



Deep-sea fishes in a sauna: Viperfishes dominate a submarine caldera

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ABSTRACT

Barbeled dragonfishes (family Stomiidae) are considered rare, solitary deep-sea predators. We document the fish fauna of the Kurose Hole, a submarine caldera within Japanese waters. The area has been surveyed on three occasions: twice in 2000 during the RV 'Natsushima' cruise and once in 2020 during the RV 'Kaimei' cruise. Within the span of twenty years, the base of the caldera warmed from 11.1 °C to 17.8 °C at 790 m. No dragonfishes were observed during the 2000 'Natsushima' expedition while over 1500 viperfishes (genus *Chauliodus*) were observed during a five and a half hour period in the 2020 'Kaimei' expedition. Viperfishes have never been seen at such high densities, accounting for 61.4% of fish observations with 6.7 viperfish per 100 m³ within the benthic boundary layer. All captured dragonfishes were juveniles, suggesting that this population arose from larvae becoming trapped within the caldera as they developed.

1. Introduction

Barbeled dragonfishes, family Stomiidae, comprise twenty-nine genera throughout the Atlantic, Pacific, and Indian Oceans (WoRMS Editorial Board, 2022). They are solitary mesopelagic predators, using highly specialized bioluminescent chin barbels to hunt. Although over 300 species are currently recognized (WoRMS Editorial Board, 2022), their intense specialization means that many species are uncommon. Dragonfishes are close relatives of the bristlemouths (family Gonostomatidae), lightfishes (family Phosichthyidae), and hatchetfishes (family Sternoptychidae), with all of these groups reported to be more abundant and present at higher biomasses than dragonfishes throughout their range (Gjøsæter and Kawaguchi, 1980; Miya et al., 1995; Sutton et al., 2008). The waters around Japan are no exception, with bristlemouths providing the largest contribution to the midwater fish community around the Boso Peninsula and in Sagami Bay, and with abundances and biomass peaking between June and August (Miya et al., 1995; Miya and Nemoto, 1986).

Water temperature plays a key role in determining midwater fish distribution (Flores et al., 2008; Eduardo et al., 2020a; Olivar and

Beckley, 2022; Watanabe et al., 1999). Many representatives in the family Stomiidae are diel vertical migrators, meaning they can withstand large temperature changes as they migrate to the surface at night (Eduardo et al., 2020b; Sutton and Hopkins, 1996). Throughout its range, the viperfish *Chauliodus sloani* have been recorded in waters ranging from 4 to 14.5 °C (Butler et al., 2001; Eduardo et al., 2020a; Farrag, 2016; Poulain et al., 2007; Sutton and Hopkins, 1996), undergoing daily temperature changes up to 7 °C as they migrate to 400 m depth at night (Eduardo et al., 2020a).

The Izu-Bonin Island Arc, located to the south of the Bozo Peninsula and Sagami Bay, hosts nineteen species of dragonfishes within the family Stomiidae (Tatsuta et al., 2014). The island arc contains nine undersea calderas, most of which are hydrothermally active (Glasby et al., 2000), including the Kurose Hole (Fig. 1). The Kurose Hole is a semi-closed caldera around 5–7 km in diameter at its summit, with the depth of its rim being around 250 m at its deepest point and 114 m at its shallowest point, and with the maximum depth of the caldera floor being 790 m below the sea surface. Geological surveys have reported that circa. 1987, hydrothermal activity within the caldera had ceased, despite having a bottom water temperature of 13.2 °C (Glasby et al.,

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2000). When the Kurose Hole was surveyed again in the year 2000, the bottom water temperature was 11.1 °C while the bottom water temperature outside of the caldera was around 4 °C at the same depth as the caldera floor (Hidaka-Umetsu and Lindsay, 2017).

Warm deep sea areas are rare, with similarly warm temperatures at depth found only in the Mediterranean Sea (Poulain et al., 2007), Sulu Sea (Grossmann et al., 2015) and Red Sea (Manasrah et al., 2004). Previous work has surveyed the gelatinous zooplankton community within the Kurose Hole (Hidaka-Umetsu and Lindsay, 2017), but the fish community remains unreported and warrants study. Here, we analyze the diversity and ecology of fishes within the Kurose Hole, particularly fishes in the family Stomiidae.

2. Methods

2.1. Survey Site

Three dives were conducted within the Kurose Hole, which are summarized in Table 1; the first dive on 24 Sept. 2000 by the remotely operated vehicle (ROV) *Dolphin-3K* was Dive 3K488, the second on Oct. 17, 2000 by the human-occupied vehicle (HOV) *Shinkai 2000* was Dive 2K1227, and the third on Dec. 23, 2020 by the ROV *Kaimei-ROV* was Dive KM143.

The ROV *Dolphin-3K* was equipped with a Victor/JVC KY-F32 three chip CCD camera and six lights: three 400-SeaArc HMI/MSR forward-facing metal halide lamps and three 250 W SeaLine SL-120/250 halogen lamps. Video footage was recorded on BCT-D124L Digital Betacam tapes. Environmental parameters (including depth,

temperature, conductivity, and dissolved oxygen concentration) were measured using a SeaBird SBE19 CTD with an SBE13 oxygen sensor.

