

Diversity and distribution of the Siphonophora (Cnidaria) in Sagami Bay, Japan, and their association with tropical and subarctic water masses

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Abstract Siphonophores were sampled using stratified 1.67-m²-mouth 330- μ m mesh nets during both day- and nighttime in Sagami Bay (35°0.50'N, 139°20'E), off south-eastern Japan during a 9-day period in March 2006, when the Kuroshio Current was in an offshore non-large meander phase. The samples were collected at 50-m intervals spanning from 1,000 m depth to the surface. Fifty-eight species and 11 eudoxid forms of unknown parentage were collected, of which 5 represent first-time records from Japanese waters, and *Clausophyes laetmata* Pugh and Pagès 1993, *Eudoxia cf. galathea* Moser 1925 and *Lensia panikkari* Daniel 1970 were recorded for the first time not only from Japan but from the entire Pacific Ocean. The highest abundance and diversity was found below the thermocline during the day, and above it at night. A second peak in abundance, around 400 m depth, associated with a decrease in diversity, could be linked to the increase in abundance of a single species—*Dimophyes arctica* (Chun 1897). The siphonophore communities could be related to the different water masses in the Bay, with an important influence of lateral transport of both tropical and subarctic species into the Bay by the different water masses.

Keywords Ecological niche · Kuroshio · Offshore non-large meander · Oyashio · Diversity · Eudoxid stage · Lateral transport

1 Introduction

The oceans around Japan have been shown to house an extremely high biodiversity of benthic and pelagic organisms (Fujikura et al. 2012). This could be explained by the wide variety of chemical and physical environments present. This diversity is uneven, however, with waters off south-eastern Japan housing a much higher diversity than those on the Japan Sea side (e.g., Lindsay and Hunt 2005).

The surface waters along the southern and eastern coasts of Japan are greatly influenced by two large oceanic currents: the Oyashio, formed north of Japan and flowing southwards along the eastern coast, and the Kuroshio, flowing north-eastwards along the southern coast of Japan from its origin near Taiwan. These two currents, the cold and warm western boundary currents of the Pacific subarctic and subtropical gyres, respectively, have specific physico-chemical characteristics, and are known to have water mass-specific associated planktonic fauna of copepods, chaetognaths and appendicularians (e.g., Hidaka 2008; Kâ and Hwang 2011; Kidachi and Ito 1979; Kobari et al. 2008; Miyamoto et al. 2012; Oh et al. 1991; Shimode et al. 2006). Although the main body of these currents heads eastwards across the Pacific as part of the North Pacific oceanic gyre, when the two currents meet off eastern Japan, part of the Oyashio gets subducted, creating the Intermediate Oyashio Water, and flows south-westwards along the south-eastern coast of Japan, between 300 and 500 m depth (Yang et al. 1993a).

Sagami Bay, a semi-circular bay off south-eastern Japan, is one of the most studied bays in Japan, and several studies have been made on the cnidarians present in the bay, using various sampling methods (Kawamura 1954; Kitamura 1997, 2000, 2009; Kitamura et al. 2003; Hunt and Lindsay 1999; Lindsay and Hunt 2005; Lindsay et al.

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1998; Toyokawa et al. 1998). However, it is also one of the most complex bays, hydrographically speaking. Indeed, as well as seasonal stratification events, waters in the Bay can be periodically influenced, at the surface, by runoff water from the surrounding land and from Tokyo Bay, by branches of the Kuroshio Current and, in the mesopelagic zone, by mixtures of Low Salinity Water, and, at times, by intrusions of Oyashio Intermediate Water (Senju et al. 1998; Yang et al. 1993b), as well as by periodic passages of typhoons in the summer and autumn months.

Although copepod, chaetognath (Kâ and Hwang 2011), and appendicularian (Hidaka 2008) species are known to be transported from the South China Sea into waters off northern Taiwan and southern Honshu (Kidachi and Ito 1979) by association with the Kuroshio Current, and copepod and chaetognath species specific to Oyashio and polar waters have been recorded in the mesopelagic layers of Sagami Bay (Miyamoto et al. 2012; Oh et al. 1991; Shimode et al. 2006), no studies have yet been made on the possible extent of the lateral transport of pelagic cnidarians, a major predator group, into Sagami Bay by these current systems.

The abundance, diversity, and community structure of cnidarians of the order Siphonophora, collected in March 2006 in Sagami Bay from 1,000 m depth to the surface in 50-m layered samples were studied. Physical characteristics of the water column, measured during the tows by a net-mounted CTD, gave information on the structure of the water column at the time of sampling, and allowed the observed biological results to be placed into an environmental context and compared with the distributions of the tropical and subarctic waters present in the bay.

2 Materials and methods

The MULTIPLE Sampling PLATform Survey of wHOLE ecosystem (MULTI-SPLASH) cruise took place in Sagami Bay ($35^{\circ}0.50'N$, $139^{\circ}20'E$) (Fig. 1) in March 2006, aboard the R/V “Kaiyo” (KY06-03). Intelligent Operated Net Environmental Sampling System (IONESS) net (Kitamura et al. 2001) tows were performed in 6 segments, 3 during the day (labeled ‘Day’) and 3 during the night (‘Night’), from 1,000 to 700 m, from 700 to 400 m, and from 400 m to the surface (Table 1). The current survey was performed as part of a wider study to compare the communities of Sagami Bay with the oceanic areas east of Oshima and off Kamogawa, and priority was given to sampling the same depth layers in different areas during consecutive days. As a result, the sampling in Sagami Bay was performed over a period of 9 days. The nighttime net towed between 300 and 350 m was removed from the analysis due to contamination by surface plankton, and the daytime net towed between 700 and 750 m was removed due to the low filtered volume (239.55 m^3). The sampled depth strata were of 50–100 m in vertical extent (Table 1). The mouth of the IONESS measured 173 by 123 cm and the tow angle was 51.5° on average, resulting in an effective mouth area of 1.67 m^2 . The nylon mesh size was $330 \mu\text{m}$, and the nets were towed at speeds of 1.1–2.7 knots ($0.57\text{--}1.39 \text{ m/s}$) versus the water. Samples were preserved in 5 % seawater-buffered formalin. A Sea-Bird MicroCAT CTD (SBE-37SIP) attached to the IONESS frame recorded pressure, temperature, and conductivity, from which depth, salinity and density were calculated.

Fig. 1 **a** Schematic diagram of Sagami Bay, with, in black, the estimated path of the surface current and, in white, the estimated path of the midwater Low Salinity Water at the time of sampling with, in white, the MULTI-SPLASH IONESS sampling location; **b** the flow of the Kuroshio current between 7 and 14 March (lighter gray), and between 14 and 21 March (darker gray) 2006 (modified after: Japan Coast Guard); black box the location of the inset

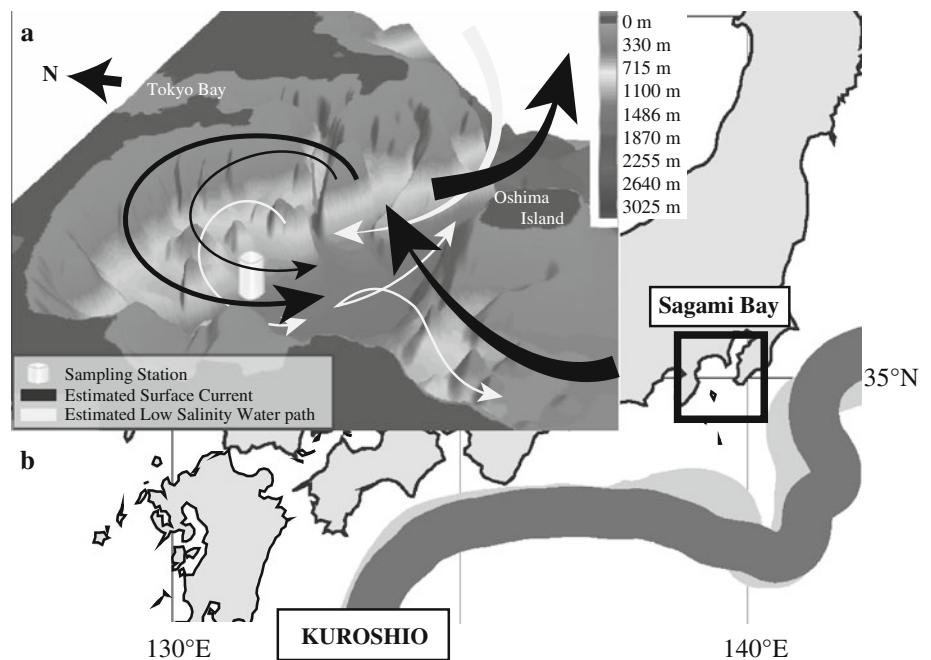


Table 1 Characteristics of the MULTI-SPLASH IONESS net tows performed in Sagami Bay in March 2006

