphotype has been observed in Sagami and Suruga Bays (Kitamura et al. 2008b), and outside the Sumisu Caldera (present study).

**Hormiphora palmata Chun, 1898**—Two individuals
Fig. 5. Comparative vertical distribution of cnidarians for each 50-m depth stratum outside and inside the Sumisu Caldera, excluding Narcomedusae.

Fig. 6. Comparative vertical distribution of Narcomedusae for each 50-m depth stratum outside and inside the Sumisu Caldera.
of *H. palmata* were observed at 624 m and 661 m (9.32 & 8.67°C, 34.31 & 34.28, 2.7 & 2.5 ml L⁻¹) outside the Sumisu Caldera. *Hormiphora palmata* possessed a teardrop-shaped body, with an extending mouth and a slightly flattened aboral end; body colour transparent; eight comb rows of equal length, extending 2/3–4/5 total body length from aboral end, with the comb rows evenly spaced; tentacle bulbs long and narrow, placed quite close and parallel to the stomodaeum; broad tentacle sheaths ran toward aboral end in a gentle curve, opening at approximately 1/6 body length from aboral end; white tentacles with numerous thread-like tentilla arising slightly aboral to the mid-point of the tentacle bulbs.

**Remarks:** *Hormiphora palmata* is a common cydippid ctenophore, usually found in open-ocean, surface waters. However, the present study is the deepest-yet observation record for the species, at 661 m depth.

According to the original description of the species (Chun 1898), immature individuals possess palm-shaped tentilla on their tentacles, and these are so large that they are unable to be retracted into the tentacle sheaths. However, the present morphotype has been reported to only have simple, thread-like tentilla, even at a body length of only 8 mm (Minemizu et al. 2015). Developmental studies on *H. palmata* should be carried in the future. *Hormiphora japonica* Moser, 1907 is a synonym.

**Cydippida sp. “White tear drop”—**Two individuals of Cydippida sp. “White tear drop” were observed at 588 m and 618 m (10.64 & 9.62°C, 34.27 & 34.32, 2.9 & 2.8 ml L⁻¹) outside Sumisu Caldera, and one individual was observed at 696 m (10.45°C, 34.37, 2.9 ml L⁻¹) inside the caldera. This cydippid morphotype has a white-coloured, elongated teardrop-shaped body; tentacle sheaths open near the aboral end, or there is an extensive groove between adjacent subtentacular comb rows that make it seem so; tentacles possess simple, thread-like tentilla.

**Remarks:** Cydippida sp. “White tear drop” appears to belong to the Pleurobrachiidae or perhaps an undescribed family (personal observations).

**Cydippida spp.—**Two individuals assignable only to Cydippida spp. were observed at 555 m and 866 m (11.3 & 10.5°C, 34.39 & 34.30, 3.0 & 1.6 ml L⁻¹) outside the caldera, and two individuals were observed at 320 m and 786 m (16.9 & 10.2°C, 34.61 & 34.35, 3.6 & 2.8 ml L⁻¹) inside the caldera. These individuals were ovoid in shape, possessed two extended tentacles with tentacle bases not being near the external surface, and had 8 comb rows.

**Ctenophore spp.—**One individual, identifiable only to Phylum, was observed at 413 m (15.45°C, 34.56, 3.5 ml L⁻¹) inside the Sumisu Caldera. Ovoid body and bright comb rows were visible.

### 2.2 Cnidaria

A total of 30 morphotaxa of Cnidarians were observed at the Sumisu Caldera. Siphonophores were sparsely distributed throughout all depth strata both inside and outside the caldera (Fig. 5). Hydromedusae were infrequent, except for two remarkable species: the very abundant hydromedusa *Earleriа bruuni* (Navas, 1969) inside the caldera, and the frequently observed deep-sea narcomedusa *Salmisius incisa* sensu lato, respectively (Fig. 5, Fig. 6). Scyphomedusae were only observed below 580 m depth.

#### 2.2.1 Siphonophores

A total of 16 siphonophore morphotaxa were observed, with 10 morphotaxa identifiable to genus level (described genera) or lower, and with 9 of the 16 morphotaxa definitely belonging to separate, distinct species. The number of observed siphonophoran morphotaxa outside and inside the caldera was 9 vs. 11, respectively. There were no significant patterns (Fig. 5).

**Agalma elegans (pro parte M. Sars, 1846)—**One individual of *A. elegans* was observed at 288 m (18.2°C, 34.76, 3.8 ml L⁻¹) above the outside of the Sumisu Caldera. *Agalma elegans* possessed an evenly-elongated colony shape with a linearly arranged stem, and with the siphosome being much longer, but the same width, as the nectosome; the pneumatophore had a long stalk, causing it to almost always be oriented vertically; adjacent gastrozooids were very widely spaced and were the only zooids that were visibly pigmented.

**Remarks:** The widely spaced gastrozooids and the siphosome being equal to or more slender than the nectosome are critical characters to distinguish it from *Agalma okeni* Eschscholtz, 1825. Most of the original description of *A. elegans*, apart from the structure of the tentilla, was based on the morphology of *Nanomia cara* Agassiz, 1865 (Sars 1846).

**Erenna sp.—**One individual of *Erenna* sp. was observed at 705 m depth (10.4°C, 34.33, 2.8 ml L⁻¹) inside the Sumisu Caldera. *Erenna* sp. possessed a thick nectosome, had conspicuous nematocyst patches on the ostia of the nectophores and tips of the bracts, and the distance between adjacent gastrozooids was short.

**Remarks:** The macromorphology of this individual closely resembled *Erenna insidiator* Pugh & Haddock, 2016, although the diagnostic characters for the species were not readily evident in the video footage.