The HOV *Shinkai 2000* was equipped with a Victor GF-S1000 HU three chip, CCD camera. There were eight lights: five 250 W SeaLine SL-120/250 halogen lamps and three 400 W SeaArc HMI/MSR metal halide lamps. Video footage was recorded on BCT-D124L Digital Betacam tapes. The Digital Betacam tapes used in both the ROV *Dolphin-3K* and the *Shinkai 2000* contained video recorded at a resolution corresponding to 480x720 pixels@29.97 fps. Environmental data was recorded using a SeaBird SBE19 CTD with an SBE13 oxygen sensor, as above.

The *Kaimei* ROV was equipped with a pan-tiltable high-definition (HD) video camera (Mini Zeus, Insite Pacific Inc.). There were seven lights: four ROS LED Spot or Floodlights, two DSP&L Sealite Sphere SLS6100 lights, and one ROS MV-LEDII light. Video was recorded on a KiPro Quad recorder (AJA video systems). The ROV was outfitted with a pair of Hero5 Stereo GoPro cameras, a single Hero4+ GoPro camera, and a stereo video camera system (stereo 4KVPR) developed at JAMSTEC and composed of a pressure housing containing a pair of 4K video cameras (Rovocam, AJA video systems), recorded internally on a pair of Ki Pro Quad recorders (AJA video systems). Data for the GoPro cameras was recorded on a micro-SD card, with video files downloaded at the end of each dive. Data for the Stereo 4KVPR camera was recorded on two sets of two 1 GB AJA Pak SSD cards which were removed from the AJA Ki Pro Quad recorders after the end of the dive. Environmental parameters (including depth, salinity, temperature, and density) were recorded in real time using a Seabird SBE 49 Fast CAT CTD system. The 4KVPR and main HD video streams were recorded in Apple ProRes HQ (4:2:2)

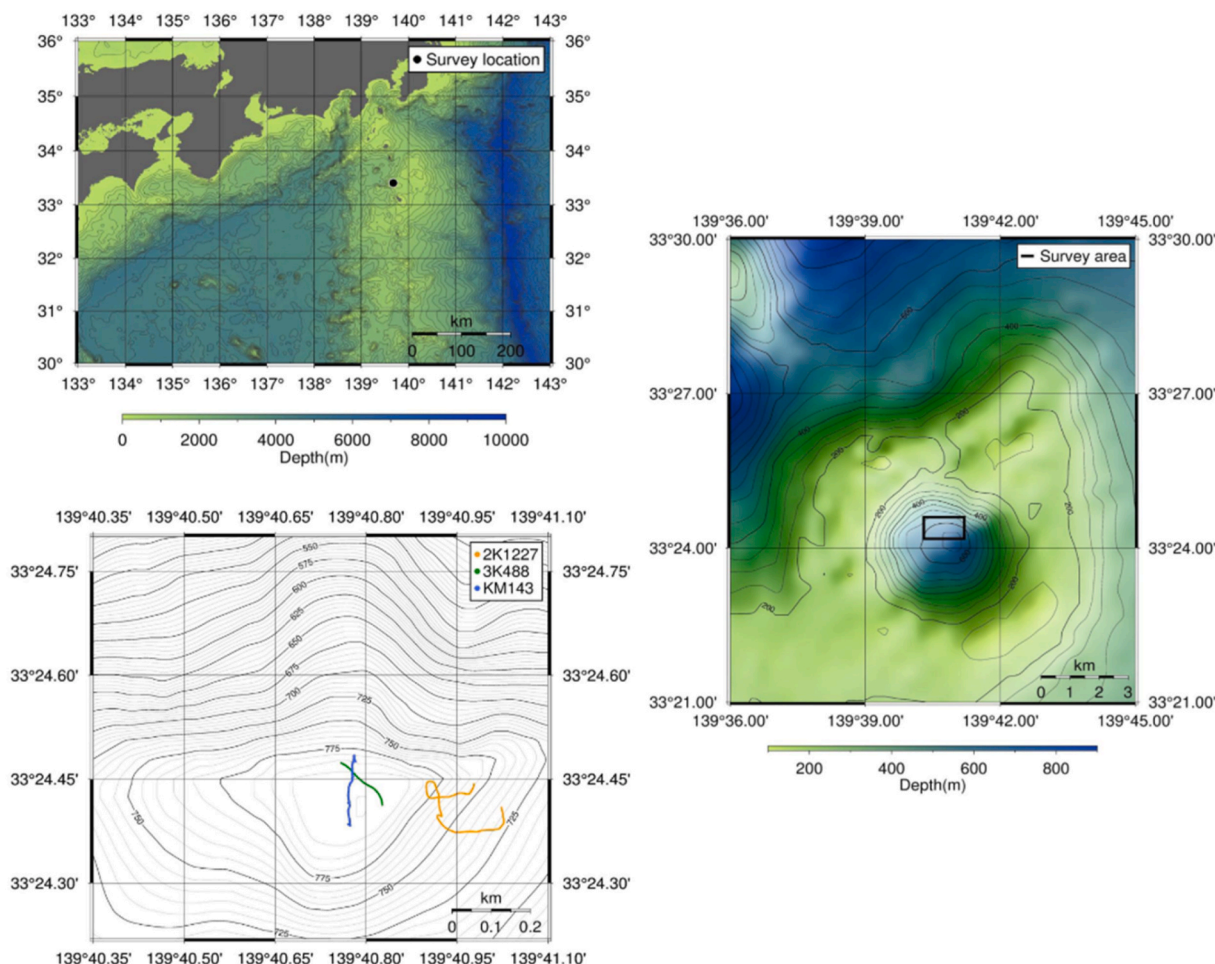


Fig. 1. Map of survey area. Includes the Izu-Bonin Island Arc and the Kurose Hole. The three survey dives within the Kurose Hole are shown in the bottom left.