Daytime				Nighttime			
Depth stratum (m)	Date	Start time	Filtered volume (m ³)	Depth stratum (m)	Date	Start time	Filtered volume (m ³)
0–50	19-3-06	16:32	815.3	0–78	19-3-06	23:44	869
50–100	19-3-06	16:22	1,007.99	78–200	19-3-06	23:28	1,465.88
100–200	19-3-06	16:11	1,245.35	200–250	19-3-06	23:15	584.57
200–300	19-3-06	15:55	1,343.16	250–300	19-3-06	23:05	473.38
300–350	19-3-06	15:44	905.91	300–350	–	–	–
350–400	19-3-06	15:30	1,111.97	350–400	19-3-06	22:36	737.24
400–450	23-3-06	17:12	1,487.64	400–450	15-3-06	4:12	1,640.83
450–500	23-3-06	17:01	1,228.81	450–500	15-3-06	4:00	1,573.09
500–550	23-3-06	16:49	1,166.63	500–550	15-3-06	3:49	1,482.16
550–600	23-3-06	16:38	1,114.69	550–600	15-3-06	3:38	1,331.26
600–650	23-3-06	16:23	1,566.04	600–650	15-3-06	3:25	1,614.65
650–700	23-3-06	16:09	1,349.32	650–700	15-3-06	3:15	1,268.47
700–750	–	–	–	700–750	14-3-06	23:59	1,675.3
750–800	19-3-06	12:39	758.37	750–820	14-3-06	23:42	2,005.38
800–850	19-3-06	12:27	580.36	820–850	14-3-06	23:33	960.29
850–900	19-3-06	12:15	480.71	850–900	14-3-06	23:17	1,743.52
900–950	19-3-06	12:05	536.93	900–950	14-3-06	23:08	971.84
950–1,000	19-3-06	11:53	447.59	950–980	14-3-06	22:59	1,001

All siphonophore parts were counted and identified to the lowest taxonomic level possible using the most recent taxonomic guides to each group (Bouillon et al. 2004; Mapstone 2009; Pugh 1992, 1999a, b, 2001, 2006; Totton 1965a) and/or the original descriptions, especially for species of the genus *Lensia*. Siphonophore terminology follows Mapstone (2009), with ‘polygastric stage’ referring to the adult asexual colony, be it cystonect, physonect, or calycophoran, and ‘eudoxid’ referring to the free eudoxid stage produced by the Abylidae, Amphicaryoninae, all Clausophyidae apart from the Clausophyinae, all Diphyidae except the Sulculeolariinae, the Nectopyramidinae, and Sphaeronectidae. The maximum number of zooids comprising a single physonect, hippopodiid, or prajid individual was estimated from submersible-caught samples or video footage from Japanese waters (Table 2). Calycophoran polygastric stages were counted as the number of complete colonies plus the highest number of either anterior or posterior nectophores. For those species producing free eudoxid stages, these were estimated to be the number of entire eudoxids plus the highest number of either bracts or gonophores, except in the family Abylidae, where it was estimated there were 2 gonophores for every bract (personal observation). This methodology was preferred over the counting of bracts alone, due to the large number of *Chuniphyes* spp. eudoxids, for which the bracts were not big enough to be reliably sampled by the 330- μ m mesh. Eudoxids of the genera *Chuniphyes* and *Kephyes* could not

be identified to species level and were considered a single form in each case. This may represent an underestimate of the number of forms present, as polygastric stages of 2 species of each of these genera were collected. Despite not being linked to any polygastric stage, 4 types of eudoxid stage and 7 other types of bract, to which gonophores could not be reliably be linked, were identified. Five types of gonophores could be recognized, but were not included in the study, as it was considered probable that their associated bracts were accounted for under a separate name. Because of the presence and considerable abundance of these eudoxid stages that could not be linked to a single, known polygastric stage, it was not possible to study species, but rather each developmental stage of a species was considered separately, and these entities were called forms. Although conspecific, the different forms of a given species will have different swimming behaviors and predation mechanisms inherent to their size and morphology (Mackie et al. 1987), and, therefore, presumably different ecological niches. Abundance was estimated in number of individuals 1,000 m⁻³, the filtered volume being estimated by a flow-meter situated just above the mouth of the net (Table 1). Shannon’s diversity (H') and Pielou’s evenness (J') indices were calculated in natural logarithm base using the R package “BiodiversityR”.

A hierarchical cluster analysis was performed on square-root-transformed abundance data using the software PRIMER v.6 (Clarke and Warwick 2001) with an average

Table 2 Estimated number of zooids composing a single physonect, prayid or hippopodiid colony in the present study

Species	<i>n</i>	Maximum no. nectophores	Maximum no. bracts	References	Reference locality
<i>Apolemiidae</i> spp.	8	10	n/a	BISMaL data portal (2012) and Lindsay and Miyake (2009)	Sagami Bay
<i>Bargmannia amoena</i>	8	22	n/a	BISMaL data portal (2012) and Lindsay and Miyake (2009)	Sagami Bay
<i>Erenna richardi</i>	2	45	30+	Pugh (2001)	Caribbean
<i>Frillagalma vityazi</i>	5	8	n/a	BISMaL data portal (2012) and Lindsay and Miyake (2009)	Sagami Bay
<i>Halistemma rubrum</i> ^a	n/a	30	n/a	Totton (1965a)	Mediterranean Sea
<i>Marrus orthocanna</i>	6	40+	n/a	BISMaL data portal (2012) and Lindsay and Miyake (2009)	Sagami Bay
<i>Nanomia bijuga</i>	10	20	n/a	BISMaL data portal (2012) and Lindsay and Miyake (2009)	Sagami Bay
<i>Desmophyes annectens</i>	2	2	30+	BISMaL data portal (2012) and Lindsay and Miyake (2009)	Sagami Bay
<i>D. aff. villafrancae</i>	0	2 ^b	n/a ^b		
<i>Rosacea plicata</i>	1	1 N1 + 1 N2	30+	BISMaL data portal (2012) and Lindsay and Miyake (2009)	Japan Trench (38°56.10'N, 143°05.60'E), Okinawa (24°51.15'N, 23°49.94'E)
<i>Vogtia</i> spp.	1	10	n/a	BISMaL data portal (2012) and Lindsay and Miyake (2009)	Sagami Bay

^a *Halistemma rubrum* sensu Totton 1965a

^b Estimated from other *Desmophyes* species; bracts unknown

linkage and Bray–Curtis similarity index. A Similarity Percentage (SIMPER) routine was carried out on the groups obtained in order to determine the forms contributing most to the Bray–Curtis dissimilarity between clusters, and a 2-dimensional Multi-Dimensional Scaling (MDS) analysis was performed. The groups obtained by the cluster analysis were superimposed on the MDS plot. The inter-form interactions were studied by performing a hierarchical cluster analysis with a Bray–Curtis similarity and average linkage on the forms contributing at least 5 % to the total abundance of a given net sample, after standardization of the abundance of each form by the total abundance of the considered form (R-mode analysis). Artwork was created from photographs of preserved specimens using Adobe Illustrator CS5.1.