**Bargmannia amoena Pugh, 1999—**One individual of *B. amoena* was observed at 486 m depth (13.6°C, 34.48, 3.4 ml L⁻¹) outside the Sumisu Caldera, while two individuals were observed at 580 m and 581 m depth (11.2 & 11.2°C, 34.40 & 34.39, 3.0 & 3.0 ml L⁻¹) inside the caldera. *Bargmannia amoena* possessed a longitudinally extended and laterally flattened nectosome with distinctive, elongated nectophores (up to 32); the siphosome was thinner and cormidia indistinct compared to *Bargmannia elongata* Totton, 1954 (see p. 161 of Minemizu et al. 2015 for comparison of macromorphologies); whitish gastrozooids were positioned sparsely but in a regular manner on the stem.

**Remarks:** The flaccidity of the siphosome contrasts with that of *B. elongata*.

**Bargmannia sp.—**Only one individual of *Bargmannia* sp. was observed, at 540 m depth (12.1°C, 34.42,
3.2 ml L\(^{-1}\)) outside the Sumisu Caldera. *Bargmannia* sp. possessed a longitudinally extended and laterally flattened nectosome and had distinctive elongated nectophores.

**Remarks:** The characteristic sinusoidal swimming behavior allowed easy identification to genus level.

**Physophora gilmeri** Pugh, 2005—Two individuals of *P. gilmeri* were observed inside the Sumisu Caldera at 274 m and 390 m depth (17.7 & 15.7°C, 34.8 & 34.6, 3.8 & 3.5 ml L\(^{-1}\)). *Physophora gilmeri* possessed an elongated dome-shaped nectosome with a long and narrow pneumophore; siphosome not elongated but rather in a corn just below the nectosome; palpons long and well-developed, encircling the colony in a manner reminiscent of a grass skirt, palpon tips pigmented bright orange, развит, spirally-coiled siphosome longer than half entire colony length; nectosome, due to having low variation in size of the nectophores; the siphosome dissociates and the colony was angled obliquely to vertically.

**Remarks:** Two species in the genus *Physophora* have been described: *P. gilmeri* and *Physophora hydrostatica* Forsskål, 1775. If they are mature, it is easy to distinguish them by the different shape and colour of their pneumatophores, and coloration of palpons, etc. (for detailed comparisons see Pugh 2005). When viewed laterally, the nectophores of *P. hydrostatica* have a translucent circle corresponding to the cross section of the T-shaped nectosome, while *P. gilmeri*, which has a Y-shaped nectosome, does not have this translucent circle.

**Forskalia asymmetrica** Pugh, 2003—One individual of *F. asymmetrica* was observed at 602 m depth (10.1°C, 34.34, 2.8 ml L\(^{-1}\)) outside the Sumisu Caldera, two individuals were observed at 495 m and 582 m depth (14.1 & 11.2°C, 34.52 & 34.40, 3.4 & 3.0 ml L\(^{-1}\)) inside the caldera. *Forskalia asymmetrica* possessed a cylindrical, rather than tapering, nectosome, due to having low variation in the size of the nectophores; the siphosome dissociates and changes shape easily; spirally-coiled siphosome shorter than half entire colony length; nectophores flattened in the upper-lower plane; gastrozooids positioned a long distance from the sipho- somal stem, the gastrozooids medium in size and number.

**Forskalia formosa** Keferstein & Ehlers, 1860—One individual of *F. formosa* was observed inside the Sumisu Caldera at 638 m depth (10.7°C, 34.31, 2.9 ml L\(^{-1}\)). *Forskalia formosa* possessed an elongated, tapering nectosome; the pneumophore extended considerably anterior to the main body of the nectosome; fin tree-shaped siphosome tapering posteriorly, thickness of the anterior end of the siphosome much wider than the width of nectosome when relaxed; spirally-coiled siphosome longer than half entire colony length; nectophores flattened in the upper-lower plane; gastrozooids positioned a long way from the siphosomal stem, the gastrozooids medium in size and number.

**Remarks:** The characteristic sinusoidal swimming behavior allowed easy identification to genus level.

**Physophora gilmeri** Pugh, 2005—Two individuals of *P. gilmeri* were observed inside the Sumisu Caldera at 274 m and 390 m depth (17.7 & 15.7°C, 34.8 & 34.6, 3.8 & 3.5 ml L\(^{-1}\)). *Physophora gilmeri* possessed an elongated dome-shaped nectosome with a long and narrow pneumophore; siphosome not elongated but rather in a corn just below the nectosome. Spinning swimming behavior is often observed in *Forskalia*.

**Physophora hydrostatica** Pugh, 2003—One individual of *P. hydrostatica* was observed at 802 m (10.2°C, 34.36, 2.8 ml L\(^{-1}\)) inside the Sumisu Caldera. *Physophora hydrostatica* has a corm-like siphosome with large palpons radiating out just below the nectosome. Spinning swimming behavior is often observed in *Forskalia*.

**Remarks:** During ROV observations, a pneumatophore usually appears as a bright white spot or bubble, attached to the anterior pole of the nectosome. Some physonect siphophore species retract the pneumatophore into an apical hollow in the nectosome.

**Clausophyes sp.**—One individual of *Clausophyes* sp. was observed at 802 m (10.2°C, 34.36, 2.8 ml L\(^{-1}\)) inside the Sumisu Caldera. *Clausophyes* sp. possessed two non-rigid nectophores that were heteromorphic and linearly opposed, and with the anterior nectophore tapering apically to a point; siphosome held within hydroecial flaps of posterior nectophore and therefore curving along lower line of posterior nectophore.

