



## A new species of clausophyid calycophoran siphonophore (Cnidaria: Hydrozoa), *Kephyes hiulcus* sp. nov., widely distributed throughout the world's oceans

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### Abstract

A new species of clausophyid siphonophore, *Kephyes hiulcus* sp. nov. is described. It can most easily be differentiated from its congener *Kephyes ovata* by the shape of the hydroecium in the anterior nectophore of the polygastric stage. This is open over the entire height of the nectophore in *K. hiulcus* sp. nov., and it is this character from which its specific name is derived. This species was found in the eastern and western Pacific Ocean, as well as the Celebes and Mediterranean Seas, indicating that this species is both relatively common and geographically widespread.

**Key words:** Clausophyidae, mesopelagic, taxonomy, new species

### Introduction

Clausophyid siphonophores are a conspicuous component of the gelatinous macroplankton community at meso- and bathypelagic depths throughout many of the world's oceans (eg. Mapstone 2009). Because of their relatively large size, most members of this family are easily observable by crewed submersibles and remotely-operated vehicles (Silguero & Robison 2000; Lindsay *et al.* 2015). A recent review by Pugh (2006) finally sorted out the convoluted taxonomy of the family, erecting a new genus, *Kephyes* Pugh, 2006, and providing a redescription of *Kephyes ovata* (Keferstein & Ehlers, 1860). Unfortunately, an oversight in that paper, where an undescribed *Kephyes* species was inadvertently included in the studied *K. ovata* material, had gone unrecognized, and this mistake subsequently has been perpetuated (eg. Mapstone 2014). Before the taxonomy of this group once again becomes convoluted, the species *Kephyes hiulcus* sp. nov., is described below based on the material of Pugh (2006) and further material from off Japan, the Celebes Sea and the Mediterranean Sea.

### Materials and methods

Material for this study was collected using several different ships and survey platforms around the world over the course of many years (Table 1). The type material was collected at 1189 m in Monterey Canyon by the ROV ‘*Tiburon*’ (dive T0980-D4, 10 May 2006, 36°36′11.909″N, 122°22′31.998″W). Material from Japan was collected on cruises of the T.R.V. *Tokaidaigaku Maru Nisei* in Suruga Bay (34°51.0′N, 138°38.3′E) from 1980 to 1992 using a 160 cm-diameter ring net with 2 mm mesh size (Kubota *et al.*, 1992; Kubota & Sawamoto 1993), during the MULTIPLE Sampling PLATform Survey of wHole ecosystem (MULTI-SPLASH) cruise in Sagami Bay (35°0.5′N, 139°2.0′E) in March 2006, aboard the R.V. *Kaiyo* (KY06-03) in 2006 using an Intelligent Operated Net Environmental Sampling System (IONESS) net (Kitamura *et al.* 2001), and during cruises KT10-11, KT11-03 and KT12-07 of the T/V *Tansei Maru* in Sagami Bay, Japan, from 24–28 June 2010, 8–12 March 2011 and 22–26 April 2012, respectively, using an obliquely-towed ORI net. Further information on the MULTI-SPLASH cruise,

including water mass structure, has been given by Grossmann & Lindsay (2013). Specimens from the Celebes Sea (2°25'N, 122°28'E) were collected during cruise KH-00-1 of the R.V. *Hakuho Maru* on the 19th of February 2000 (Grossmann *et al.* 2015). Material from the Balearic Sea, north-western Mediterranean Sea (40°47.74'N 01°33.57'E – 41°49.35'N 03°33.59'E), was collected during the 2012 FISHJELLY cruises aboard the R.V. *García del Cid* from 20 June–24 July 2012 (Lindsay *et al.* 2014) using a MOCNESS net (Weibe *et al.* 1976). Line drawings were made by tracing from photographs using Adobe Illustrator v5.1 supplemented by observations under a Leica MZ16 dissecting scope.

## Results

### Systematics

#### Class Hydrozoa Owen, 1843

#### Order Siphonophorae Eschscholtz, 1829

#### Suborder Calyphorae Leuckart, 1854

#### Family Clausophyidae Totton, 1965

**Diagnosis.** Calyphorae with dissimilar nectophores, typically two, both possessing a somatocyst and with anterior nectophore partially apposed to and partially linearly adjoined to the elongate posterior one; atypically only anterior one developed (genus *Heteropyramis*). Nectophore(s) either with longitudinal ridges or smooth; mouthplate absent in anterior nectophore (except in *Clausophyes laetmata*), present or absent in posterior nectophore; somatocyst in both nectophores typically simple, swollen, and reaching anterior end of nectophore. Cormidia with bracts, except in genera *Clausophyes* (eudoxids not developed) and *Crystallophyes* (produces a unique sexual stage termed the fuseudoxid); bract with phyllocyst variously shaped, with two fine basal branches (bracteal canals) extending down into neck-shield.

#### Genus *Kephyes* Pugh, 2006

Type species. *Kephyes ovata* (Kieferstein & Ehlers, 1860).

**Diagnosis.** Clausophyidae with two nectophores, lacking ridges and cusps, and with descending surface diverticula in both nectophores; cormidia with bracts, released as free-living eudoxids, each comprising a bract with two bracteal canals and a phyllocyst, a gastrozoid and tentacle, and a gonophore without distinctive ridges.