3 Results

3.1 Water column environmental parameters

The vertical profiles of water mass parameters were similar during the 3 sampling periods, with the exception of the layer between 200 and 350 m, where the water encountered at night on 19 March had a salinity 0.045 units higher, and a temperature 0.9 °C higher, than during the day on the same date (Fig. 2). Additionally, the daytime water masses encountered in the 700–1,000 m stratum differed greatly

from those sampled in the 400–700 m stratum, 4 days before. At 700 m, on 19 March, the waters sampled by the lower tows were up to 0.03 units less saline and up to 0.55 °C warmer than at 699 m on 23 March.

Between 14 and 21 March, the Kuroshio Current was in an offshore non-large meander phase (Japan Coast Guard 2006; Kawabe 1995), and did not intrude into Sagami Bay (Fig. 1). The surface mixed layer was characterized by the highest temperatures (≥ 15.3 °C) and the highest salinities (≥ 34.6) of the water column (Fig. 2) and surface currents did not exceed 0.3 knots (0.15 m/s) (Japan Coast Guard 2006). A marked thermocline was present, between 82 and 88 m during the day and between 78 and 82 m at night. Below the thermocline, the temperature decreased steadily to 1,000 m. The salinity decreased to around 550 m, before increasing again to reach values of 34.44 and 34.42 at 1,000 m during the Day and Night tows, respectively. The lowest salinity value (34.32) was recorded at night between 497 and 502 m on 15 March. The Low Salinity Water (LSW), found between the 26.5 and 27.1 isopycnals (Senjyu et al. 1998), was located between 235.5 and 635.4 m during the day and between 281.9 and 614.1 m at night. These depth differences were most likely due to the fact that the net samplings were not performed consecutively but over a period of up to 9 days (Night on 15 March, Day on 24 March), rather than to any diel pattern. The LSW has been associated with Oyashio Intermediate Water (Senjyu et al. 1998; Yang et al. 1993a), but in the

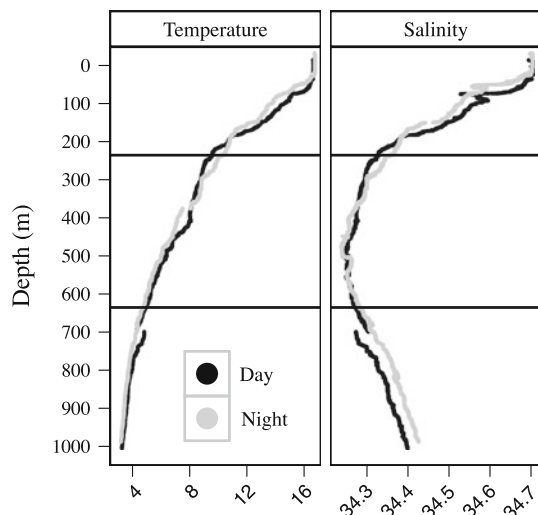


Fig. 2 **a** Temperature (°C) and **b** salinity profiles at the different sampling times. Black horizontal lines indicate the maximal extent of the Low Salinity Water, defined by Senjyu et al. (1998) as being located between the 26.5 and 27.1 isopycnals

present dataset, the salinity was consistently higher than the 34.2 indicative of that water mass (Sekine and Uchiyama 2002; Senjyu et al. 1998), therefore possibly representing a mixture of waters of northern origin.

3.2 Siphonophore diversity and vertical distribution

Fifty-eight species were identified in the MULTI-SPLASH IONESS samples (Table 3): 8 physonects and 50 calyphorans, of which 31 were of the family Diphyidae and 20 of those were of the genus *Lensia* Totton 1932. *Eudoxia macra* Totton 1954, *E. cf. galathea* Moser 1925 and nine previously undescribed eudoxid stages were recorded. These records have been added to the Ocean Biogeographic Information System via the Biological Information System for Marine Life (BISMaL) portal (Grossmann and Lindsay 2013). Eleven species and two eudoxid stages of unknown polygastric stages (Table 3, in bold) were recorded for the first time from Sagami Bay. Of these, *Heteropyramis crystallina* (Moser 1925), *Kephyes* sp. A, *Lensia ajax* Totton 1941, *L. cordata* Totton 1965b and *L. zenkevitchi* Margulis 1970 represent first-time records from Japanese waters (Table 3^c), while *Clausophyes laetmata* Pugh and Pagès 1993, *Lensia panikkari* Daniel 1970, and *E. galathea* were recorded for the first time not only from Japan but from the entire Pacific Ocean (Table 3^d). Other calyphoran genera, such as *Abyla*, *Praya*, *Sphaeronectes*, *Sulculeolaria*, the physonects *Agalma*, *Cordagalma*, *Forskalia*, *Lychnagalma*, and *Physophora*, and all cystonect genera are known to be present in the sampling area (Bigelow 1913; Hunt and Lindsay 1999; Kawamura 1954; Kitamura 1997, 2000, 2009; Kitamura et al. 2003; Lindsay

and Hunt 2005; Lindsay and Miyake 2009; Moser 1925), but were not found in the present IONESS samples. While most of the species recorded for the first time from Sagami Bay have previously been found in neighboring areas such as Suruga Bay or the Ogasawara Islands (Kitamura 2009; Pagès et al. 2006), the bipolar species *Muggiaea bargmannae* Totton 1954 was collected twice, at night, between 400 and 450 m and between 550 and 600 m, while the only previous records from Japanese waters were in the Japan Sea (Park and Won 2004).

There were on average 17 forms per depth stratum, but form numbers varied greatly, both between samples and sampling times, from a minimum of 7 (Night, 250–300 m) to a maximum of 28 (Day, 950–1000 m) (Fig. 3).

Total siphonophore abundance per net was relatively low, with a mean value of 240 individuals 1000 m⁻³, and a maximum of only 1148.5 individuals 1000 m⁻³ (Night, 0–78 m). There were 2 marked peaks in abundance over the water column (Fig. 3): between 50 and 100 m during the day and 0–78 m at night, and between 350 and 400 m at both sampling times. A smaller peak in abundance could be observed between 800 and 850 m during the day. At the upper peak in abundance, *Eudoxoides spiralis* (Bigelow 1911) eudoxids were the most abundant form during the day (Table 4), while *Muggiaea atlantica* Cunningham 1892 polygastric stages dominated the uppermost net at night. This difference could be due to the differences in sampling strata performed during the day and night (200–100–50–0 m during the day, 200–78–0 m at night) which could influence the estimation of abundance of animals present in only a 5 or 10 m stratum of the sampled depth. Indeed, while the uppermost daytime net spent about 13 s sampling each meter of the water column (50–0 m in 11 min), the nighttime net spent only half that amount of time (78–0 m in 8 min, or about 6.4 s m⁻¹). Between 350 and 400 m, where the second peak of abundance could be observed, *Dimophyes arctica* (Chun 1897) polygastric stages dominated, and it was at these depths that the maximal abundance of this species in any given sampling series could be found. Between 800 and 850 m during the day, at the smaller peak in abundance, the dominant form was Eudoxid A (Table 4).

Of the 44 forms collected both during the day- and nighttime, the physonect *Nanomia bijuga* was the only one to display clear diel vertical migration patterns, the peak of abundance found between 100 and 200 m during the day being found between 0 and 78 m at night. However, because the upper 300 m of the water column was sampled in different depth strata during the day and night (Table 1), patterns of diel vertical migration may have been difficult to distinguish. In the mesopelagic zone, all species showed relatively stable patterns of both abundance and vertical distribution between day and nighttime, despite the sampling having been performed on different days (not shown).