**Clausophyidae sp.** (Not *Clausophyes* sp., Not *Physophoraeidae*)—Twelve individuals assignable only to the morphaxon *Physophoreidae* due to poor video quality were observed outside the Sumisu Caldera between 260 m–824 m depth (18.4–5.4°C, 34.77–34.30, 3.9–1.7 ml L\(^{-1}\)) and five were observed inside between 328 m–627 m depth (16.6–10.7°C, 34.61–34.37, 3.6–2.9 ml L\(^{-1}\)). Physonectae were identified by the presence of a gas-filled apical organ called a "pneumatophore" and an array of swimming bells called "nectophores" beneath the pneumatophore.

**Remarks:** Two individuals of Clausophyidae sp. were observed at 244 m (18.3°C, 34.38, 3.0 ml L\(^{-1}\)) inside the caldera. *Clausophyidae* sp. possessed a spirally-coiled siphosome but all clausophyids we observed had two.

**Diphyomorph sp.**—One individual assignable to either the Clausophyidae or Diphyidae and recorded here as "Diphyomorph sp." was observed at 244 m (18.3°C, 34.77, 3.9 ml L\(^{-1}\)) above the inside of the caldera. Diphyomorphs typically possess two dissimilar, linearly-adjointed nectophores.

**Remarks:** Taxonomically, Clausophyidae also includes siphonophores with a single nectophore but all clausophyids we observed had two.

**Diphyomorph sp.**—One individual assignable to either the Clausophyidae or Diphyidae and recorded here as "Diphyomorph sp." was observed at 244 m (18.3°C, 34.77, 3.9 ml L\(^{-1}\)) above the inside of the caldera. Diphyomorphs typically possess two dissimilar, linearly-adjointed nectophores.

**Remarks:** Diphyomorph spp. observed in deep waters by ROVs are more likely to be Clausophyids than other
diphyomorphs due to the larger colony sizes of members of this family. 

**Sphaeronectes sp.**—One individual of *Sphaeronectes* sp. was observed at 357 m (16.7°C, 34.69, 3.5 ml L⁻¹) outside the caldera. It possessed a single sub-spherical nectophore. **Remarks:** Sphaeronectes spp. within the Sphaeroneectidae are the only siphonophores to possess a single sub-spherical nectophore, with other single nectophore species having a streamlined, rocket-shaped nectophore. The Prayid subfamily Amphicaryoninae also looks spherically but has two nectophores, with one cradled by the other.

**Prayinae sp.**—One individual of Prayinae sp. was observed at 564 m (11.3°C, 34.39, 3.0 ml L⁻¹) outside the Sumisu Caldera. It possessed a pair of opposed, rounded nectophores, similar in size to each other.

**Remarks:** The form and branching pattern of the nectophoral mantle canals and presence/absence of a somatophoral mantle canals and presence/absence of a somato-nectophore. Similar to the genus *Stephanophyes* because, exceptionally within the Prayinae, this genus often has more than two opposing nectophores.

**Calycopehrae sp.** (Not Hippopodidae)—One individual of Calycophehrae sp. was observed at 200 m (18.63°C, 34.80, 4.0 ml L⁻¹) above the outside of the caldera. The bright white spot indicative of an anterior pneumatophore was absent and one or two nectophores were present.

**Remarks:** When a siphonophoran colony has only one or two nectophores and no pneumatophore present, but it is impossible to tell whether there is only one nectophore (Sphaeroneectidae, Nectopyramidinae, Enneagonum, Heteropyramis, Muggiaea, Clausophyes laetmata Pugh & Pages, 1993, *Diphyes chamissonis* Huxley, 1859) or whether the nectophores are opposed (Prayomorph) or linearly adjoined (Diphyomorph) it was treated as Calycophehrae sp.

**Siphonophorae spp.** (Not Physalliidae, Not Rhodaliidae)—Seven colonies identifiable only as Siphonophorae were observed within the Sumisu Caldera between 271–756 m depth (18.3–6.4°C, 34.77–34.28, 3.8–2.0 ml L⁻¹) and two inside at 380 m and 432 m (15.8 & 15.1°C, 34.64 & 34.36, 3.5 & 3.5 ml L⁻¹). The term Siphonophorae spp. refers to an elongated cnidarian colony where it is impossible to determine whether a pneumatophore or nectophores were present or not. This morphotaxon can include any kind of siphonophore except the cystonect Physalliidae (e.g., Portuguese man o’ war, *Physalia physalis* (Linnaeus, 1758)) and the physonect Rhodaliidae (benthic siphonophores with a corncob-like siphone).

### 2.2.2 Hydromedusae

A total of 10 morphotaxa of Hydromedusae were observed (Fig. 5, Fig. 6), with 5 morphotaxa identifiable to genus level (described genera) or lower, and with 7 of the 10 morphotaxa definitely belonging to separate, distinct species. The number of observed hydromedusan morphotaxa outside and inside the caldera was 6 vs. 7, respectively.

The leptomedusa *Earleria bruuni* was highly abundant inside the caldera. Narcomedusae differ from other hydromedusae in primarily preying on gelatinous prey and, because they therefore belong to a different functional group, their distribution has been graphed separately (Fig. 6). *Solmissetus incisa* sensu lato were relatively abundant both inside and outside the caldera and their population peak was in the 600–650 m depth stratum (Fig. 6).

**Pandea conica** (Quoy & Gaimard, 1827)—One individual of *P. conica* was observed at 245 m (18.63°C, 34.80, 4.0 ml L⁻¹) above the inside of the caldera. *Pandea conica* possessed a vertically-elongated, transparent exumbrella; frilled lips and well-developed gonads on the slender manubrium, manubrium length half the bell height; filiform tentacles with wide bulbs, numbering less than 40.