Table 1

Summary of the three dives completed within the Kurose Hole. The name of the cruise, the dive number within the cruise, the date, start and end locations, survey time, bottom depth and temperature are given for each dive.

Cruise	Dive	Date	Start	End	Survey Time (hh:mm)	Bottom Depth (m)	Bottom Temperature (°C)
RV <i>Natsushima</i> NT00-10	3K488	Sept 24, 2000	33°24.500'N; 139°40.500'E	33°24.835'N; 139°40.334'E	02:36	774	11.1
RV <i>Natsushima</i> NT00-11	2K1227	Oct 17, 2000	33°24.505'N; 139°40.594'E	33°24.330'N; 139°41.057'E	07:20	778	11.1
RV <i>Kaimei</i> KM20-11	KM143	Dec 23, 2020	32°06.344'N; 139°52.050'E	2°06.325'N; 139°52.075'E	05:32	788	17.9

codec. The 4KVPR videos had a resolution of 3840x2176@29.97fps, while the HD video had a resolution of 1920x1080 pixels@29.97fps.

Seafloor bathymetry measurements were recorded from the R/V *Kaimei* based Multi-beam sonar system and were converted to grid files. High resolution 50 m grid files made at the Kurose Hole were used to generate the color map of the KM143 survey area using the GMT Mapping software (Wessel et al., 2019). Low resolution 500 m grid files were used to generate color maps of the Kurose Hole and the Izu-Bonin Island arc using the same software tools.

2.2. Sample collection

Biological samples were collected during the KM143 dive with a suction sampler (hose diameter 90 mm), and were later identified and imaged using a stereo dissecting microscope (Leica M165C and Canon EOS Kiss X7i with NY1S Micronet lens). A sample of mixed midwater fishes was collected at 777 m (sample UUID KM0143SS1B). The sample was preserved in borax-buffered 10% formalin-seawater. For each individual within the sample the total length, wet weight, maturity, and stomach contents were recorded. Total length was assessed using a ruler to the nearest millimeter and wet weight was obtained to the nearest milligram with an analytical balance (A&D GR-202). Dissection was performed after total length and wet weight were assessed. Maturity was determined using the macroscopic appearance of the gonads (Brown-Peterson et al., 2011). One additional sample of midwater crustaceans was collected along the seafloor at 777 m (sample UUID KM0143SS1C). The sample was preserved in borax-buffered 10% formalin-seawater. The cephalothorax length was measured for each crustacean within the sample.

2.3. Video analysis

Data on observations made during dives 3K488 and 2K1227 were completed in Excel. Observations from KM143 were annotated in Squidle+ (Friedman, 2021). Only the ROV's primary video camera and the stereo 4KVPR cameras were used to identify organisms. If an individual was seen in more than one camera, the observer linked the multiple observations together to indicate they were of the same individual. Only the primary annotations (the first record of an individual between the three separate cameras) were used in the analysis. Organisms were identified to the lowest taxonomic level possible using recent keys and guides (21, 29–31). Statistical analysis to determine depth preference and pie charts were completed in R Studio version 4.0.5 (R Core Team, 2020) using the packages ggplot2 version 3.3.5 (Wickham, 2016) and RColorBrewer version 1.1–2 (Neuwirth, 2014).

Density of *Chauliodus* within Dive KM143 was calculated from the starboard stereo 4KVPR camera. The density calculation was completed using the resolution of the cameras, the opening horizontal angle (70.6°), and the opening vertical angle (39.7125°). The forward viewing range of the camera at which *Chauliodus* could be identified reliably was found to be 4.5 m. At this range, the horizontal field of view (6.32 m) and the vertical field of view (3.56 m) give a maximum imaging window of 22.53 m². The length of the ROV track along a transect 10 m from the seafloor was 341.2 m; this multiplied by the imaging window gives us

the maximum imaging volume of the camera in m³ (7089 m³). In just the starboard camera, there were a total of 474 primary *Chauliodus* observations; linked observations were not used in this analysis. By dividing the number of *Chauliodus* by the maximum imaging volume, the total number of *Chauliodus* per image volume of the track was determined.

3. Results

The salinity during Dive KM143 was 34.80 in the upper mixed layer and decreased within the halocline (150–420 m) to 34.75, staying largely stable in the deeper layers but reaching a minimum of 34.73 at the floor of the caldera (CTD profile in Fig. 2). The temperature in the upper 0–150 m depth layer ranged from 21.6 to 22.0 °C, dropping from 21.6 °C at 150 m to 18.4 °C at 420 m within the thermocline, with the temperature near the seafloor being 17.8 °C. Seawater density mirrored water temperature, ranging from 24.1 to 24.2 Sigma-T in the upper 0–150 m depth range, increasing to 25.0 at 420 m at the base of the pycnocline, and gradually increasing to 25.1 near the seafloor.