Table 3 Depth range and mean depth (weighted by abundance) of the siphonophore forms collected in Sagami Bay during the March 2006 MULTI-SPLASH cruise, with literature-based information on their known depth and geographic ranges

			Depth range (m)	Mean depth (m)	Known depth range (m)	Depth references	Atlantic ocean	Other oceans	Location references
Physonectae									
Agalmatidae	<i>Halistemma rubrum</i> ^a	p	100–200	150	0–500	Pugh (1999b)	60°N–42°S	I, M, P	Alvariño (1971) and Pugh (1999b)
	<i>Nanomia bijuga</i>	p	0–1,000	262.58	0–400	Pugh (1999b)	55°N–59°S	I, M, P	Alvariño (1971) and Pugh (1999b)
Apolemiidae	Apolemiidae A	p	650–850	773.31					
	Apolemiidae B	p	450–950	712.06					
Erennidae	<i>Erenna richardi</i>	p	850–950	898.62	700–1,000	Pugh (1999b)	35°N–31°S	I, P	Alvariño (1971), Daniel (1985) and Pugh (1999a)
Pyrostephidae	<i>Bargmannia amoena</i>	p	350–1,000	666.55	200–910	Pugh (1999a)	37°N–45°S	I, P	Alvariño (1971) and Pugh (1999b)
Incertae sedis	<i>Frillagalma vityazi</i>	p	350–820	503.84	0–2000	Mapstone (2009)	36°–0°N	I, P	Mapstone (2009)
	<i>Marrus orthocanna</i>	p	600–1,000	796	0–700	Mapstone (2009)	60°–35°N	I, M, P	Mapstone (2009)
Calycophorae									
Abylidae	<i>Abylopsis eschscholtzi</i>	p	0–100	48.09	0–200	Pugh (1999b)	40°N–40°S	I, M, P	Alvariño (1971) and Pugh (1999b)
		e	0–100	63.31					
	<i>A. tetragona</i>	p	0–200	88.15	0–200	Pugh (1999b)	57°N–45°S	I, M, P	Alvariño (1971) and Pugh (1999b)
		e	0–400	170.37					
	<i>Bassia bassensis</i>	p	0–100	46.32	0–200	Pugh (1999b)	60°N–49°S	I, M, P	Alvariño (1971) and Pugh (1999b)
Clausophyidae		e	0–200	49.78					
	<i>Chuniphyes moserae</i>	p	600–850	766	>1,000	Pugh (1999b)	50°N–67°S	I, M, P	Alvariño (1971) and Pugh (1999b)
	<i>Ch. multidentata</i>	p	200–700	427.51	300–800+	Pugh (1999b)	60°N–63°S	I, M, P	Alvariño (1971) and Pugh (1999b)
	<i>Ch. spp.</i>	e	78–998	446.73					
	<i>Clausophyes galeata</i>	p	450–950	727.7	>1,000	Pugh (1999b)	47°N–67°S	P	Alvariño (1971) and Pugh (1999b)
	<i>Cl. laetmata</i> ^d	p	550–850	780.93	1,800	Pugh (1999b)	59°–62°S		
	<i>Cl. moserae</i>	p	500–900	665.58	500–1,000+	Pugh (1999b)	60°N–65°S	I, M, P	Alvariño (1971), Mapstone (2009) and Pugh (1999b)
	<i>Heteropyramis crystallina</i> ^e	e	500–700	576.26	400–1,000	Pugh (1999b)	60°N–67°S	I, P	Mapstone (2009) and Pugh (1999b)
	<i>Kephyes ovata</i>	p	78–1,000	613.7	0–700	Mapstone (2009)	50°S–46°N	I, M, P	Alvariño (1971) and Mapstone (2009)
	<i>K. sp. A</i> ^c	p	450–1,000	776.89					
Diphyidae	<i>K. spp.</i>	e	350–1,000	596.83					
	<i>Chelophyes appendiculata</i>	p	78–200	146.72	0–300	Pugh (1999b)	55°N–56°S	I, M, P	Alvariño (1971) and Pugh (1999b)
	<i>C. contorta</i>	p	0–600	231.74	0–200	Pugh (1999b)	SW Africa	I, M, P	Alvariño (1971) and Pugh (1999b)
	<i>Dimophyes arctica</i>	p	78–1,000	403.66	0–600	Pugh (1999b)	74°N–67°S	I, M, P	Alvariño (1971) and Pugh (1999b)
		e	78–1,000	581.98					
	<i>Diphyes bojani</i>	p	0–50	25.5	0–100	Pugh (1999b)	44°N–40°S	I, M, P	Alvariño (1971) and Pugh (1999b)

Table 3 continued

		Depth range (m)	Mean depth (m)	Known depth range (m)	Depth references	Atlantic ocean	Other oceans	Location references
	e	0–200	87.4					
<i>Dip. dispar</i>	e	50–100	75	0–200	Pugh (1999b)	47°N–45°S	I, M, P	Alvariño (1971) and Pugh (1999b)
<i>Eudoxoides mitra</i>	p	0–700	88.85	0–200	Pugh (1999b)	44°N–40°S	I, M, P	Alvariño (1971) and Pugh (1999b)
	e	0–550	66.07					
<i>E. spiralis</i>	p	0–700	86.43	0–250	Pugh (1999b)	60°N–60°S	I, M, P	Alvariño (1971) and Pugh (1999b)
	e	0–750	70.48					
<i>Gilia reticulata</i>	p	250–1,000	895.96	700–1,100	Pugh (1999b)	60°N–62°S	I, P	Alvariño (1971) and Pugh (1999b)
	e	800–950	862.39					
<i>Lensia achilles</i>	p	200–950	473.18	500–900	Pugh (1999b)	60°N–65°S	I, P	Alvariño (1971) and Pugh (1999b)
	e	200–1,000	633.84					
<i>L. ajax</i>^c	p	200–998	492.65	200–1,000	Pugh (1999b)	44°N–33°S	I, P	Alvariño (1971) and Pugh (1999b)
<i>L. asymmetrica</i>	p	400–1,000	862.31	200–1,000	Pugh and Pagès (1997)	–	P	Pugh and Pagès (1997)
	e	500–750	600.57			–		
<i>L.campanella</i>	p	0–100	63.31	0–100	Pugh (1999b)	54°N–38°S	I, M, P	Alvariño (1971) and Pugh (1999b)
<i>L. conoidea</i>	p	50–600	111.61	0–300	Pugh (1999b)	69°N–59°S	I, M, P	Alvariño (1971) and Pugh (1999b)
	e	50–650	119.77					
<i>L. cordata</i>^c	p	500–700	602.01	500–1,250	Zhang (2005)		I, P	Mapstone (2009) and Zhang (2005)
<i>L. exeter</i>	p	350–400	375	400–600	Pugh (1999b)	60°N–33°S		Pugh (1999b)
<i>L. fowleri</i>	p	100–700	332.81	0–300	Pugh (1999b)	61°N–45°S	I, M, P	Alvariño (1971) and Pugh (1999b)
	e	100–200	150					
<i>L. grimaldii</i>	p	200–300	250	400–600	Pugh (1999b)	53°N–43°S	P	Alvariño (1971) and Pugh (1999b)
<i>L. hardy</i>	p	50–200	83.92	0–200	Pugh (1999b)	18°N–57°S	I, P	Alvariño (1971) and Pugh (1999b)
<i>L. havock</i>	p	250–1,000	754.26	1,200–1,600	Pugh (1999b)	60°N–67°S	I, M, P	Alvariño (1971) and Pugh (1999b)
<i>L. hostile</i>	p	350–400	375	500–1,500	Pugh (1999b)	60°N–66°S	I, M, P	Alvariño (1971) and Pugh (1999b)
<i>L. leloupi</i>	p	0–750	110.68	0–200	Pugh (1999b)	44°N–2°S	I	Daniel (1985) and Pugh (1999b)
<i>L. lelouveteau</i>	p	200–1,000	548.85	600–1,000	Pugh (1999b)	60°N–33°S	I, P	Alvariño (1971) and Pugh (1999b)
<i>L. meteori</i>	p	100–200	150	200–500	Pugh (1999b)	55°N–39°S	I, M, P	Alvariño (1971) and Pugh (1999b)
<i>L. multicristata</i>	p	100–1,000	417.51	100–500	Pugh (1999b)	60°N–57°S	I, M, P	Alvariño (1971) and Pugh (1999b)
<i>L. panikkari</i>^d	p	200–400	277.54	0–200	Daniel (1985)	–	I	Daniel (1985)