#### *Kephyes hiulcus* sp. nov.

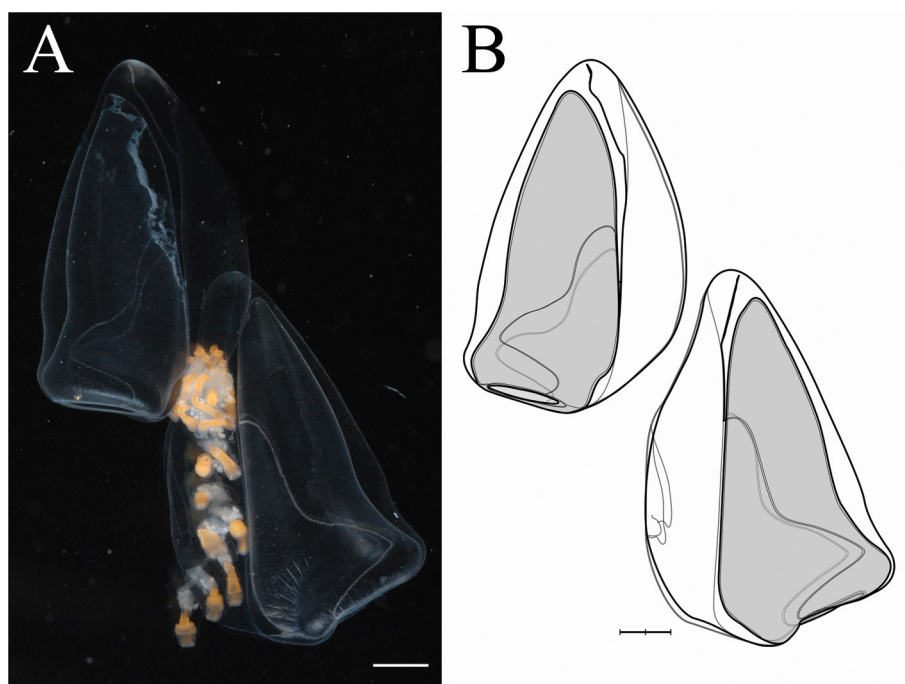
*Kephyes* sp. A. Grossmann & Lindsay 2013, Grossmann *et al.*, 2015

*Kephyes ovata*. Pugh 2006 (Figs. 1, 5A)

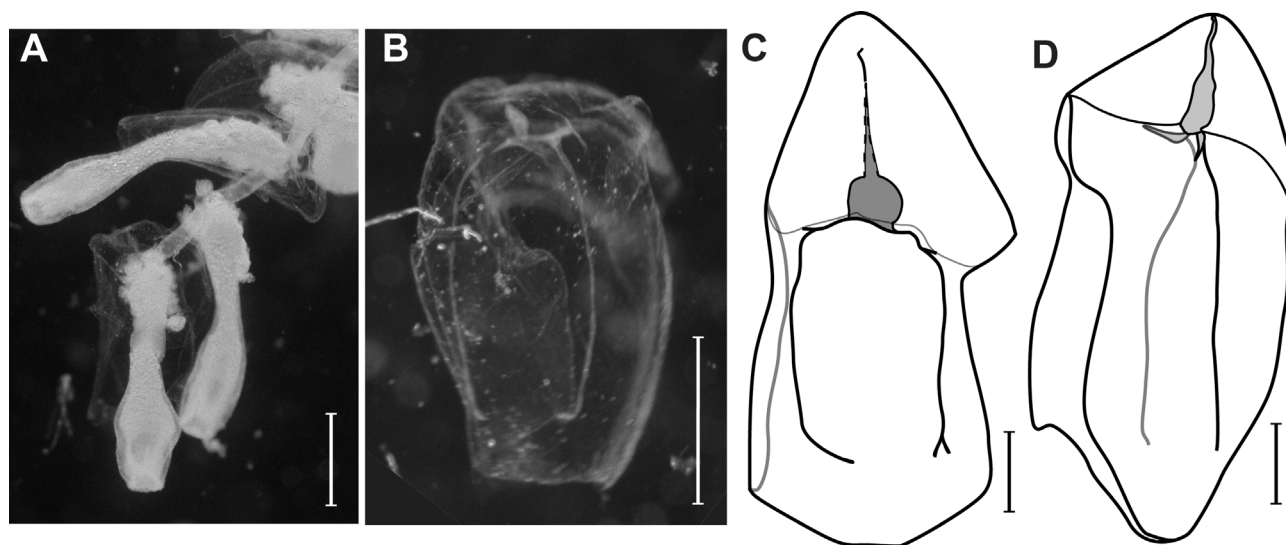
*Kephyes ovata*. Mapstone 2014 (Fig. 5D)

**Diagnosis.** Anterior and posterior nectophores conical, ridgeless, laterally compressed. Nectosac extending to 90% height of nectophores, with looped radial canals. Lateral canals arise from upper canal, either together or separately. Pedicular canal with long descending diverticulum in both nectophores. Somatocyst thin, extending to nectophore apex. Hydroecium open over entire height of both nectophores, and without median mesogloal protuberance from the hydroecial wall; hydroecial flaps ending slightly before ostial level, large hydroecial wings in posterior nectophore.

Eudoxids cannot, at present, be differentiated from those of *K. ovata*.



**FIGURE 1.** Photograph (A) and line drawing (B) of the living holotype of *Kephyes hiulcus* **sp. nov.** in lateral view. Scale bars = 2 mm. (photograph by Steven Haddock, MBARI)



**FIGURE 2.** A: Photograph of the siphosomal cormidia of the preserved holotype of *Kephyes hiulcus* **sp. nov.**, B: siphosomal bract of the preserved holotype, C, D: *Kephyes* spp. free-eudoxid bracts from Japanese waters showing the structure of the hydroecial canals. B and C in upper view, D in right lateral view. Scale bars = 1 mm.

**Material examined.** *Holotype*: Polygastric stage comprised of attached anterior and posterior nectophores, and anterior part of siphosomal stem. Collected at 1189 m in Monterey Canyon by the ROV ‘*Tiburon*’ (dive T0980-D4, 10 May 2006, 36°36’11.909” N, 122°22’31.998” W). The holotype was deposited at the Showa Memorial Institute, National Science Museum, Tokyo (NSMT-Co1579).

Additionally, twenty-one anterior nectophores and 25 posterior nectophores of *Kephyes hiulcus* **sp. nov.**, ninety-seven anterior nectophores and 35 posterior nectophores of *K. ovata*, two complete *Kephyes* spp. free-living eudoxid stages, 302 bracts and 246 gonophores were analyzed, from Japanese waters and the Celebes and Mediterranean Seas (Table 1).