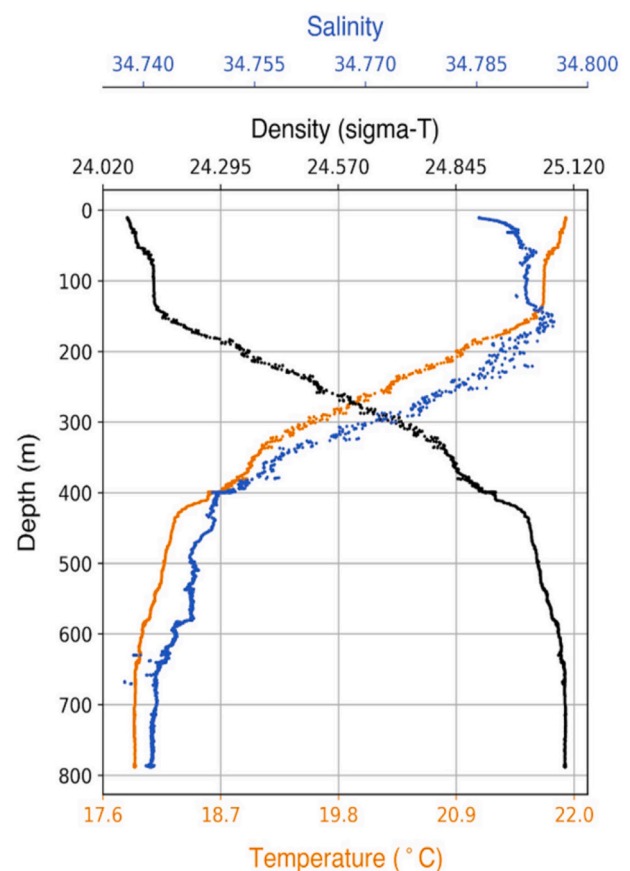


Fig. 2. CTD profile of the Kurose Hole during Dive KM143. The salinity, density, temperature, and depth are shown.

A total of 2482 observations in 28 fish genera were made during Dive KM143, while only 52 observations in 7 genera were made during the 3K488 and 2K1227 dives combined (Table 2). Fishes during Dive KM143 were observed between 413 and 788 m and 17.8–18.4 °C (Table 3). All genera observed during Dives 3K488 and 2K1227 were also observed during Dive KM143, except for the pencil smelt *Nansenia* sp. and the snapper *Etelis* sp.

Six taxa were collected with the suction sampler during Dive KM143

Table 2

Observed species and count per dive within the Kurose Hole, including dives 2K1227, 3K488, and KM143. Species are grouped by their respective higher orders. Count data from 2K1227 to 3K488 from Hidaka-Umetzu and Lindsay (2017). Individuals collected with the suction sampler are not included within the count for Dive KM143.

	Species	2K1227 (2000)	3K488 (2000)	KM143 (2020)
Subclass	<i>Squalus</i> spp.			3
Elasmobranchii	<i>Centrophorus</i>			2
	<i>atromarginatus</i>			
Order	<i>Tetronarce tokiosis</i>			8
	<i>Avocettina</i> spp.			8
Anguilliformes	Unidentified			1
	Nemichthyidae			
Order	<i>Synaphobranchus kaupii</i>			21
	<i>Nansenia</i> spp.	2		
Argentiniformes	Unidentified			14
	Bathylagidae			
Order	Unidentified			23
	Alepocephalidae			
Order	<i>Cyclothone</i> spp.			4
	Stomiiformes	5		22
Order	Sternoptychinae			
	<i>Chauliodus</i> spp.			1524
Order	<i>Stomias</i> spp.			27
	<i>Astronesthes</i>			1
Order	<i>indopacificus</i>			
	<i>Melanostomias</i> spp.			154
Order	<i>Eustomias</i> sp.			1
	<i>Melanostomias</i>			2
Order	<i>pauciradius</i>			
	<i>Pachystomias</i>			1
Order	<i>microdon</i>			
	<i>Tactostoma macropus</i>			2
Order	<i>Malacosteus niger</i>			1
	<i>Photostomias guernei</i>			1
Order	<i>Photostomias</i> sp.			1
	<i>Idiacanthus</i> spp.			26
Order	Unidentified			288
	Stomiidae			
Order	<i>Alepisaurus ferox</i>			1
	Aulopiformes			1
Order	Unidentified	7	1	118
	Myctophidae			
Order	<i>Beryx decadactylus</i>			1
	Berciformes			
Order	<i>Hoplostethus crassispinus</i>	1		33
	<i>Trachurus japonicus</i>			4
Order	<i>Seriola lalandi</i>			1
	<i>Ruvettus pretiosus</i>	1		5
Order	<i>Thyrsooides marleyi</i>			10
	Unidentified		1	
Order	Gempylidae			
	<i>Benthodesmus tenuis</i>			12
Order	<i>Trichiurus lepturus</i>			7
	<i>Aphanopus arigato</i>			2
Order	<i>Evoxymetopon taeniatus</i>			1
	Unidentified	30		84
Order	Trichiuridae			
	<i>Etelis</i> sp.	1		
Order	<i>Pentaceros japonicus</i>			29
	Unidentified Fishes	3		30
	Total	50		2474

and later identified (8), including Sloan's viperfish *Chauliodus sloani*, the Pacific black dragonfish *Idiacanthus antrostomus*, the barbeled dragonfishes *Melanostomias* sp. stet and *Eustomias* sp. stet, the lanternfish *Benthosema* sp. stet, and two oceanic lightfish *Vinciguerria nimbaria*; information for each specimen is provided in Table 4. Additionally, a sample of pelagic crustaceans was collected at the base of the caldera and later identified; information for each specimen is given in Table 5.