Table 3 continued

			Depth range (m)	Mean depth (m)	Known depth range (m)	Depth references	Atlantic ocean	Other oceans	Location references
	<i>L. quadriculata</i>	p	500–1,000	876.73	678–1,049	Pagès et al. (2006)	42°N	P	Pagès et al. (2006)
	<i>L. subtilis</i>	p	50–200	93.34	0–200	Pugh (1999b)	55°N–39°S	I, M, P	Alvariño (1971) and Pugh (1999b)
	<i>L. zenkevitchi</i> ^c	p	350–650	527.83	0–2,540	Margulis (1970)	10°S	P	Margulis (1970) and Mapstone (2009) ^b
	<i>Muggiaea atlantica</i>	p	0–1,000	50.93	0–100	Pugh (1999b)	55°N–37°S	I, M, P	Alvariño (1971) and Pugh (1999b)
		e	0–998	100.95					
	<i>M. bargmannae</i>	p	400–600	507.83	200–500	Pugh (1999b)	42–67° N/S	I, P	Alvariño (1971), Park and Won (2004), Pugh (1999b)
	<i>M. delsmanni</i>	p	50–100	75				I, P	Alvariño (1971)
Hippopodiidae	<i>Vogtia glabra</i>	p	50–250	163.71	100–500	Pugh (1999b)	62°N–56°S	I, M, P	Alvariño (1971) and Pugh (1999b)
	<i>V. pentacantha</i>	p	200–300	250		Alvariño (1971)	46°N–32°S	I, M, P	Alvariño (1971)
	<i>V. serrata</i>	p	300–950	504.62	400–800	Pugh (1999b)	66°N–65°S	I, M, P	Alvariño (1971) and Pugh (1999b)
Prayidae	<i>Amphicaryon acaule</i>	p	350–400	375	0–100	Pugh (1999b)	60°N–37°S	I, M, P	Alvariño (1971) and Pugh (1999b)
		e	100–450	231.12					
	<i>Desmophyes annectens</i>	p	200–500	348.67	0–200	Zhang (2005)	North Atlantic	I, M, P	Zhang (2005)
	<i>D. aff. villafrancae</i>	p	500–550	525					
	<i>Nectadamas richardi</i>	e	550–750	575	0–1,000	Mapstone (2009)	60°–0°N	P	Mapstone (2009)
	<i>Rosacea plicata</i>	p	200–950	441.99	200–500	Pugh (1999b)	60°N–65°S	I, M, P	Alvariño (1971) and Pugh (1999b)
Incertae sedis (aff. Diphyidae)	<i>Eudoxia macra</i>	e	50–200	81.89	0–200	Zhang (2005)	34°S–11°N	I, P	Mapstone (2009) and Zhang (2005)
	<i>Eudoxia cf. galathea</i> ^d	e	78–1,000	434.59	0–3,000	Moser (1925)	15°N–64°S		Moser (1925)
	Eudoxid A	e	200–1,000	795.54					
	Eudoxid B	e	0–700	335.38					
	Bract C	e	0–1,000	218.04					
	Bract D	e	50–600	209.49					
	Bract E	e	700–750	725					
	Bract F	e	500–650	568.21					
	Bract G	e	100–200	150					
	Bract H	e	100–350	174.73					
	Bract I	e	100–700	563.44					

Species in bold mark first-time records from Sagami Bay

e Eudoxid, p polygastric stage, I Indian Ocean, M Mediterranean Sea, P Pacific Ocean

^a *Halistemma rubrum* sensu Totton 1965a

^b As *Lensia hostile* (based on Fig. 51)

^c First-time records from Japanese waters

^d First-time records from the Pacific Ocean

Fig. 3 Form richness, total abundance in individuals $1,000 \text{ m}^{-3}$, diversity and evenness over the water column in each sampling series. Marks represent the mean sampling depth for each net

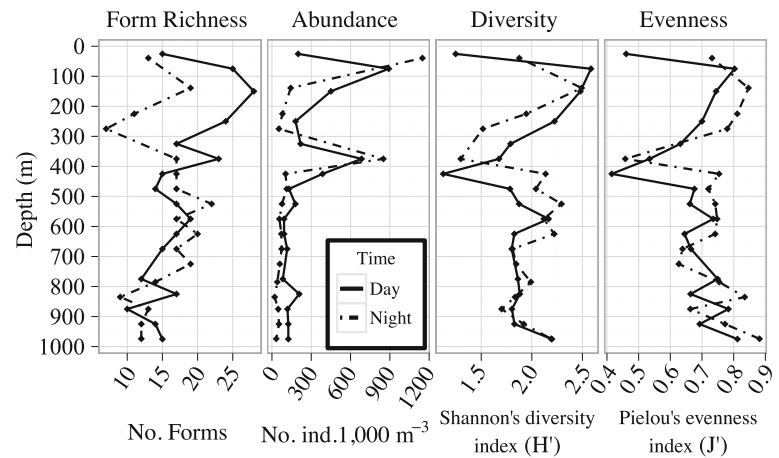


Table 4 Most abundant form per depth stratum and sampling time

Day time depth range (m)		Night time depth range (m)	
0–50	<i>Muggiaea atlantica</i> e. (142.3)	0–78	<i>M. atlantica</i> p. (359.0)
50–100	<i>Eudoxoides spiralis</i> e. (210.3)	78–200	<i>E. spiralis</i> p. (24.6)
100–200	Bract C e. (128.5)	200–250	Eudoxid B e. (22.2)
200–300	<i>Dimophyes arctica</i> p. (67.7)	250–300	Eudoxid B e. (25.3)
300–350	<i>D. arctica</i> p. (89.4)	300–350	–
350–400	<i>D. arctica</i> p. (301.3)	350–400	<i>D. arctica</i> p. (558.9)
400–450	<i>D. arctica</i> p. (266.2)	400–450	<i>D. arctica</i> p. (21.9)
450–500	<i>D. arctica</i> p. (52.1)	450–500	<i>D. arctica</i> e. (31.1)
500–550	<i>D. arctica</i> p. (75.4)	500–550	<i>D. arctica</i> e. (28.3)
550–600	<i>D. arctica</i> e. (37.7)	550–600	<i>D. arctica</i> e. (19.5)
600–650	<i>D. arctica</i> e. (49.2)	600–650	Eudoxid A e. (21.1)
650–700	Eudoxid A (46.7)	650–700	Eudoxid A e. (33.1)
700–750	–	700–750	Eudoxid A e. (29.8)
750–800	<i>D. arctica</i> e. (36.9)	750–820	Eudoxid A e. (16.0)
800–850	Eudoxid A e. (81.0)	820–850	Eudoxid A (8.3)
850–900	<i>D. arctica</i> e. (41.6)	850–900	Eudoxid A (25.8)
900–950	<i>D. arctica</i> e. (52.2)	900–950	Eudoxid A (22.6)
950–1,000	<i>D. arctica</i> e. (35.7)	950–980	<i>Gilia reticulata</i> p. (7.0)

Abundance in individuals $1,000 \text{ m}^{-3}$ in parentheses

e eudoxid, p polygastric stage

Both diversity and evenness indices were globally high over the whole water column, except for the uppermost daytime net, and for the 400–450 m stratum during the day and the 350–400 m stratum at night (Fig. 3). Shannon's diversity index (H') varied between 1.1 and 2.6 and Pielou's evenness index (J') had an average value of 0.7. The highest diversity was found in the daytime nets sampled between 50 and 300 m and in the nighttime nets sampled between 78 and 300 m. The uppermost daytime net, the only one to have sampled exclusively above the thermocline, showed very low diversity and evenness indices ($H' = 1.25$, $J' = 0.46$). The low diversity and evenness

values around 400 m corresponded to the midwater peak in total abundance and the relative increase in abundance of *Dimophyes arctica*.