**Remarks:** We were not able to count the tentacles accurately, so the possibility exists that it might be *Pandea cybeles* Alvariño, 1988, which has 40 tentacles compared to the 20 of *P. conica*.

However, according to a description of *P. conica* from Japan (by Shin Kubota in Minemizu et al. 2015), the number of tentacles can be up to 44.

**Earleria bruuni** (Navas, 1969)—Twenty-three individuals of *E. bruuni* were observed only inside the Sumisu Caldera between 714–769 m (10.4–10.2°C, 34.36–34.34, 2.8 ml L⁻¹). *Earleria bruuni* possessed a fairly flattened umbrella with a small, dark red or brownish-pigmented manubrium; four cream-coloured, ellipsoidal gonads on the distal half of each radial canal, not extending onto the upper half; tentacles crowded and numerous so that it seems like the outer edge of the bell is white.

**Remarks:** *Earleria bruuni* was not observed even once outside the caldera, even though it was the most dominant species observed inside the Sumisu Caldera. Hidaaka-Umetsu & Lindsay (2017) discussed the possibility that medusae of the genus *Earleria* favour semi-closed submarine topography.

**Geryoniidae sp.**—One individual of Geryoniidae sp. was observed at 245 m (18.7°C, 34.79, 4.0 ml L⁻¹) above the outside of the caldera. Geryoniidae sp. possessed a hemispherical, transparent bell; a long, conical, gelatinous peduncle that protruded below the margin of the bell, and 4–6 long marginal tentacles.

**Remarks:** Geryoniidae includes only two species, *Geryonia proboscidalis* (Forsskål, 1775) and *Liriope tetraphylla* (Chamisson & Eysenhardt, 1821). They are easily distinguished by the number of radial canals and tentacles, and the shape of the gonads. *Geryonia proboscidalis* usually has 6 radial canals, 6 flat heart-shaped gonads on the radial canals, and 6 long tentacles alternating with 6 small tentacles. *Liriope tetraphylla* usually has 4 radial canals, 4 flat leaf-shaped gonads on the radial canals, and 4 long tentacles alternating with 4 small tentacles. We could not accurately count the number of tentacles in the present video.

**Halicreas minimum** Fewkes, 1882—Two individuals of *H. minimum* were observed at 701 m and 878 m (7.5 & 5.1°C, 34.28 & 34.29, 2.2 & 1.6 ml L⁻¹) outside the Sum-
isu Caldera, while one individual was observed at 661 m (10.6°C, 34.32, 2.9 ml L⁻¹) inside the caldera. \textit{Halicreas minimum} possessed a vertically-compressed, hemispherical bell with a prominent gelatinous projection arising from the apex; body transparent, except for whitish to orange radial canals and tentacles; 8 broad radial canals containing whitish gonads; 8 clusters of gelatinous papillae on the exumbrella overlying the radial canals, difficult to observe from a distance. Tentacles numbered in the hundreds and were prominent, being near transparent in the proximal half and intense white or reddish-coloured in the stiff, needle-like distal half.

\textit{Remarks:} when viewed laterally, the radial canals lie in the same plane and are therefore visible as a bright white horizontal line, while the mass of tentacles, when contracted, form a thicker white band. The combination of two white parallel lines/bands of similar length formed by the radial canals and tentacles, the apical projection, and the angularity of the dorsal margins of the exumbrella allow us to easily identify this species in \textit{situ}. Currently, \textit{H. minimum} is considered the only valid species in the genus.

\textit{Colobonema sericeum} Vanhöffen, 1902—Four individuals of \textit{C. sericeum} were observed between 468–644 m (14.2–8.7°C, 34.51–34.29, 3.4–2.5 ml L⁻¹) outside the caldera, and two individuals were observed at 581 and 663 m depth (11.2 & 10.6°C, 34.39 & 34.32, 3.0 & 2.9 ml L⁻¹) inside the caldera. \textit{Colobonema sericeum} possessed a transparent, hemispherical exumbrella and conical subumbrella; well-developed velum; eight narrow radial canals, linear gonads attached to canals along most of their length; long, white stomach without peduncle; tentacles numbered up to 32, tentacle colour near-transparent proximally, becoming whiter distally, and with distal portions frequently curled up when stationary and in fishing position. Tentacles were often jettisoned when the medusae were stimulated.

\textit{Remarks:} Tentacle colour sometimes appears to be blue during \textit{in situ} ROV observations.

\textit{Rhopalonematidae} \textit{spp.}—One individual assignable only to Rhopalonematidae \textit{spp.} was observed at 819 m depth (5.5°C, 34.30, 1.6 ml L⁻¹) outside, while the other was observed at 428 m depth (15.2°C, 34.58, 3.5 ml L⁻¹) inside the Sumisu Caldera. These individuals had transparent, hemispherical exumbrellas, eight radial canals and lacked gastric peduncles. The gonads on the radial canals were near the manubrium in the individual from 819 m depth.

\textit{Remarks:} The morphology of the individual from 819 m depth suggests it may have been \textit{Arctapodema} \textit{spp.}, especially since it jettisoned many fine tentacles when escaping—a behavior most commonly observed in \textit{Arctapodema} \textit{spp.}

\textit{Trachymedusae} \textit{spp.}—One hydromedusa assignable only to Trachymedusae \textit{spp.} was observed at 615 m depth (10.8°C, 34.35, 3.0 ml L⁻¹) inside the Sumisu Caldera. \textit{Trachymedusae} \textit{spp.} possessed a hemispherical exumbrella; a number of thick white tentacles, and swam rapidly with vigorous pulses. The tentacles seemed to be whiter distally, suggesting that it may have belonged to the family Halicreas-\textit{atidae} (\textit{Halicreas}?).