Perciformes was the most frequently observed teleost order during Dive 3K488, comprising 62% of the observed fish fauna (Table 3). The dominant taxa within this order were the cutlassfishes (family Trichiuridae). Two Pacific black scabbardfishes, *Aphanopus arigato*, were observed during Dive KM143. This species is notably rare, with only a handful of reports after its description (Lauth, 1997). All previous reports have been from benthic or midwater trawls, making the two individuals observed during this survey the first *in situ* observations of the species (*in situ* video can be seen in Movie S1). Although both the diversity and number of observations within this order were higher during Dive KM143 than during Dive 3K488, they only contributed 5.5% of the total number of observed fish during Dive KM143, while *Chauliodus* accounted for over 84% of fish observations (Fig. 3). Within the benthic boundary layer, there were an average of 6.7 per 100 m³ *Chauliodus* observed with a maximum density of 40.8 fish per 100 m³ (*in-situ* image in Fig. 4).

4. Discussion

The Kurose Hole has the highest ambient water temperature of the nine calderas within the Izu-Bonin Island Arc, with no hydrothermal activity reported within the three dives. A geological survey circa. 1985 to Kaikata Caldera, another submarine caldera within the Izu-Bonin Island Arc which has a caldera rim at 500 m and a base at 900 m, revealed that the bottom water temperature was about 7 °C, over two degrees warmer than the water temperature at the same depth outside of the caldera (Urabe et al., 1987). Subsequent visual surveys to the caldera described the hydrothermal vent fauna (Hashimoto and Yamane, 2005; Ono et al., 1996), but did not report the midwater fauna. Additional visual surveys to Kaikata Caldera should be conducted to compare the midwater fish fauna between the two calderas. Moreover, further geological work within the Kurose Hole should be conducted to determine the cause behind the elevated water temperature at depth.

The increase in species diversity between Dive 3K488 and Dive KM143 is partly due to the higher recording quality of the cameras used, allowing for observers to better identify the fishes observed and to identify fishes further from the camera. The three cameras used in Dive KM143 also provided a larger viewing area to analyze than the single CCD cameras used in Dives 3K488 and 2K1227. Nevertheless, the warmer water temperatures seen in Dive KM143 had a profound effect on the local fish community within the Kurose Hole. Several new maximum temperature and/or depth records for fish taxa are reported here, summarized in Tables 6 and 7, respectively.

Many species within the family Trichiuridae, including *Evoxymetopon taeniatus*, *Trichiurus lepturus*, and *Benthodesmus tenuis*, are found in tropical and subtropical waters (Nakamura and Parin, 1993). While the large temperature range expansion for *Aphanopus arigato* is likely because the fish is rare, *T. lepturus* has been reported in the Mediterranean Sea at 19.9 °C (Aykol et al., 2013; Theoharatos and Tselepidaki, 1990) and *B. tenuis* is reported in the Sulu Sea at 11.8 °C (National Museum of Natural History, 2007). *E. taeniatus* is not recorded in either the Mediterranean or the Sulu Seas, with the Kurose Hole representing the first report of the species in a warm deep sea area.

The presence of *Synaphobranchus kaupii* within the Kurose Hole during Dive KM143 is surprising, considering this fish is also not reported in the Mediterranean and Sulu Seas and generally avoids high water temperatures (Scott and Scott, 1988). Similarly, *Beryx decadactylus* is rarely reported in the Western Mediterranean, being more common on continental slopes (Di Blasi et al., 2018; Paxton, 1999). The

Table 3

Summary of fish fauna observed within the Kurose Hole during Dive KM143, indicating depth and temperature at which they were observed. The species, number of individuals observed, depth range and average, and temperature range and average are given. Averages are only given for species with three or more observations. This table excludes individuals collected with the suction sampler.