**Description of Holotype.** *Nectosome*: Anterior nectophore (Figure 1): The type specimen was 12.6 mm in height and 3.6 mm wide in its preserved state. It was conical in shape, laterally flattened, without ridges; nectosac

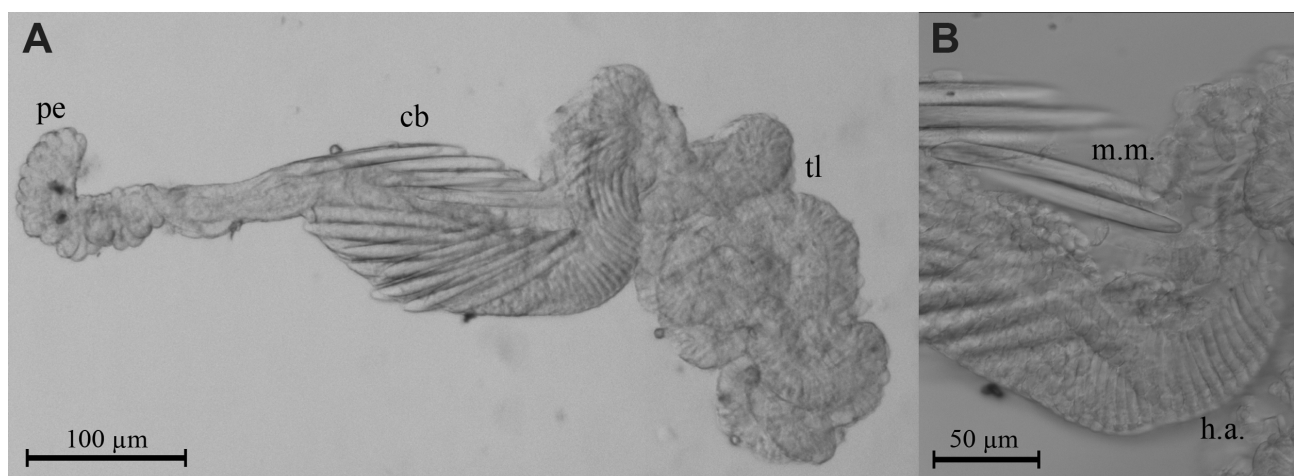
extending to 90% of nectophore height; no mouth plate; lateral radial canals arising from upper radial canal, with origins of right and left canals staggered, following a looped course, and inserting onto ostial ring canal in its lower lateral half; insertion point of pedicular canal at 40% nectophore height from the ostium; descending diverticulum from the pedicular canal remaining in contact with the hydroecium, extending at least to posterior end of hydroecial flaps; somatocyst remained in contact with hydroecium to 60% nectophore height before penetrating into the mesogloea, ending close to the apex of the nectophore; hydroecium open over the whole height of the nectophore, 20 to 45% of the nectophore width; hydroecial wings smooth and rounded, ending slightly anterior of the ostium, small projection of thickened mesogloea on external edge of hydroecial wings 1/3 nectophore height from the ostium.

Posterior nectophore 12.9 mm in height and 4 mm wide in its preserved state; conical in shape, laterally flattened, without ridges; nectosac extended to 90% of the nectophore in height; no mouthplate; lateral radial canals arising together from upper radial canal, following a looped course, joining ostial ring canal in its lower lateral half; insertion point of pedicular canal 60% nectophore height from the ostium; descending branch of the pedicular canal remaining in contact with the hydroecium, extending at least to posterior end of hydroecial flaps; somatocyst remaining in contact with hydroecium for half its length before penetrating into the mesogloea, ending close to the apex of the nectophore; hydroecium open over the whole height of the nectophore; hydroecial wings large, ending slightly anterior of the ostium, with medial flaps on internal surface.

**Siphosome:** Siphosomal cormidia composed of a bract and a tentacle-bearing gastrozoid (Figure 2A). No gonophores could be observed. The bracts could not be distinguished from those described by Pugh (2006) for *Kephyes ovata*, or from any of the material of both species we have examined.

Gastrozooids pale tangerine in colour when alive.

Cnidoband of tentacle tentilla long and slender (Figure 3). Although discharged nematocysts were not observed, the size and shape of the capsules suggested they were long thin microbasic mastigophores, measuring up to 112  $\mu\text{m}$  in length, and smaller, elongate homotrichous anisorhizas measuring up to 41  $\mu\text{m}$  in length. The terminal filament was covered in small, spherical nematocysts.



**FIGURE 3.** A: a detached tentillum from the holotype of *Kephyes hiulcus* sp. nov. B: close-up of the cnidoband nematocytes. cb: cnidoband, h.a.: homotrichous anisorhiza, m.m.: microbasic mastigophores, pe: pedicel, tl: terminal filament.

Bracts measured up to 2.38 mm in length. Flattened apically, expanded laterally to grip the stem (Figure 2B); neck-shield extensive, with small indentations on the posterior lateral corners; central phyllocyst spindle-shaped, extending to the apex of the headpiece; 2 longitudinal bracteal canals, up to 4/5 the neck-shield in length, sometimes curving sharply inwards in their most distal part, the right (when the neck-shield is downwards), being longer than the left.

Gonophore not observed.

**Etymology.** The specific name *hiulcus* is Latin meaning split or open, and refers to the wide-open or gaping hydroecium of the anterior nectophore of this species in comparison with the more-closed one of *K. ovata*.

**Distribution.** Type locality: Monterey Canyon, Eastern Pacific Ocean (36°36'11.909" N, 122°22'31.998" W)

*Kephyes hiulcus* sp. nov. samples have been collected in Monterey Canyon, in Japanese waters (Grossmann &

Lindsay 2013, as '*Kephyes* sp. A'), in the Celebes Sea (Grossmann *et al.*, 2015, as '*Kephyes* sp. A'), as well as in the Catalan Sea, north-western Mediterranean Sea (Table 1). The *Kephyes hiulcus* **sp. nov.** holotype was collected at 1189 m in Monterey Bay, but specimens from Japanese waters were found throughout mesopelagic depths. Nectophores were found to be roughly the same size, and were often collected concurrently with *K. ovata*. All of the MULTI-SPLASH net samples containing *K. hiulcus* **sp. nov.** also contained *K. ovata*, and 50% of the net samples from Suruga Bay contained both *Kephyes* species. There was no obvious segregation between the two species, or between polygastric and eudoxid stages, with depth, salinity or water temperature. The holotype was collected in waters with a temperature of 3.5°C, salinity of 34.46 and a dissolved oxygen concentration of 0.56 mL.L<sup>-1</sup>, while the *K. hiulcus* **sp. nov.** specimens from the Catalan Sea (Mediterranean Sea) were collected in waters with temperatures above 13.0°C, salinity 38.18–38.50 and dissolved oxygen concentrations between 4.14 and 5.87 mL.L<sup>-1</sup>.