\textit{Solmissus incisa sensu lato}—Five individuals of \textit{S. incisa} \textit{s.l.} were observed between 578–614 m (11.1–9.6°C, 34.37–34.32, 3.0–2.7 ml L⁻¹) outside the caldera, and seven individuals were observed between 448–688 m (14.7–10.5°C, 34.58–34.35, 3.4–2.9 ml L⁻¹) inside the caldera.

\textit{Remarks:} At least two morphotypes of \textit{Solmissus incisa} \textit{s.l.} occurred. One morphotype was nicknamed "white socks" (see Hidaka-Umetsu & Lindsay 2018), and this morphotype seems to correspond to \textit{S. incisa} form B in Toyokawa et al. 1998. The other morphotype possessed a convex hemispherical bell and 24 triangular stomach pouches with perradial tentacles. The tips of the tentacles were curled and this morphotype does not seem to correspond to either form A or form B of \textit{S. incisa} in Toyokawa et al. (1998), nor the morphotype reported by Lindsay et al. (2015).

\textit{Narcomedusa} \textit{spp.}—Three hydromedusae, assignable only to \textit{Narcomedusa} \textit{spp.}, were observed between 600–660 m (10.1–8.7°C, 34.31–34.30, 2.8–2.5 ml L⁻¹) outside the Sumisu Caldera. \textit{Narcomedusa} \textit{spp.} possessed a flat, disk-like bell with tentacles arising from partway up the exumbrella, and lacked oral arms.

\textit{Remarks:} \textit{Narcomedusa} \textit{spp.} resembled \textit{Solmissus}.

\textit{Hydromedusa} \textit{spp.}—Three medusae, assignable only to \textit{Hydromedusa} \textit{spp.}, were observed between 284–585 m (18.2–10.8°C, 34.77–34.34, 3.8–3.0 ml L⁻¹) outside the caldera, and two individuals were observed at 225 and 619 m (18.6 & 10.8°C, 34.80 & 34.38, 4.0 & 3.0 ml L⁻¹) inside the caldera. \textit{Hydromedusa} \textit{spp.} possessed a transparent, hemispherical bell, had numerous short tentacles, and lacked oral arms.

\textit{Remarks:} \textit{Hydromedusa} \textit{spp.} probably includes several species.

2.2.3 Scyphomedusae

A total of 4 morphotaxa of Scyphomedusae were observed (Fig. 5). All of the Scyphomedusae occurred deeper than 583 m depth. The most abundant scyphomedusa \textit{Periphylla periphylla} (Pérón & Lesueur, 1810) was only observed outside the Sumisu Caldera.

\textit{Ulmaridae gen. et sp. nov.}—One individual of \textit{Ulmaridae gen. et sp. nov.} was observed at 813 m (10.2°C, 34.30, 2.8 ml L⁻¹) inside the Sumisu Caldera. \textit{Ulmaridae gen. et sp. nov.} possessed a hemispherical umbrella with the bell margin cleft into 8 broad lobes (lappets); thick, transparent mesogela; reddish to brown-coloured stomach and oral arms; base of stomach cross-shaped when viewed directly from above; a total of 16 canals arose from the base of the stomach; dozens of subumbrellar tentacles.

\textit{Remarks:} This undescribed species was also observed at 843 m depth (10.1°C, 34.34, 2.8 ml L⁻¹) during the same dive inside the caldera (HPD0084), but it was not treated in the semi-quantitative analysis because it was filmed during the ascent. Because of absorption of red light by seawater the stomach and oral arms can appear brown or even grey when the medusa is observed from a distance.

\textit{Periphylla periphylla} (Pérón & Lesueur, 1810)—Five
individuals of *P. periphylla* were observed between 704–751 m (7.5–6.7°C, 34.29–34.23, 2.2–2.0 ml L\(^{-1}\)) outside the Sumisu Caldera. *Periphylla periphylla* possessed a steep conical or dome-shaped bell that was usually higher than wide; body colour transparent or brownish, conical stomach pigmented in cardinal red; whitish U- or J-shaped gonads in 4 pairs, near the base of the stomach; solid marginal tentacles arising from clefts between the lappets.

**Remarks:** *Periphylla periphylla* is considered a cosmopolitan species, being absent only in the Arctic Ocean and the Sea of Japan (Minemizu et al. 2015). The genus *Periphylla* is currently considered monotypic, although evidence exists that there may be more than one species (Lindsay 2005, Minemizu et al. 2015).

*Atolla* sp.—One individual of *Atolla* sp. was observed at 694 m depth (7.9°C, 34.23, 2.3 ml L\(^{-1}\)) outside the Sumisu Caldera. *Atolla* sp. possessed a flat exumbrella with an obvious coronal furrow; brownish-coloured body with whitish tentacles; tentacles numbered more than 8 and it was also dragging a single, extremely long, hypertrophied tentacle.

**Remarks:** Based on the colour of the individual, it was not *Atolla vanhoffeni* Russell, 1957, which possesses a transparent bell.

*Coronatae* sp. (Not Atollidae, Not Paraphyllinidae, Not Periphyllidae)—One individual of Coronatae sp. was observed at 583 m depth (11.2°C, 34.39, 3.0 ml L\(^{-1}\)) inside the Sumisu Caldera. Coronatae sp. possessed a coronal furrow on the exumbrella; transparent body colour; more than 6 tentacles; tips of tentacles with terminal knob.