Species	N	Depth m (range)	Depth m (avg)	Temperature °C (range)	Temperature °C (avg)
<i>Squalus</i> spp.	3	781.0–785.2	782.5	17.8–17.9	17.9
<i>Centrophorus atromarginatus</i>	2	777.2–780.3		17.9	
<i>Tetronarce tokiosis</i>	8	783.5–786.7	785.2	17.8–17.9	17.9
<i>Avocettina</i> spp.	8	638.0–760.6	689.4	17.8–17.9	17.9
Unidentified Nemichthyidae	1	672.8		17.8	
Unidentified Bathylagidae	14	454.4–786.7	645.2	17.8–18.2	18.0
Unidentified Alepocephalidae	23	454.3–786.8	636.5	17.8–18.2	17.9
Unidentified Evermannellidae	3	738.0–714.3	722.2	17.8–17.9	17.8
<i>Cyclothone</i> spp.	4	765.1–786.5	780.3	17.8–17.9	17.8
Unidentified Sternoptychinae	22	457.8–786.6	679.0	17.8–18.2	17.9
<i>Chauliodus</i> spp.	1524	413.2–788.1	774.1	17.8–18.4	17.8
<i>Stomias</i> spp.	27	544.1–769.3	699.6	17.8–18.0	17.9
<i>Astronesthes indopacificus</i>	1	785.419		17.8894	
<i>Melanostomias</i> spp.	155	692.8–788.1	768.6	17.8–17.9	17.8
<i>Eustomias</i> sp.	1	783.5		17.8	
<i>Melanostomias pauciradius</i>	2	783.5–785.4		17.8–17.9	
<i>Pachystomias microdon</i>	1	786.5		17.8	
<i>Tactostoma macropus</i>	2	646.4–785.2		17.8–17.9	
<i>Malacosteus niger</i>	1	760.6		17.8	
<i>Photostomias guernei</i>	1	783.5		17.9	
<i>Photostomias</i> sp.	1	783.5		17.8	
<i>Idiacanthus</i> spp.	26	545.6–786.6	765.3	17.8–17.9	17.8
Unidentified Stomiidae	288	543.8–787.8	772.0	17.8–17.9	17.9
Unidentified Myctophidae	118	489.4–787.9	712.4	17.8–18.1	17.9
<i>Synaphobranchus kaupii</i>	21	764.7–785.2	773.8	17.8–17.9	17.9
<i>Alepisaurus ferox</i>	2	574.9–586.8		17.9–18.0	
<i>Beryx decadactylus</i>	1	786.2		17.9	
<i>Hoplostethus crassispinus</i>	33	782.4–788.1	785.5	17.8–17.9	17.8
<i>Trachurus japonicus</i>	4	541.5–786.6	725.2	17.8–18.0	17.9
<i>Seriola lalandi</i>	1	786.3		17.8	
<i>Ruvettus pretiosus</i>	5	764.7–786.5	777.7	17.8–17.9	17.8
<i>Thyrstoides marleyi</i>	10	541.4–644.5	564.6	17.8–17.9	17.9
<i>Benthodesmus tenuis</i>	12	542.2–786.4	634.5	17.8–17.9	17.9
<i>Trichiurus lepturus</i>	7	490.3–786.8	715.1	17.8–18.1	17.9
<i>Aphanopus arigato</i>	2	648.1–648.2		17.8–17.9	
<i>Evoxymetopon taeniatus</i>	1	695.9		17.9	
Unidentified Trichiuridae	84	482.0–787.7	663.8	17.8–18.1	17.9
<i>Pentaceros japonicus</i>	29	764.9–788.0	777.9	17.8–17.9	17.8
Unidentified Fishes	30	525.5–788.0	663.0	17.8–18.1	17.9

Table 4

Summary of fishes caught with the suction sampler at 777m in Dive KM143, sample KM0143SS1B. The total length, wet weight, maturity, and stomach contents of each specimen within the sample are given.

Identification	Total Length (cm)	Wet Weight (g)	Stomach	Maturity
<i>Bentosema</i> sp. stet	1.6	0.06	–	Immature
<i>Chauliodus sloani</i>	11	2.57	1 <i>Nematobranchion</i> 1 <i>Actinopterygii</i> stet	Immature
<i>Eustomias</i> sp. stet	2.6	0.08	–	Immature
<i>Idiacanthus antrostomus</i>	5.9	0.85	–	Immature
<i>Melanostomias</i> sp. stet	3.0	0.11	–	Immature
<i>Melanostomias</i> sp. stet	2.9	0.09	–	Immature
<i>Vinciguerria nimbara</i>	2.5	0.19	–	Female; gravid
<i>Vinciguerria nimbara</i>	2.4	0.22	1 Ostracoda indet, 1 Crustacea stet, 1 Gastropoda indet	Male

presence of these species within the Kurose Hole indicates their thermal tolerance is more flexible than previously thought. These new records, coupled with the large increase in dragonfishes within the caldera, are

Table 5

Summary of crustaceans captured with the suction sampler in Dive KM143, KM0143SS1C. The carapace length and maturity are given.

Identification	Cephalothorax Length (mm)	Notes
<i>Euphausia</i> sp. stet	1.5	–
<i>Nematobranchion flexipes</i>	5	–
<i>Nematobranchion flexipes</i>	4.5	–
<i>Pasiphaea japonica</i>	13	Female; gravid
<i>Pasiphaea japonica</i>	13	–
<i>Pasiphaea japonica</i>	6	–
<i>Pasiphaea japonica</i>	3	–

important in understanding the potential effects of climate change on the deep ocean.

No dragonfishes, including *Chauliodus*, have ever been recorded in such high abundance. Midwater trawl surveys around the northeastern Boso Peninsula in September reported an average of 0.001 *Chauliodus sloani* per 100 m³, far less than the abundance of the deepwater bristlemouth *Cyclothone atraria* (family Gonostomatidae; 0.25 individuals per 100 m³) and Garman's lanternfish *Diaphus garmani* (family Myctophidae; 0.02 individuals per 100 m³) (Miya et al., 1995). A similar beam-trawl survey in December 2010 in the nearby Ogasawara Islands also reported *Chauliodus* as being less numerous than the lanternfishes *Bentosema*, *Diaphus* and *Lampanyctus* (Tatsuta et al., 2014). Abundance of some lanternfish larvae is reported to decline within Sagami Bay in December, but viperfish larvae also exhibited a similar decline and