*Kephyes ovata* and *K. hiulcus* **sp. nov.** are the only members of the Clausophyidae for which the polygastric stage has been reported from the Mediterranean Sea.

**Remarks.** First figured as a photograph (Fig. 5A: 1002) in Pugh's (2006) reclassification of *Clausophyes ovata* (Keferstein & Ehlers, 1860) into the genus *Kephyes*, the present species *K. hiulcus* **sp. nov.** is similar in size, shape and general aspect to *K. ovata*. However, it can easily be differentiated by the extent of the hydroecium in the anterior nectophore of the polygastric stage. In *K. ovata*, this extends to 70% of the nectophore in height from the ostium (Pugh 2006), whereas in *K. hiulcus* **sp. nov.**, the hydroecium is open over the entire height of the anterior nectophore. Additionally, the hydroecial wings do not extend to ostial level in *K. hiulcus* **sp. nov.**, as they do in *K. ovata*, but end slightly anterior of the ostium, both in the anterior and posterior nectophores. In the posterior nectophores of *K. hiulcus* **sp. nov.**, the anterior part of the somatocyst lies close to the apex of the nectophore, as in the anterior nectophore, while in *K. ovata*, the somatocyst does not reach the apex of the nectophore in the posterior nectophore.

The origin of the lateral radial canals on the anterior nectophores of *K. hiulcus* **sp. nov.** showed a great deal of variability, arising either from the upper radial canal, or from the insertion point of the pedicular canal, right and left canals not always arising together. It is interesting to note that on all anterior *K. ovata* nectophores studied where the radial canals were visible, the lateral radial canals originated from the insertion point with the pedicular canal, as was the case in specimens from the north-eastern Pacific (Mapstone, 2009). Pugh (2006), when describing the variability of the origin of the lateral radial canal in *K. ovata*, used, by way of an example of the canals arising from the upper radial canal, the animal shown in his figure 5A (Pugh, 2006: 1002), which is, in fact, *K. hiulcus* **sp. nov.** However, it is clear from Patrì's (1969) specimens from the Mediterranean that in *K. ovata* the lateral radial canals may also arise separately, and from the upper radial canal.

In *Kephyes hiulcus* **sp. nov.**, neither the stem nor the posterior nectophore are attached level with the base of the somatocyst of the anterior nectophore, but rather some way down the hydroecial cavity. This can be clearly seen in the photograph of the living sampled holotype (Figure 1A). Although no scar could be observed on the preserved material, it is supposed that the stem and posterior nectophore join at the start of the somatocyst of the latter, as in species of the genus *Clausophyes*, and that in *K. hiulcus* there is an extremely elongate 'somatocyst along the hydroecium' somatocyst portion (Haddock *et al.* 2005) from the origin of the stem attachment point to the penetrating somatocyst of the anterior nectophore.

The free-living eudoxid stages of the two *Kephyes* species cannot, at present, be differentiated. The eudoxid bracts of *Kephyes* spp. examined in the present study measured between 2.98 and 7.22 mm in length. The longitudinal canals were usually reduced, while the hydroecial canals extended to 15–20% of bract height from the posterior edge. On many bracts, the hydroecial canals ran in a smooth and slight curve towards the centre of the neckshield (Figure 2D), resembling those drawn by Pugh for *K. ovata* (2006, Fig. 3A: p.1000). However, other bracts had hydroecial canals curving sharply inwards at their posterior ends, as observed on the small *K. hiulcus* **sp. nov.** siphosomal bracts (Figure 2B), or again had one hydroecial canal bending inward at its posterior end, while the second had a bifurcated tip (Figure 2C). The phyllocyst observed in free eudoxid stage bracts was more tapered in its anterior part than in the attached siphosomal bracts. It extended to or close to the apex of the head-piece (Figure 2). A well-developed hydroecial flap was present on the right hydroecial wing of all eudoxid stage gonophores studied.

**TABLE 1.** List of samples examined for the present study. \*: *Kephyes hiulcus* **sp. nov.** Holotype specimen; a.n.: anterior nectophore; b.: bract; g.: gonophore; e.: eudoxid; pol.: polygastric stage; p.n.: posterior nectophore.

Species	Zooid (No.)	Depth range (m)	Date	Latitude	Longitude	Location	Time	Temperature (°C)	Salinity	Dissolved Oxygen (mL/L)
<i>Kephyes hiulcus</i> <b>sp. nov.</b>	pol.(1)*	1189	10-May-2006	36.603	-121.376	Monterey Canyon	Day	3.52	34.46	0.6
	p.n.(1)	0–750	21-Jun-2012	40.966	2.064	Catalan Sea	Night	13.01–23.07	38.18–38.5	4.1–5.9
	p.n.(1)	0–750	21-Jun-2012	40.966	2.064	Catalan Sea	Night	13.01–23.07	38.18–38.5	4.1–5.9
	p.n.(2)	900–1000	19-Feb-2000	2.472	122.480	Celebes Sea	Night	4–5	34.55–34.6	1.8–1.9
	a.n.(1)	750–800	15-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	3.76–4.00	34.32–34.34	1.2–1.5
	a.n.(1)	800–850	15-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	3.53–3.76	34.34–34.37	1.2–1.4
	a.n.(3)	850–900	22-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	3.34–3.42	34.37–34.38	1.1–1.2
	a.n.(1)	450–500	23-Mar-2006	35.008	139.333	Sagami Bay	Day	6.34–7.18	34.25–34.26	1.8–2.1
	a.n.(6)	500–550	23-Mar-2006	35.008	139.333	Sagami Bay	Day	5.72–6.35	34.25–34.25	1.7–1.8
	p.n.(3)	750–820	14-Mar-2006	35.008	139.333	Sagami Bay	Night	3.65–3.89	34.33–34.36	1.3–1.4
	p.n.(1)	0	9-Mar-1980	25.200	124.600	Suruga Bay	Night	n/a	n/a	n/a
	a.n.(1)	397	27-Mar-1984	34.800	138.620	Suruga Bay	Day	8.36	n/a	n/a
	p.n.(2)	480	27-Nov-1986	34.850	138.637	Suruga Bay	Day	6.88	n/a	n/a
	p.n.(5)	494.1	9-Mar-1980	25.200	124.600	Suruga Bay	Night	n/a	n/a	n/a
	p.n.(1)	790	13-Nov-1992	34.858	138.633	Suruga Bay	Night	3.94	34.36	n/a
	a.n.(1)	990	15-Mar-1985	40.487	142.658	Suruga Bay	Day	n/a	n/a	n/a
	a.n.(7)	1049	28-Mar-1985	34.795	138.617	Suruga Bay	Day	3.16	n/a	n/a
	a.n.(2)	1105	27-Nov-1986	34.850	138.637	Suruga Bay	Day	3.93	n/a	n/a
	p.n.(2)	1105	27-Nov-1986	34.867	138.638	Suruga Bay	Night	3.93	n/a	n/a
	a.n.(1)	400–450	8-Nov-1991	34.888	138.632	Suruga Bay	Day	7.16–6.73	34.257–34.302	n/a
	p.n.(4)	n/a	1980	n/a	n/a	Suruga Bay	n/a	n/a	n/a	n/a
<i>Kephyes ovata</i>	a.n.(1)	350–400	24-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	7.08–8.25	34.23–34.28	2.3–2.6
	a.n.(3)	350–400	25-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	6.70–8.18	34.22–34.29	2.3–2.6
	a.n.(1)	400–450	24-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	6.473–7.226	34.22–34.26	2.2–2.4
	a.n.(3)	450–500	24-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	5.82–6.48	34.20–34.25	2.0–2.3