**Remarks:** This individual seems to belong either to the genus *Nausithoe* or *Atorella*.

### 2.3 Thaliacea

A total of ten morphotaxa of thaliaceans were observed, with 2 morphotaxa identifiable to genus level (described genera) or lower, and with 4 of the 10 morphotaxa definitely belonging to separate, distinct species. The number of observed thaliacean morphotaxa outside and inside the caldera was 6 vs. 7, respectively. While *Cyclosalpa* or salps belonging to the subfamily Cyclosalpinae were abundant in the upper subsurface layers (Fig. 7), salps belonging to the subfamily Salpinae were abundant at rather deeper depths both inside (HPD0083) and outside the Sumisu Caldera (HPD0084).

**Doliolid nurse**—A doliolid nurse colony was observed at 147 m depth (18.8°C, 34.81, 4.1 ml L\(^{-1}\)) above the inside of the caldera. One transparent, simple, barrel-shaped zooid pulled behind it a long, fuzzy tail-like structure, presumably zooids attached to its dorsal spur.

**Remarks:** Doliolid nurses can seem like siphonophores sometimes when observed in the video record. However, the siphosomes of siphonophores invariably possess obvious clusters of cormidia on their stems, visible as alternating white-clear areas, so that they can be distinguished from doliolids. The escape responses of siphonophores and doliolid nurses also differ, with nurses jetting back in the...
direction of the dorsal spur to form a V-shape.

**Cyclosalpa sp. solitary zooid**—One solitary zooid of *Cyclosalpa* sp. was observed at 181 m depth (18.7°C, 34.77, 4.0 ml L$^{-1}$) above the inside of the caldera. *Cyclosalpa* sp. solitary zooid possessed a single transparent test with a straight gut overlying the gill bar, which lay obliquely in the middle of the tunic; more than five light organs were arranged on both sides of the tunic; it bore a coiled stolon ventrally.

**Cyclosalpa spp. aggregate zooids**—Five chains of *Cyclosalpa* spp. aggregate zooids” were observed between 103–241 m (18.8–18.7°C, 34.81–34.80, 4.1–4.0 ml L$^{-1}$) above the outside of the caldera, three were observed between 172–313 m (18.7–17.0°C, 34.76–34.64, 4.0–3.7 ml L$^{-1}$) above the inside of the caldera. Chain morphology was wheel-like or when composed of only a couple of zooids was chain-like, with zooids being conjoined tenaciously with a short peduncle. Each zooid possessed two tail-like projections arising from the posterior part of the tunic and a ringed yellow gut lay at the base of the projections.

**Remarks:** *Cyclosalpa* spp. aggregate zooids were likely either *Cyclosalpa barkeri* Ritter, 1905 or *Cyclosalpa foxtoni* Van Soest, 1974. However, to identify the species it is necessary to observe the shape of the dorsal tubercle, which was not visible in the present video record.

**Cyclosalpinae spp. solitary zooid**—An individual of *Cyclosalpinae* sp. was observed at 176 m depth (18.8°C, 34.81, 4.1 ml L$^{-1}$) above the outside of the caldera, and one at 637 m depth (10.7°C, 34.31, 2.9 ml L$^{-1}$) inside the caldera. *Cyclosalpinae* sp. solitary zooid possessed a single transparent test, with a straight gut overlying the gill bar, which lay obliquely in the middle of the tunic. The individual observed outside the caldera (HPD0083) bore a coiled stolon ventrally, while the shape of the gut was not determinable in the video of the second individual.

**Salpinae cf. Salpa spp. aggregate zooids**—Two chains of *Salpa* spp. aggregate zooids were observed at 549 m and 608 m depth (12.0 & 10.9°C, 34.41 & 34.38, 3.2 & 3.0 ml L$^{-1}$) inside the caldera. Salpinae cf. *Salpa* spp. aggregate zooids formed linear chains; each blastozoooid had pointy projections on both anterior and posterior ends.

**Salpinae sp. solitary zooid**—One individual of Salpinae sp. was observed at 478 m depth (13.8°C, 34.53, 3.3 ml L$^{-1}$) inside the caldera. “Salpinae sp. solitary zooid” possessed a single transparent test and had a spherical gut.

**Salpinae spp. aggregate zooids**—Nine chains of *Salpinae* spp. zooids were observed between 502–621 m (13.8–9.3°C, 34.50–34.32, 3.3–2.7 ml L$^{-1}$) outside the caldera, while eight were observed between 269–631 m (18.1–10.5°C, 34.75–34.37, 3.8–2.9 ml L$^{-1}$) inside the caldera. “Salpinae spp. aggregate” chains were straight chains and the zooid guts were spherical, appearing as bright white spots.

**Salpida sp. solitary zooid**—One individual of Salpida sp. was observed at 478 m depth (13.8°C, 34.53, 3.3 ml L$^{-1}$) outside the caldera. “Salpida sp. solitary zooid” possessed a transparent barrel-shaped tunic and had a gill bar that lay obliquely in the middle of the tunic.

**Pyrosoma atlanticum** Péron, 1804—one colony of *P. atlanticum* was observed at 705 m depth (7.5°C, 34.28, 2.2 ml L$^{-1}$) outside the caldera. *Pyrosoma atlanticum* was a long, finger-shaped colony that had a pinkish colour. No spines/projections occurred around the open end of the colony and the width to length ratio of the colony was less than 0.16.