Random measurements of 271 *Dimophyes arctica* anterior nectophores (from apex to ostium) and 217 bracts (from apex of the headpiece to end of neckshield) present in 27 of the nets, showed the bracts to measure 3.7 mm on average (Fig. 4), with the complete eudoxids being up to 50 % longer (personal observation). Apart from 2 large anterior nectophores more than 8 mm long, the median length of the anterior nectophores was 1.8 mm. No posterior nectophores of a size suitable for the small anterior

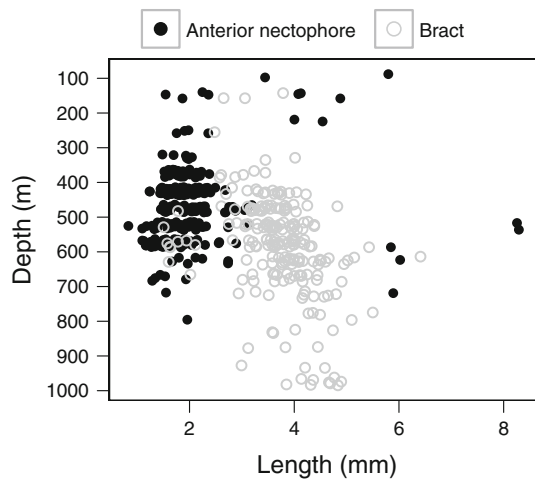


Fig. 4 Length (mm) of the bract of the eudoxid (gray) and anterior nectophore of the polygastric (black) stages of *Dimophyes arctica*

nectophores were found, and it may be possible *D. arctica* polygastric stages do not produce posterior nectophores until they attain a certain size, as was described for the diphyid species *Chelophyes appendiculata* (Patriiti 1964). However, even with these approximations, the eudoxid stages being at least twice the length of the polygastric ones pointed to the presence of different generations within the *D. arctica* population.

3.3 Community structure analysis

The multivariate cluster analysis performed on square-root-transformed abundance data produced 5 clusters at a 40 % cut-off (Fig. 5), with between 1 and 19 net samples per cluster. Cluster A contained the daytime 0–50 m net sample, the only one to have sampled exclusively above the thermocline. This net sample was dominated by *Muggiaea atlantica* polygastric stages. Cluster B contained the nets having sampled through the thermocline, down to 200 m depth. *Eudoxoides spiralis* eudoxids and polygastric stages caused the highest discrimination with the other clusters (Table 5). Cluster C contained the nighttime nets towed between 200 and 300 m. The nets in this cluster corresponded to the warmer, more saline waters found at these depths during the night, and Eudoxid B was the form causing the highest discrimination with the deeper nets, while the absence of *Chuniphyes* spp. eudoxids differentiated it from the daytime nets in the 200–300 m stratum. In cluster D, which contained all nets towed between 300 and 600 m, as well as the daytime nets towed between 200 and 300 m and between 600 and 650 m, *Dimophyes arctica* polygastric stages (Table 5) contributed the most to the dissimilarity of this cluster with Cluster E, which contained all the remaining nets.

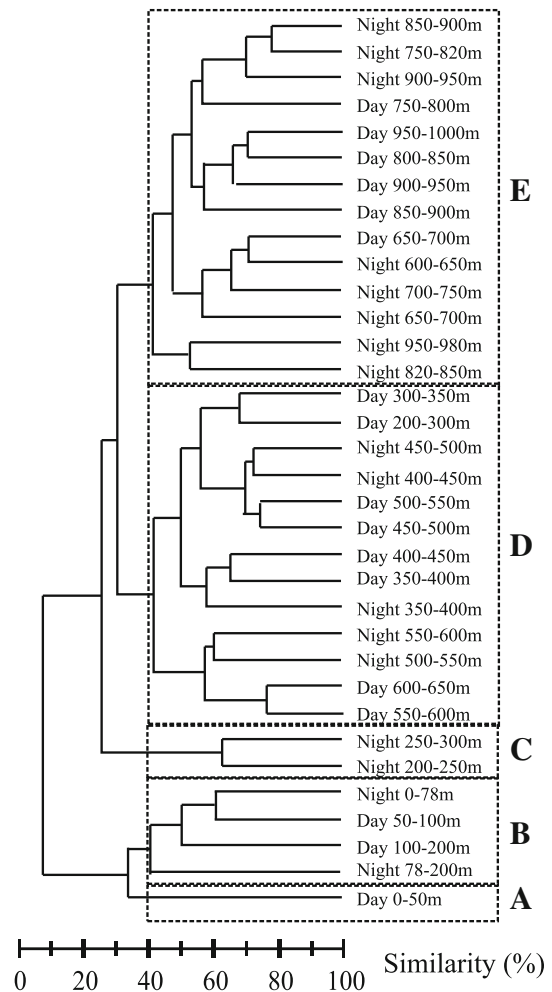


Fig. 5 Community structure analysis dendrogram, (clustering performed on square-root-transformed abundance data, with an average linkage and Bray–Curtis similarity)

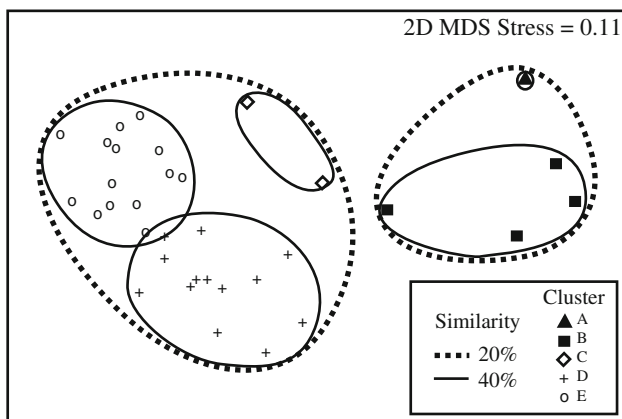
The 2D MDS (Fig. 6), with a stress value of 0.11, showed clusters A, B, and C to be well defined, while clusters D and E showed very small distances in the area corresponding to the daytime sampling depths around 650 m (cluster D: 600–650 m; cluster E: 650–700 m). The 3D MDS analysis (stress = 0.08) showed a clear separation of these latter 2 clusters (data not shown).

The inter-species cluster analysis produced 5 main groups at a 20 % similarity cutoff, and 5 forms did not cluster (*Clausophyes moserae*, *Kephyes ovata*, *Lensia conoidea* and *L. cordata* polygastric stages, and *Muggiaea atlantica* eudoxids). The 5 assemblages could be linked with the depth distribution and origin of the different forms they contained (Fig. 7). The 2 distinct mesopelagic clusters could be differentiated by the origin of the forms they contained. Indeed, the first, composed of *Lensia achilles* and Eudoxid B, represented temperate mesopelagic species, as opposed to the second group, containing

Table 5 Forms contributing the most to the dissimilarity between clusters (average dissimilarity ≥ 5 in terms of percentage abundance for each pair of clusters)