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TABLE 1. (Continued)

Species	Zooid (No.)	Depth range (m)	Date	Latitude	Longitude	Location	Time	Temperature (°C)	Salinity	Dissolved Oxygen (mL/L)
	a.n.(1)	900–950	15-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	3.27–3.38	34.39–34.41	0.9–1.2
	a.n.(1)	400–450	20-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Night	8.63–9.41	34.03–34.33	2.6–3.0
	a.n.(1)	950–1000	22-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	3.10–3.24	34.40–34.42	1.6–1.1
	p.n.(1)	0–1075	24-Apr-2012	34.986	139.334	Sagami Bay	Day	3.29–19.95	n/a	n/a
	p.n.(2)	0–1128	22/23-Apr-2012	34.968	139.405	Sagami Bay	Night	3.18–20.27	n/a	n/a
	p.n.(1)	0–1412	27-Jun-2010	34.150	139.283	Sagami Bay	n/a	n/a	n/a	n/a
	p.n.(1)	0–634	22-Apr-2012	34.963	139.409	Sagami Bay	Night	5.22–20.19	n/a	n/a
	p.n.(1)	0–982	8-Mar-2011	35.010	139.291	Sagami Bay	Night	n/a	n/a	n/a
	a.n.(3)	400–450	15-Mar-2006	35.008	139.333	Sagami Bay	Night	6.78–7.86	34.25–34.27	2.1–2.2
	a.n.(4)	400–450	24-Mar-2006	35.008	139.333	Sagami Bay	Night	6.72–7.72	34.25–34.27	2.1–2.2
	p.n.(1)	400–600	22-Apr-2007	35.008	139.333	Sagami Bay	Night	4.77–6.62	34.22–34.27	n/a
	a.n.(2)	450–500	15-Mar-2006	35.008	139.333	Sagami Bay	Night	6.00–6.78	34.23–34.25	1.8–2.1
	a.n.(2)	450–500	24-Mar-2006	35.008	139.333	Sagami Bay	Night	6.01–6.76	34.24–34.25	1.8–2.1
	a.n.(3)	450–500	23-Mar-2006	35.008	139.333	Sagami Bay	Day	6.34–7.18	34.25–34.26	1.8–2.1
	a.n.(10)	500–550	23-Mar-2006	35.008	139.333	Sagami Bay	Day	5.72–6.35	34.25–34.25	1.7–1.8
	a.n.(2)	500–550	15-Mar-2006	35.008	139.333	Sagami Bay	Night	5.42–6.01	34.23–34.26	1.7–1.8
	a.n.(2)	500–550	24-Mar-2006	35.008	139.333	Sagami Bay	Night	5.50–6.01	34.25–34.26	1.7–1.8
	a.n.(1)	750–820	14-Mar-2006	35.008	139.333	Sagami Bay	Night	3.65–3.89	34.33–34.36	1.3–1.4
	a.n.(8)	78–100	19-Mar-2006	35.008	139.333	Sagami Bay	Night	14.65–15.74	34.55–34.64	3.4–3.7
	p.n.(1)	800–1000	19-Mar-2006	35.008	139.333	Sagami Bay	Night	3.26–4.04	34.32–34.40	1.2–1.3
	a.n.(1), p.n.(1)	800–850	23-Mar-2006	35.008	139.333	Sagami Bay	Night	3.40–3.83	34.34–34.38	1.2–1.3
	a.n.(2)	800–850	19-Mar-2006	35.008	139.333	Sagami Bay	Day	3.70–3.97	34.33–34.35	1.2–1.3
	a.n.(3), p.n.(2)	820–850	14-Mar-2006	35.008	139.333	Sagami Bay	Night	3.47–3.59	34.36–34.37	1.2–1.3
	a.n.(3)	900–950	19-Mar-2006	35.008	139.333	Sagami Bay	Day	3.44–3.59	34.36–34.38	1.2
	p.n.(1)	0	9-Mar-1980	25.200	124.600	Suruga Bay	Night	n/a	n/a	n/a
	p.n.(2)	2	11-Aug-1980	35.033	138.688	Suruga Bay	Night	24.09	n/a	n/a
	a.n.(3)	397	27-Mar-1984	34.800	138.620	Suruga Bay	Day	8.36	n/a	n/a

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TABLE 1. (Continued)