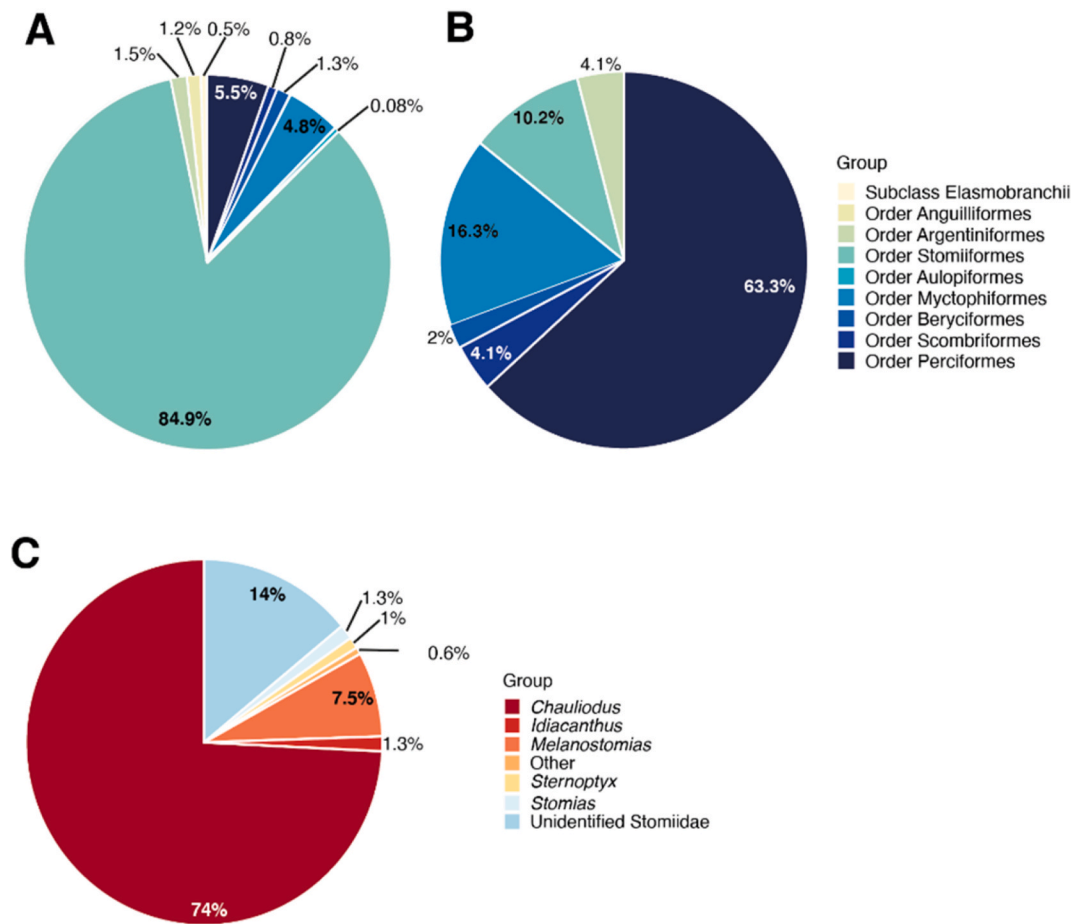


Fig. 3. A. Percentage of each fish group seen within Dive KM143. Percentages are out of the total number of fish observations within the dive (can be found in Table 2) minus the number of unidentified fishes: 2443. B. Percentage of each fish group seen within Dives 3K488 and 2K1227, combined. C. Percentage of each genus within family Stomiidae. The “Other” category combines the following genera: *Astronesthes*, *Cyclothone*, *Eustomias*, *Malacosteus*, *Photostomias*, *Pachystomias*, and *Tactostoma*.

remained less abundant than both lanternfishes and bristlemouths (Sassa and Kawaguchi, 2006).

Dragonfishes are lie-and-wait predators, evidenced by the lowered C + N in their muscle tissue, lack of a swim bladder, low haematocrit count, low blood viscosity, and less red musculature compared to actively-hunting deep-sea teleosts (Lindsay, 2003; Blaxter et al., 1971). This lifestyle has benefits, particularly in the deep sea where food can be scarce, due to the lower energy requirements for maintenance and reduced muscle activity (Childress et al., 1980). Energy consumption is higher at increased temperatures (Torres et al., 1979) but this does not explain why dragonfishes are not found in similarly high abundance around other calderas within the Izu-Bonin Arc (Tatsuta et al., 2014).

Barbeled dragonfishes, family Stomiidae, typically have little intraspecific diet variation, specializing in either fishes, cephalopods, or pelagic crustaceans (Sutton and Hopkins, 1996; McGonagle, 2021). Pacific viperfish, *Chauliodus macouni*, have been recorded to eat fish in Japanese waters (Gordon et al., 1985). Contrastingly, *C. sloani* is primarily a fish predator (Eduardo et al., 2020a) that also consumes a mixture of fishes and pelagic crustaceans throughout its range (Sutton and Hopkins, 1996; Clarke, 1982; Battaglia et al., 2018). Although all other barbeled dragonfishes captured during this survey (see Table 4) had empty stomachs, *C. sloani* contained one krill *Nematobrachion* sp. (family Euphausiidae) and one unidentified fish. Pelagic crustaceans were abundant during Dive KM143 and several were captured serendipitously with the suction sampler (Table 5). Moreover, *C. sloani* has been reported to feed on other dragonfishes (Sutton and Hopkins, 1996) and conspecifics (Eduardo et al., 2020a; Battaglia et al., 2018), although

records for both are uncommon. One viperfish was observed during this survey attacking a second (Movie S2). This appears to be a failed attempt at feeding, despite the two fishes being roughly equal in size, as the attacker bit the incomer twice behind the head before swimming away. The less-specialized diet of viperfishes may partially explain why they were the most abundant of the dragonfishes during Dive KM143, and opportunistic cannibalism would be beneficial when this species is the most abundant within the caldera.