**Remarks:** size up to 60 cm.

**Pyrosomatidae spp.**—One colony of Pyrosomatidae spp. was observed at 705 m depth (7.5°C, 34.29, 2.2 ml L$^{-1}$) above the inside of the caldera and three were observed between 497–801 m (14.0–10.2°C, 34.50–34.36, 3.4–2.8 ml L$^{-1}$) inside the caldera. Pyrosomatidae spp. colonies were long and cylindrical, colored pinkish, and some colonies could be seen to be tapered into a tip.

**Discussion**

**Taxonomic identification based on ROV video records**

Identications of morphotaxa or morphospecies from ROV video records for ecological investigations are usually based on only a few morphological characters, due to priority being given to gathering quantitative data, and observation time per individual is often short. Hence, traditional identification methods, such as the use of hierarchical taxonomic keys, do not always work well. In particular, microscopic analyses are all but impossible. In this respect, in order to assess the pelagic fauna occurring above deep-sea mineral deposits for Environmental Impact Assessments using ROVs, the establishment of a field guide based on morphological characters visible with the naked eye or a lower resolution video camera is a pressing need. In expectation of this future demand, the present study described the morphological and behavioral characters for each taxon that we were able to observe in the ROV video record. As a result, a total of 61 gelatinous zooplankton morphotaxa: 21 ctenophore morphotaxa; 16 siphonophore morphotaxa; 10 hydromedusan morphotaxa; 4 scyphomedusan morphotaxa; 10 thaliacean morphotaxa were observed and recognized. Some of these morphotaxa were higher taxa, based on classical taxonomy, while some morphotaxa were described here independently of the existing, flawed higher taxonomy (e.g., “little ruby” cydippid).

The morphological characters that allow us to identify each morphotaxon in the video record are usually not one, but rather a combination of possession and/or absence of several morphological features. For instance, two genera of lobate ctenophores, *Eurhamphaea* and *Kiyohimea*, both possess two triangular projections on their aboral ends and this character is exceptional among the presently-described lobate morphotaxa. *Eurhamphaea* also possesses one flexible filament on the distal extreme of each of these projections, while *Kiyohimea* lacks these filaments. On the ba-
sis of these two morphological characters alone, combined with the presence of “lobes”, we can easily identify these two genera. Although taxonomic identification based on ROV images is not always easy, adopting practical morphological characters for taxon identifications is imperative for conducting ecosystem-level community characterizations in the future. Furthermore, we recommend that care should be taken when preparing taxonomic papers, such as new species descriptions, to include macromorphological characters allowing distinctions between morphotaxa to be made based on video and/or image data alone.

In his description of Physophora gilmeri, Pugh described comparative characteristic differences between the new species and Physophora hydrostatica in his discussion in a meticulous manner (Pugh 2005). For instance, he described and compared the colours and shapes of the pneumophores, and colours and shapes of the palpons, etc. Thanks to the comparisons given in the discussion, we were able to clearly distinguish these congeners in the present video records. In another of Pugh’s papers, he published photographs of the colonies of each species of the physosnet siphonophore Bargmannia, along with their descriptions (Pugh 1999). With net-collected samples, siphonophore colonies are invariably broken into pieces and, therefore, most species descriptions of siphonophores have focused on the morphology of different zooid types, with morphological information at the whole colony level rarely being included. However, in accordance with developments concerning in situ survey methodologies, more and more image-based investigations are expected to be carried out. Therefore, concrete descriptions of the major macromorphological characters that are observable from a distance and can serve to distinguish between morphotaxa observed in situ, are invaluable.

Amon et al. (2007a, b) anticipated this need and created an atlas of benthic and benthopelagic megafauna based on the videos and still images recorded by ROVs and Autonomous Underwater Vehicles (AUVs) at the Clarion-Clipperton Zone (CCZ). There are in situ photographs and short descriptions of the species for a wide number of morphotaxa. In Japanese waters, there are two seminal papers that include taxonomic notes for identifying gelatinous zooplankton morphotaxa in situ. Toyokawa (1998) gave notes on a total of 14 morphotaxa of cnidarians and ctenophores using the human-occupied submersible vehicle Shinkai 2000, while Lindsay et al. (2015) described a total of 28 cnidarian, ctenophoran and appendicularian morphotaxa based on the video record from the ROV Hyper-Dolphin. The present study adds to this legacy.

High gelatinous zooplankton concentrations in deep-sea calderas: ecological comparison

In the present study, the numbers of gelatinous zooplankton morphotaxa observed outside and inside the caldera were 39 (n=106) vs. 41 (n=124) respectively, while the total time of observation was 140 vs. 109 min. Despite the observation time inside the caldera being 30 minutes shorter than outside, the number of observed morphotaxa was approximately equal to or higher, and the number of observed individuals was higher, inside the caldera. In particular, large numbers of three gelatinous zooplankton morphotaxa, Lobata sp. “Boli” (ctenophore), undescribed Lobata “No auricles” (ctenophore) and Earleria bruuni (Leptomedusae), were observed inside the Sumisu Caldera. “Boli” occurred both inside and outside the caldera, but was most abundant inside the caldera in the 300–450 m depth stratum, which is somewhat deeper than the caldera rim (about 200 to 450 m depth). In contrast, “No auricles” was abundant just above the caldera floor in the depth range from 826 to 864 m. The distribution of E. bruuni was extremely concentrated, with most individuals observed at 700–750 m depth. Hidaka-Umetsu & Lindsay (2017) conducted another similar ROV survey at a hydrothermally inactive deep-sea caldera (Kurose Hole), 218 km north of the Sumisu Caldera, on 24 September 2000, and also reported high population densities of E. bruuni only inside the caldera. In that study, however, high concentrations of lobate ctenophores were not observed. In that previous study, the number of gelatinous zooplankton morphotaxa observed outside and inside the caldera were 23 (n=38) vs. 10 (n=69) respectively, while the total time of observations was about 43 min both outside and inside. Similarly, in both studies, the calderas were filled with an isothermic, warm-water mass at a temperature of more than 10°C. Kurose Hole possesses a shallow rim (107 m depth), while the rim of the Sumisu Caldera possesses channels at around 200–450 m depth. The most different feature between the calderas is the existence (Sumisu) or not (Kurose) of an active hydrothermal vent with associated chemosynthetic ecosystems.