Species	Zooid (No.)	Depth range (m)	Date	Latitude	Longitude	Location	Time	Temperature (°C)	Salinity	Dissolved Oxygen (mL/L)
	a.n.(3)	480	27-Nov-1986	34.850	138.637	Suruga Bay	Day	6.88	n/a	n/a
	a.n.(5)	480	27-Nov-1986	34.850	138.637	Suruga Bay	Day	6.88	n/a	n/a
	p.n.(4)	494.1	9-Mar-1980	25.200	124.600	Suruga Bay	Night	n/a	n/a	n/a
	a.n.(2)	625	24-Feb-1982	34.860	138.633	Suruga Bay	Day	5.88	n/a	n/a
	p.n.(3)	790	13-Nov-1992	34.858	138.633	Suruga Bay	Night	3.94	34.36	n/a
	p.n.(3)	823	27-Mar-1984	34.800	138.618	Suruga Bay	Night	4.45	n/a	n/a
	p.n.(4)	996	12-Nov-1981	34.889	138.646	Suruga Bay	Night	3.55	n/a	n/a
	a.n.(7)	1049	28-Mar-1985	34.795	138.617	Suruga Bay	Day	3.16	n/a	n/a
	p.n.(2)	1073	28-Mar-1985	34.817	138.650	Suruga Bay	Night	3.16	n/a	n/a
	a.n.(3)	1090	6-Nov-1984	34.817	138.620	Suruga Bay	Day	3.52	n/a	n/a
	p.n.(1)	1092	19-Oct-1985	34.842	38.630	Suruga Bay	Night	3.51	n/a	n/a
	a.n.(2)	1105	27-Nov-1986	34.850	138.637	Suruga Bay	Day	3.93	n/a	n/a
	p.n.(2)	1105	27-Nov-1986	34.867	138.638	Suruga Bay	Night	3.93	n/a	n/a
	a.n.(1)	400–450	8-Nov-1991	34.888	138.632	Suruga Bay	Day	7.16–6.73	34.26–34.30	n/a
	a.n.(3)	449–496	24-Feb-1989	34.867	138.625	Suruga Bay	Night	5.91–5.23	34.29–34.31	n/a
	a.n.(4)	530–650	6-Oct-1990	34.862	138.638	Suruga Bay	Night	6.26–5.54	34.29–34.32	n/a
	p.n.(1)	850–990	24-Feb-1989	34.867	138.625	Suruga Bay	Night	4.2–3.77	34.38–34.40	n/a
	p.n.(2)	n/a	1990	n/a	n/a	Suruga Bay	n/a	n/a	n/a	n/a
	p.n.(5)	n/a	1980	n/a	n/a	Suruga Bay	n/a	n/a	n/a	n/a
<i>Kephyes</i> spp.	g.(1)	900–1000	19-Feb-2000	2.472	122.480	Celebes Sea	Night	4.00–5.00	34.55–34.60	1.8–1.9
	b.(1)	350–400	25-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	6.70–8.18	34.22–34.29	2.3–2.6
	b.(1)	400–450	25-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	6.68–7.37	34.24–34.27	2.2–2.4
	b.(11)	400–450	24-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	6.47–7.23	34.22–34.26	2.2–2.4
	b.(10)	450–500	24-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	5.82–6.48	34.20–34.25	2.0–2.3
	b.(10)	450–500	25-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	6.04–6.69	34.25–34.27	2.0–2.3
	b.(3)	500–550	25-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	5.70–6.06	34.24–34.26	1.8–2.2

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TABLE 1. (Continued)

Species	Zooid (No.)	Depth range (m)	Date	Latitude	Longitude	Location	Time	Temperature (°C)	Salinity	Dissolved Oxygen (mL/L)
	b.(5)	500–550	24-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	5.60–5.85	34.19–34.22	1.8–2.2
	b.(3)	550–600	25-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	5.16–5.70	34.25–34.26	1.6–2.0
	g.(3)	550–600	24-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	5.26–5.61	34.22–34.26	1.6–2.0
	b.(5)	600–650	25-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	4.89–5.17	34.26–34.28	1.4–1.7
	b.(1)	650–700	25-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	4.36–4.89	34.28–34.32	1.3–1.7
	g.(9)	650–700	24-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	4.01–5.01	34.28–34.32	1.3–1.7
	b.(4)	700–750	15-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	3.98–4.66	34.31–34.33	1.3–1.5
	b.(1)	750–800	15-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	3.76–4.00	34.32–34.34	1.2–1.5
	g.(1)	750–800	15-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	3.59–3.75	34.34–34.36	1.3–1.5
	b.(2)	800–850	15-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	3.53–3.76	34.34–34.37	1.2–1.4
	g.(2)	800–850	15-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	3.44–3.60	34.36–34.38	1.2–1.4
	b.(1)	850–900	15-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	3.38–3.53	34.34–34.39	1.0–1.4
	g.(4)	900–950	15-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	3.13–3.35	34.39–34.41	0.9–1.2
	b.(3)	950–1000	15-Mar-2006	34.700	139.832	east of Oshima (Japan)	Day	3.21–3.27	34.41–34.41	0.9–1.3
	g.(1)	950–1000	15-Mar-2006	34.700	139.832	east of Oshima (Japan)	Night	3.02–3.14	34.41–34.42	0.9–1.3
	b.(2)	300–350	20-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	9.74–10.79	34.33–34.39	3.0–3.2
	b.(1)	400–450	20-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Night	8.63–9.41	34.3–34.33	2.6–3.0
	b.(1)	400–450	21-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	8.64–9.50	34.27–34.32	2.6–3.0
	b.(1)	450–500	21-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	6.43–8.65	34.22–34.28	2.4–2.9
	b.(3)	500–550	21-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	6.01–6.48	34.22–34.24	1.7–2.5
	b.(8)	550–600	21-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	4.43–6.02	34.23–34.28	1.6–2.1
	g.(6)	550–600	20-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Night	4.86–6.13	34.23–34.28	1.6–2.1
	b.(15)	600–650	21-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	4.09–4.48	34.27–34.29	1.3–1.7
	g.(4)	600–650	20-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Night	4.22–4.86	34.27–34.28	1.3–1.7
	b.(1)	650–700	21-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	3.93–4.12	34.29–34.33	1.2–1.6
	g.(9)	650–700	20-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Night	3.59–4.29	34.27–34.35	1.2–1.6

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TABLE 1. (Continued)