The *C. sloani* individual sampled during the present survey was immature at 9.5 cm standard length (Table 4) – less than a third of the maximum standard length of 35 cm (Nakabo, 2013). Reports about the minimum age of sexual maturity in dragonfishes are scarce and vary by location, but viperfishes have been reported to reach maturity at a minimum of 9.55 cm standard length in the Gulf of Mexico (Marks et al., 2020) and 15.4 cm standard length around Hawaii (Clarke, 1983). Fish larvae and post-transformation adults generally have larger thermal ranges when compared to reproductive adults and embryos (Dahlke et al., 2020), which may partly explain the prevalence of juvenile dragonfishes. High temperatures are known to cause transgenerational plasticity, which can affect body size and growth rate in fishes (Shama and Wegner, 2014; Salinas and Munch, 2012). Fish raised in high water temperatures whose parents were acclimated to similarly high temperatures are known to have larger body sizes (Dahlke et al., 2020). Further work should attempt to quantify morphological variations and growth rates of dragonfishes in response to warmer water temperatures, especially within the semi-closed Kurose Hole. Examination of methylation and regulation within the genome of dragonfishes within the Kurose



Fig. 4. **Top:** Cropped HD *in-situ* image of *Chauliodus* sp. in Dive KM143 with a dorsal ectoparasite. The image was taken at 00:20:43 (UTC) at 738 m depth. **Bottom:** Microscope image of preserved, juvenile *Chauliodus sloani* captured with the ROV suction sampler in Dive KM143. Scale bar = 3 mm.

Table 6
Comparison between previous and new thermal maxima for six species observed within the Kurose Hole. The reference and location for the previous thermal maxima is also given.

Species	New Thermal Maxima (°C)	Previous Thermal Maxima (°C)	Location	Reference
<i>Aphanopus arigato</i>	17.8	5	West Coast USA	Lauth, 1997
<i>Benthodesmus tenuis</i>	17.9	11.8	Sulu Sea	National Museum of Natural History (2007)
<i>Beryx decadactylus</i>	17.9	11.6	Bay of Biscay	Uiblein et al. (2003)
<i>Chauliodus sloani</i>	18.4	14.5	Mediterranean	Farrag, 2016; Poulain et al. (2007)
<i>Evoxymetopon taeniatus</i>	17.9	16.5	Brazil	Haimovici et al. (1994)
<i>Synaphobranchus kaupii</i>	17.9	9.58	Bay of Biscay	Uiblein et al. (2003)

Hole might also help determine how resistant they are to high temperatures and whether their resistance is transgenerational (Veilleux et al., 2018).

The larvae of some deep-sea fish within Sagami Bay, just north of the Kurose Hole, stay below or within the thermocline, and *C. sloani* larvae are known to transform into juveniles at a depth of 400–800 m (Sassa and Kawaguchi, 2006). It is possible that the larval viperfishes within the Kurose Hole became trapped within it as they transformed, as the rim of the caldera is above the thermocline and above 400 m depth (see Figs. 1 and 2). During dives 3K488 and 2K1227, a gravid population of the hydromedusa *Earleria brunii* was the dominant midwater taxon (Hidaka-Umetu and Lindsay, 2017). The height of the rim of the caldera

Table 7
Comparison between previous and new depth maxima for three species observed within the Kurose Hole. The reference and location for the previous depth maxima is also given.

Species	New Depth Maxima (m)	Previous Depth Maxima (m)	Location	Reference
<i>Evoxymetopon taeniatus</i>	695.9	300	Brazil	Haimovici et al. (1994)
<i>Trachurus japonicus</i>	786.7	275	Japan	Sassa et al. (2019)
<i>Trichiurus lepturus</i>	754.8	587	Brazil	Martins et al. (2005)

combined with the depth of the thermocline and warm waters can potentially foster these highly localized single-species aggregations. This would partially explain why similar midwater aggregations have not been reported in Kaikata Caldera considering that the rim of the caldera is much lower, although midwater surveys should be undertaken to assess this. Additional work focusing on viperfish larval abundance, comparison of genetic relatedness between individuals, and histological analysis of gonad development throughout different size ranges should be completed to better understand this population within the Kurose Hole while also assessing the importance of heightened temperature and topological characteristics. Moreover, continued monitoring of the Kurose Hole could provide insight into the temporal dynamics of mesopelagic communities despite the isolated location of the caldera.

5. Conclusions

With an increasing interest in the effects of ocean warming on the deep sea, surveys like the ones undertaken within the Kurose Hole further our understanding of how warm water temperatures affect deep-sea ecosystems. The water temperature at the base of the caldera warmed by 6.7 °C between the years 2000 and 2020, with the fish community changing from being predominantly cutlassfishes to viperfishes. Many fishes observed within the Kurose Hole have more resilience to high water temperatures than previously reported, and nearly all fish taxa observed within the caldera were more numerous during the warmer 2020 survey. While the reasons behind why the Kurose Hole is so warm at depth have yet to be determined, the deep oceans of the future may contain a similarly high abundance of dragonfishes in the family Stomiidae.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Leah A Bergman reports financial support was provided by Government of Japan Ministry of Education Culture Sports Science and Technology. Dhugal J Lindsay reports financial support was provided by Belmont Forum.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2022.103950>.

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