D	<i>Dimophyes arctica</i> p. ←			
	<i>Chuniphyes</i> spp. e. ←			
	Eudoxid A e. ↓			
C	Eudoxid A e. ↓	<i>D. arctica</i> p. ←		
	Eudoxid B e. ←	<i>Chuniphyes</i> spp. e. ↓		
	<i>D. arctica</i> p. ←	Eudoxid B e. ←		
B	<i>Eudoxoides spiralis</i> e. ←	<i>E. spiralis</i> e. ←	<i>E. spiralis</i> p. ←	
	<i>E. spiralis</i> p. ←	<i>E. spiralis</i> p. ←	<i>M. atlantica</i> p. ←	
	Bract C e. ←	<i>M. atlantica</i> p. ←	<i>E. spiralis</i> e. ←	
	<i>Muggiaea atlantica</i> p. ←	Bract C e. ←	Bract C e. ←	
	<i>Lensia leloupi</i> p. ←	<i>D. arctica</i> p. ↓	<i>L. leloupi</i> p. ←	
A		<i>L. leloupi</i> p. ←		
	<i>M. atlantica</i> p. ←	<i>M. atlantica</i> p. ←	<i>M. atlantica</i> p. ←	<i>M. atlantica</i> p. ←
	Eudoxid A e. ↓	<i>D. arctica</i> p. ↓	Eudoxid B e. ↓	<i>L. leloupi</i> p. ↓
	<i>E. spiralis</i> e. ←	<i>D. arctica</i> e. ↓	<i>D. arctica</i> p. ↓	Bract C e. ↓
	<i>D. arctica</i> e. ↓	<i>Chuniphyes</i> spp. e. ↓		
		<i>E. spiralis</i> e. ←		
	E	D	C	B

Arrows indicate which cluster, of columns or rows, a form contributes the most to
e eudoxid, *p* polygastric stage

**Fig. 6** 2D MDS diagram of the inter-net clustering, with 20 % (dotted line) and 40 % (solid line) similarity levels, each point represents one net sample, shapes refer to the clusters observed in Fig. 5

Dimophyes arctica, *Lensia multicristata* and the eudoxids of the genera *Chuniphyes* and *Kephyes*, forms that are generally more abundant in polar regions, and extremely rare in the mesopelagic zone of warm seas such as the Mediterranean (Alvariño 1971; Mapstone 2001), or Sulu Seas (Lindsay, personal observation).

3.4 Eudoxid stage descriptions

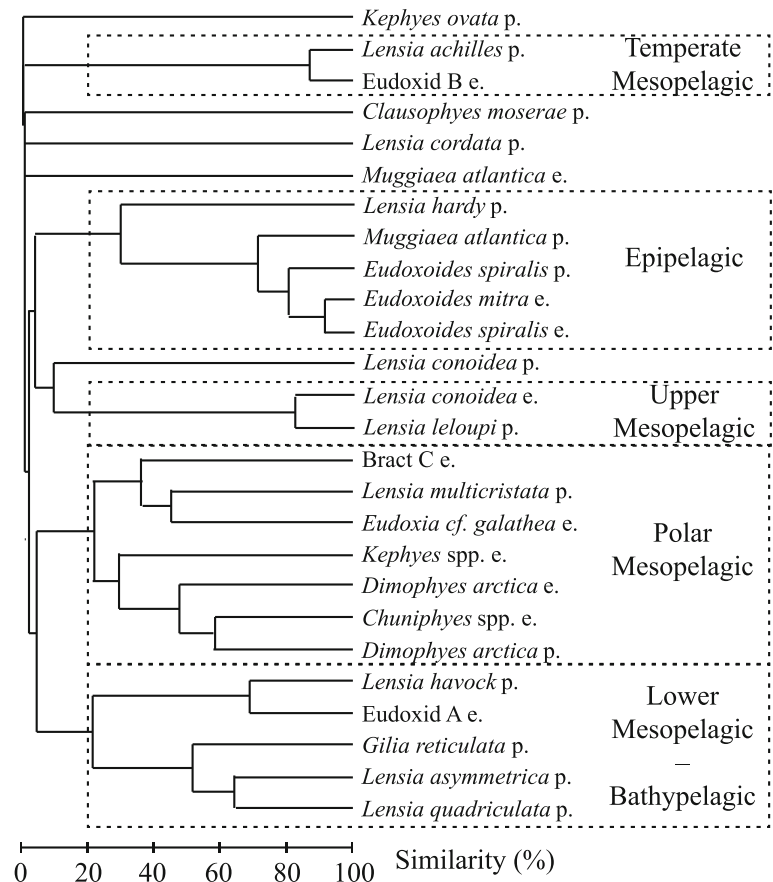
Free eudoxids could be assigned with certainty to 17 species, and a further 2 could be assigned to genus level. Eleven eudoxids of unknown polygastric stages were recorded (Table 3). Of these, four were found to contribute to the dissimilarity between clusters, as well as being the most abundant forms in several net samples (Table 4): *Eudoxia* cf. *galathea*, Eudoxid A and B, and Bract C. Although quite probably of the genus *Lensia*, the polygastric stage of these eudoxids could not be determined with certainty.

3.4.1 *Eudoxia* cf. *galathea* Moser 1925 (Fig. 8a i–iv)

Bract up to 2.92 mm tall and 1.6 mm wide; headpiece conical, without ridges; neckshield usually half the headpiece height in length, posterior margin bilobed due to wide central notch of varying height; hydroecium deep, evenly rounded; phyllocyst globular and asymmetrical, without pedicle, varying greatly in size depending on the number of oil droplets contained.

Gonophore up to 3.8 mm tall by 1.4 mm wide, without marked ridges; short rounded mouthplate; articulate surface flat; nectosac conical at apex, radial canals originating on upper side of nectosac, near the apex, running straight to

Fig. 7 Inter-species cluster analysis dendrogram (R-mode analysis: forms contributing at least 5 % to the total abundance of a given net sample, abundance standardized by total, average linkage and Bray–Curtis similarity), and the assemblages obtained at a 20 % similarity cut-off. *e* Eudoxid, *p* polygastric stage



the ostial canal; pedicular canal short, curving to the apex of the gonophore.

The length of the bract's neckshield, and the presence of a large posterior notch in it; as well as the shape of the gonophores clearly differentiate this eudoxid from that of *Lensia asymmetrica* Stepanjants 1970, the only other small, unridged diphyid-type bract to have an asymmetrical phyllocyst. The eudoxids described by Moser (1925), under the name *Eudoxia galathea*, had an average size of 3–4 mm, and the overall shape of the bract and somatocyst led us to tentatively assign our samples to this species. The original description does not mention a posterior notch or bilobed neckshield, however the illustrations on plate IV show an undulating posterior margin to the bracts, perhaps an interpretation of a shallow posterior notch.

3.4.2 Eudoxid A (Fig. 8b i–iv)

Bract up to 6.4 mm long by 1.7 mm wide; conical headpiece without marked ridges; neckshield at least as long as headpiece, wider at posterior margin, with 2 tooth-like projections, one on each baso-lateral corner; hydroecial cavity flattened; phyllocyst about half the length of the headpiece, asymmetrical in shape, containing oil droplets, orange in colour in living animals.

Gonophore 5.7 mm long by 3.2 mm wide; 6 incomplete ridges extending to 1/5 gonophore length from ostium; large rounded mouthplate; hydroecium shallow; articulate surface concave; nectosac as wide as gonophore, with rounded conical apex, radial canals straight, joining on ventral facet at about 1/5th nectosac length from its apex.

The large size of this eudoxid, its lower mesopelagic distribution, as well as the bright orange pigmentation of the phyllocyst when alive (Fig. 8b iv), would make this a likely eudoxid stage of *Lensia havock* or *L. cordata*, also present in the sampling zone and having orange-pigmented somatocysts of a similar globular shape as the phyllocyst of Eudoxid A.

3.4.3 Eudoxid B (Fig. 8c i–ii)

Bract up to 3.19 mm tall and 1.35 mm wide; headpiece conical, with 2 marked bracteal ridges extending to the apex of the headpiece; neckshield greatly reduced; hydroecium shallow; phyllocyst long and thin, without pedicle, occupying 80 % of the headpiece in height.

Gonophore up to 2.9 mm tall by 1.24 mm wide; 4 well-developed, complete ridges, the lower merging into the mouthplate; mouthplate short, square.