Species	Zooid (No.)	Depth range (m)	Date	Latitude	Longitude	Location	Time	Temperature (°C)	Salinity	Dissolved Oxygen (mL/L)
	g.(4)	700–750	25-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Night	3.48–4.10	34.29–34.36	1.2–1.5
	b.(2)	750–800	22-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	3.51–3.67	34.35–34.36	1.2–1.3
	g.(1)	750–800	25-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Night	3.43–3.51	34.36–34.36	1.2–1.3
	b.(5)	800–850	22-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	3.42–3.61	34.35–34.37	1.2
	g.(1)	800–850	25-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Night	3.30–3.44	34.36–34.37	1.2
	b.(7)	850–900	22-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	3.34–3.42	34.37–34.38	1.1–1.2
	b.(5)	900–950	22-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	3.23–3.35	34.38–34.40	1.1–1.2
	g.(1)	900–950	25-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Night	3.26–3.30	34.38–34.39	1.1–1.2
	b.(6)	950–1000	22-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Day	3.10–3.24	34.40–34.42	1.1
	g.(1)	950–1000	25-Mar-2006	34.991	140.259	off Kamogawa (Japan)	Night	3.18–3.30	34.39–34.40	1.1
	g.(1)	550–919	22-Nov-2011	n/a	n/a	Ogasawara Isl. (Japan)	n/a	n/a	n/a	n/a
	g.(3)	0–1439	24/25-Apr-2012	34.986	139.351	Sagami Bay	Night	2.41–19.35	n/a	n/a
	g.(1)	1200–1400	19-Mar-2006	35.008	139.333	Sagami Bay	Night	2.55–2.96	34.44–34.49	1.1–1.2
	b.(2)	350–400	19-Mar-2006	35.008	139.333	Sagami Bay	Night	7.29–8.589	34.27–34.3	2.2–2.4
	b.(18)	400–450	15-Mar-2006	35.008	139.333	Sagami Bay	Night	6.78–7.86	34.25–34.27	2.1–2.2
	b.(21)	400–450	24-Mar-2006	35.008	139.333	Sagami Bay	Night	6.72–7.72	34.25–34.27	2.1–2.2
	b.(7)	400–450	23-Mar-2006	35.008	139.333	Sagami Bay	Day	7.18–8.03	34.26–34.28	2.1–2.2
	b.(23)	450–500	23-Mar-2006	35.008	139.333	Sagami Bay	Day	6.34–7.18	34.25–34.26	1.8–2.1
	b.(31)	450–500	24-Mar-2006	35.008	139.333	Sagami Bay	Night	6.01–6.76	34.24–34.25	1.8–2.1
	b.(35)	450–500	15-Mar-2006	35.008	139.333	Sagami Bay	Night	6.00–6.78	34.23–34.25	1.8–2.1
	b.(25)	500–550	23-Mar-2006	35.008	139.333	Sagami Bay	Day	5.72–6.35	34.25–34.25	1.7–1.8
	e.(10), b.(10)	500–550	15-Mar-2006	35.008	139.333	Sagami Bay	Night	5.42–6.01	34.23–34.26	1.7–1.8
	e.(9), b.(13)	500–550	24-Mar-2006	35.008	139.333	Sagami Bay	Night	5.50–6.01	34.25–34.26	1.7–1.8
	b.(13)	550–600	23-Mar-2006	35.008	139.333	Sagami Bay	Day	5.23–5.73	34.25–34.26	1.6–1.7
	g.(20)	550–600	24-Mar-2006	35.008	139.333	Sagami Bay	Night	4.96–5.51	34.25–34.27	1.6–1.7
	g.(21)	550–600	15-Mar-2006	35.008	139.333	Sagami Bay	Night	5.00–5.43	34.25–34.26	1.6–1.7
	b.(26)	600–650	23-Mar-2006	35.008	139.333	Sagami Bay	Day	4.75–5.23	34.26–34.28	1.5–1.6

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TABLE 1. (Continued)

Species	Zooid (No.)	Depth range (m)	Date	Latitude	Longitude	Location	Time	Temperature (°C)	Salinity	Dissolved Oxygen (mL/L)
	g.(14)	600–650	24-Mar-2006	35.008	139.333	Sagami Bay	Night	4.60–4.96	34.27–34.28	1.5–1.6
	g.(8)	600–650	15-Mar-2006	35.008	139.333	Sagami Bay	Night	4.62–5.01	34.25–34.28	1.5–1.6
	g.(1)	600–800	19-Mar-2006	35.008	139.333	Sagami Bay	Night	4.036–5.602	34.26–34.32	1.5–1.6
	b.(7)	650–700	23-Mar-2006	35.008	139.333	Sagami Bay	Day	4.27–4.82	34.27–34.30	1.4–1.6
	g.(2)	650–700	15-Mar-2006	35.008	139.333	Sagami Bay	Night	4.14–4.623	34.28–34.31	1.4–1.6
	g.(8)	650–700	24-Mar-2006	35.008	139.333	Sagami Bay	Night	4.27–4.60	34.28–34.30	1.4–1.6
	g.(2)	700–750	14-Mar-2006	35.008	139.333	Sagami Bay	Night	3.89–4.24	34.17–34.34	1.3–1.5
	g.(4)	700–750	23-Mar-2006	35.008	139.333	Sagami Bay	Night	3.88–4.24	34.17–34.34	1.3–1.5
	b.(3)	800–850	19-Mar-2006	35.008	139.333	Sagami Bay	Day	3.70–3.97	34.33–34.35	1.2–1.3
	g.(1)	800–850	23-Mar-2006	35.008	139.333	Sagami Bay	Night	3.40–3.83	34.34–34.38	1.2–1.3
	g.(1)	820–850	14-Mar-2006	35.008	139.333	Sagami Bay	Night	3.47–3.59	34.36–34.37	1.2–1.3
	g.(2)	850–900	23-Mar-2006	35.008	139.333	Sagami Bay	Night	3.31–3.64	34.36–34.39	1.2
	g.(6)	850–900	14-Mar-2006	35.008	139.333	Sagami Bay	Night	3.33–3.475	34.34–34.39	1.2
	b.(1)	900–950	19-Mar-2006	35.008	139.333	Sagami Bay	Day	3.44–3.59	34.36–34.38	1.2
	g.(1)	900–950	23-Mar-2006	35.008	139.333	Sagami Bay	Night	3.20–3.50	34.38–34.40	1.2
	g.(3)	900–950	14-Mar-2006	35.008	139.333	Sagami Bay	Night	3.23–3.34	34.39–34.41	1.2
	b.(5)	950–1000	19-Mar-2006	35.008	139.333	Sagami Bay	Day	3.28–3.45	34.38–34.4	1.2
	g.(10)	950–998	14-Mar-2006	35.008	139.333	Sagami Bay	Night	3.10–3.23	34.41–34.42	1.2
	g.(5)	0	9-Mar-1980	25.200	124.600	Suruga Bay	Night	n/a	n/a	n/a
	b.(1)	480	27-Nov-1986	34.850	138.637	Suruga Bay	Day	6.88	n/a	n/a
	b.(1)	625	24-Feb-1982	34.860	138.633	Suruga Bay	Day	5.88	n/a	n/a
	g.(2)	530–650	6-Oct-1990	34.862	138.638	Suruga Bay	Night	6.26–5.54	34.29–34.32	n/a