Taking into account the two studies described above (this study and Hidaka-Umetsu & Lindsay 2017), three different hypotheses can be proposed as to why gelatinous zooplankton were present at high concentrations inside but not outside these deep-sea calderas. Firstly, blooming of E. bruuni was not a seasonal event (September at Kurose Hole, March at Sumisu Caldera), and it may be a ‘normal’ phenomenon in these two deep-sea calderas. As Hidaka-Umetsu & Lindsay (2017) suggested, E. bruuni seems to favor deep isolated water masses, though the occurrence of E. bruuni was not restricted to near the caldera floor in the present study. Hidaka-Umetsu & Lindsay (2017) hypothesized that steep-walled concave topography, such as calderas and deep-sea canyons, should concentrate food resources (i.e. sinking particles and vertically migrating plankton) with depth, hence high concentrations of E. bruuni occurred in the near-bottom layer where food should be most concentrated. In the Sumisu Caldera, this species was found in large numbers at the depth of active venting and therefore, presumably, where food concentrations (e.g., vent larvae, organic flocs, etc.) should be greatest.

Secondly, individuals belonging to the morphotaxa Lo-
bata sp. “Boli” were highly abundant just below the depth of the rim of the Sumisu Caldera, but were also observed outside the caldera at shallower depths. This animal was not observed just north of this area at the Kurose Hole on 24 September 2000 (Hidaka-Umetsu & Lindsay 2017). This difference may be due to “Boli” blooming seasonally and being trapped by the caldera, leading to higher local concentrations.

Thirdly, large numbers of an undescribed Lobata morphotaxa “No auricles” were only observed inside the hydrothermally-active Sumisu Caldera near the bottom. A similar morphotype of Lobata was observed around the Hatoma Knoll hydrothermal vent by Lindsay et al. (2015). This suggests that this morphotaxa may be favorably disposed to near-vent environments. The Sumisu Caldera contains chemosynthetic biological communities, including vestimentiferan tubeworms, mussels, sponges, and so on (Nishijima et al. 2010), thus these ctenophores could possibly consume the presumably abundant eggs and/or larvae of these invertebrates or be feeding directly on vent bacterial flocs sinking into the caldera basin.

Burd & Thomson (1994, 2000, 2015) examined the relationships between hydrothermal vents and zooplankton abundance, biomass, and productivity. According to their results, productivity over the total water column is highest in the regions surrounding hydrothermal vent sites. Not only gelatinous zooplankton, but also other taxa (e.g., copepods, amphipods, chaetognaths), have enhanced biomass throughout the entire water column above hydrothermal venting sites and shallow populations can exist at deeper depths (Burd & Thomson 1994, 2000, 2015). Burd & Thomson (2000) emphasized the relative importance of medusae above hydrothermal vents, however, their research was mainly based on net-sampled specimens, and the biomass and abundances of extremely fragile gelatinous zooplankton would still be underestimated. Deep-sea calderas are semi-closed environments. This indicates that the influence of high chemosynthetic primary productivity should be more potent at other vent sites and that they may also act as a topological “trap” entraining plankton within their environs.

Hypothetical food-web in a hydrothermally-active caldera

The narcomedusa Solmissus incisa s.l. is a well-known predator of gelatinous zooplankton (e.g., Raskoff 2002, Choy et al. 2017). During the present study, we also observed two S. incisa s.l. that had ingested a salp chain and a narcomedusa, respectively (details described in Hidaka-Umetsu & Lindsay 2018).

The abundant filter-feeding thaliaceans that occurred in the area (Fig. 7) could be important prey for co-occurring S. incisa s.l. Indeed, at the depths at which thaliaceans were abundant inside the caldera (Fig. 7), S. incisa s.l. was also abundant (Fig. 6), compared to outside the caldera. It is entirely plausible that heightened productivity (e.g., from chemosynthetic sources), combined with the concentration of sinking particles constrained by the funnel-like topology of calderas and entrainment of ascending particles from hydrothermal vents through turbulent mixing (Hidaka-Umetsu & Lindsay 2017), could stimulate sustained high concentrations of both filter-feeding thaliaceans and their predators around active submarine calderas, thereby also acting as hotspots for other predators of gelatinous zooplankton, including fish and other taxa.

Conclusions

Remotely-Operated Vehicle (ROV) investigations allow direct in situ observations of zooplankton in their natural state and also make investigation of topologically challenging areas for plankton-net surveys, such as closed calderas and canyons, possible. The present study provided information about the detailed distribution of abundant gelatinous zooplankton in a hydrothermally active deep-sea caldera, giving notes on morphological characters able to be identified in the video record and outlining methodological treatment of these data. Some information allowing us to discuss the possible ecology of submarine calderas was also acquired. ROVs can be a powerful tool for the investigation of gelatinous macrozooplankton and, given the high abundances of these gelatinous organisms at the studied sites, should be an integral part of any baseline studies for environmental impact assessments of areas where deep sea mining is proposed and, indeed, for the entirety of the vast global pelagic zone.

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