## Acknowledgements

We are grateful to Phil Pugh and an anonymous reviewer for their critical and constructive comments on the manuscript and nomenclature employed. We would like to express our gratitude to the scientific parties, captains and crews of the various research cruises upon which the present material was collected for their logistical support, and to Dr. Steven Haddock for use of the photograph of the live animal. Special thanks to Dr. Phil Pugh for making the holotype specimen available for study. We also thank Dr. Hiroyuki Yamamoto of the Environmental Impact Assessment Research Group, within the Research and Development Center for Submarine Resources, JAMSTEC, and Dr. Satoshi Mitarai of OIST, for their support. This work was partially funded by Japan Society for the Promotion of Science (JSPS) KAKENHI, grant numbers 24248032, 26304030 and 23405031, and JST grant CREST, the fund for Interdisciplinary Collaborative Research by the Atmosphere and Ocean Research Institute, University of Tokyo, and the Cross-ministerial Strategic Innovation Promotion Program (SIP) for the Development of New-generation Research Protocols for Submarine Resources.

## References

- Grossmann, M.M. & Lindsay, D.J. (2013) Diversity and distribution of the Siphonophora (Cnidaria) in Sagami Bay, Japan, and their association with tropical and subarctic water masses. *Journal of Oceanography*, 64 (4), 395–411.  
<https://doi.org/10.1007/s10872-013-0181-9>
- Grossmann, M.M., Nishikawa, J. & Lindsay, D.J. (2015) Diversity and community structure of pelagic cnidarians in the Celebes and Sulu Seas, southeast Asian tropical marginal seas. *Deep-Sea Research I*, 100, 54–63.  
<https://doi.org/10.1016/j.dsr.2015.02.005>
- Haddock, S.H.D., Dunn, C.W. & Pugh, P.R. (2005) A re-examination of siphonophore terminology and morphology, applied to the description of two new prayine species with remarkable bio-optical properties. *Journal of the Marine Biological Association of the United Kingdom*, 85, 695–707.  
<https://doi.org/10.1017/S0025315405011616>
- Kitamura, M., Tanaka, Y., Ishimaru, T., Mine, Y., Noda, A. & Hamada, H. (2001) Sagami Bay research report: Improvement of multiple opening/closing net, IONESS (Intelligent Operative Net Sampling System). *Journal of the Tokyo University of Fisheries*, 10, 149–158. [in Japanese]
- Kubota, T., Sawamoto, S. & Kishimoto, H. (1992) Macroplankton Project of Marine Biological Center, Institute of Oceanic Research and Development, Tokai University, 1980–1985. *Bulletin of the Institute of Oceanic Research and Development, Tokai University*, 13, 105–120.
- Kubota, T. & Sawamoto, S. (1993) Macroplankton Project of Marine Biological Center, Institute of Oceanic Research and Development, Tokai University, 1985–1992. *Bulletin of the Institute of Oceanic Research and Development, Tokai University*, 14, 151–163.
- Lindsay, D.J., Yamaguchi, A., Grossmann, M.M., Nishikawa, J., Sabates, A., Fuentes, V., Hall, M., Sunahara, K. & Yamamoto, H. (2014) Vertical profiles of marine particulates: a step towards global scale comparisons using an Autonomous Visual Plankton Recorder. *Bulletin of the Plankton Society of Japan*, 61 (1), 72–81.
- Lindsay, D.J., Umetsu, M., Grossmann, M.M., Miyake, H. & Yamamoto, H. (2015) The gelatinous macroplankton community at the Hatoma Knoll hydrothermal vent. In: Ishibashi, J., Okino, K. & Sunamura, M. (Eds.), *Subseafloor Biosphere Linked to Global Hydrothermal Systems; TAIGA Concept*. Springer, Tokyo, pp. 639–666.  
[https://doi.org/10.1007/978-4-431-54865-2\\_51](https://doi.org/10.1007/978-4-431-54865-2_51)
- Mapstone, G.M. (2009) *Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters*. NRC Research Press, Ottawa, 302 pp.
- Mapstone, G.M. (2014) Global diversity and review of Siphonophorae (Cnidaria: Hydrozoa). *PloS ONE*, 9 (2), 1–37.  
<https://doi.org/10.1371/journal.pone.0087737>
- Patriiti, G. (1969) *Clausophyes massiliana* sp. n. nouvelle espèce de siphonophore calycophore bathypélagique des eaux méditerranéennes. *Thetys*, 1 (2), 255–260.
- Pugh, P.R. (2006) Reclassification of the clausophyid siphonophore *Clausophyes ovata* into the genus *Kephyes* gen. nov. *Journal of the Marine Biological Association of the United Kingdom*, 86, 997–1004.  
<https://doi.org/10.1017/S002531540601397X>
- Silguero, J.M.B. & Robison, B.H. (2000) Seasonal abundance and vertical distribution of mesopelagic calycophoran siphonophores in Monterey Bay, CA. *Journal of Plankton Research*, 22 (6), 1139–1153.  
<https://doi.org/10.1093/plankt/22.6.1139>
- Weibe, P.H., Morton, A.W., Bradley, A.M., Backus, R.H., Craddock, J.E., Barber, V., Cowles, T.J. & Flierl, G.R. (1976) New development in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Marine Biology*, 87, 313–323.  
<https://doi.org/10.1007/BF00397811>