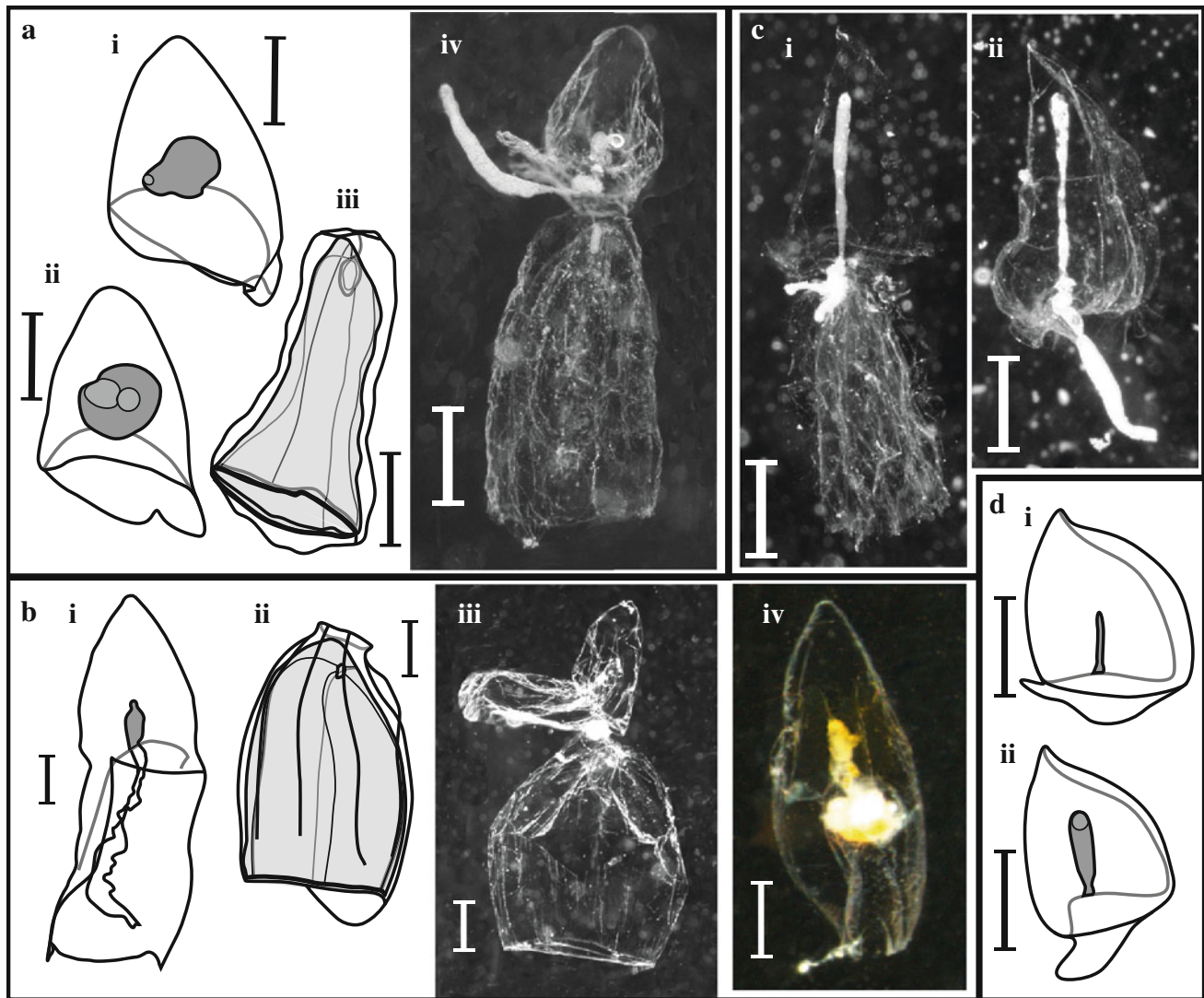


Fig. 8 **a** *Eudoxia* cf. *galathea*: *i* right lateral view, *ii* lower view of bract, *iii* upper view of gonophore, *iv* photograph of preserved eudoxid, right lateral view of bract and left lateral view of gonophore (all Day, 400–450 m, 35°0.50'N, 139°20'E); **b** Eudoxid A: *i* upper view of bract (Night, 820–850 m, 35°0.50'N, 139°20'E), *ii* right lateral view of gonophore (Night, 750–800 m, 35°0.50'N, 139°20'E), *iii* photograph of preserved eudoxid, left lateral view of bract and upper view of gonophore (Night, 700–750 m, 35°0.50'N, 139°20'E),

iv photograph of living bract in lower view (34°59.15'N, 139°21.05'E); **c** Eudoxid B: *i* photograph of preserved eudoxid, right lateral view of bract and left lateral view of gonophore (Night, 100–200 m, 34°59.43'N, 140°15.54'E), *ii* photograph of preserved bract in right lateral view (Night, 350–400 m, 34°59.43'N, 140°15.54'E); **d** *i* Bract C, right lateral view, *ii* *Lensia conoidea* bract, right lateral view (Night, 100–200 m, 35°0.50'N, 139°20'E), scale bars 1 mm

3.4.4 Bract C (Fig. 8d i)

Similar in size and shape to the bract of *Lensia conoidea* (Keferstein and Ehlers 1860) (Fig. 8d ii), Bract C (Fig. 8d i) can be differentiated by the less pronounced teardrop shape, its flattened hydroecial cavity and the shorter, thinner phyllocyst.

Bract up to 3 mm tall, with marked bracteal ridges; neck-shield 1/3 the height of the headpiece, without marked notches; hydroecial cavity flattened; phyllocyst elongate, without terminal swelling, about 50 % of the headpiece in height.

Gonophore unknown.

The abundance of this bract, its upper-mesopelagic distribution and the elongate but thin phyllocyst would make this a likely eudoxid stage of *Lensia leloupi*.

4 Discussion

With 58 species of siphonophore recorded from the MULTI-SPLASH IONESS samples, the species richness of Sagami Bay was found to be much higher than the 37 species collected by Mapstone (2009) in the Canadian Pacific from similar depth strata and using similar sampling

gear. However, that study dealt with water masses around 48.5°N, while Sagami Bay is at 35°N and, moreover, a zone of important heterogeneity when considering the temporal variability of the waters present in the Bay. Indeed, waters in the Bay can be influenced at the surface by runoff water from the surrounding land and from Tokyo Bay, by sub-branches of the Kuroshio current, and, in the mesopelagic zone, by a mixture of waters of northern origin, the LSW, and, at times, by intrusions of Oyashio Intermediate Water (OIW) (Senjyu et al. 1998).

The CTD profile and surface oceanographic maps (Japan Coast Guard 2006) during the present sampling times showed no direct influence of either Kuroshio (off-shore non-large meander type) (Fig. 1) or OIW at the sampling station, and the hydrographic characteristics in the Bay remained relatively constant during the 9-day sampling, the main differences being found at night, between 200 and 351 m, and, during the day, around 700 m. The cluster analysis and 2D MDS plot showed clear separation of the siphonophore communities based on the depth and origin of the different water masses of the Bay.

The epipelagic community, composed of clusters A and B, and spanning from 200 m to the surface, was dominated by *Muggiaea atlantica*, an epipelagic species known to undergo seasonal blooms in spring and autumn (Kitamura 2009; Mapstone 2009), and by warm-water species of the genera *Abylopsis*, *Bassia* and *Eudoxoides*, absent in the Canadian Pacific (Mapstone 2009), but recorded up to 60°N in the Atlantic (Table 3), an area influenced by a similar current system—the North Atlantic Drift. *Muggiaea delsmanni* Totton 1954, an Indian Ocean species whose Pacific records include the Fiji and South China Seas, and other tropical waters of south-east Asia (Gao et al. 2002; Rengarajan 1973), was collected in the 50–100 m net during the day, possibly above the thermocline present between 82 and 88 m.

Another primarily tropical, neritic species, *Lensia subtiloides* (Lens and van Riemsdijk 1908), was completely absent from the present dataset. It was previously found to be present from June to November, and absent in February from the upper 200 m of Sagami Bay (Kitamura 2009), so perhaps season, rather than the effect of the Kuroshio Current, may play a greater role in determining its distribution in south-eastern Japan. It is possible the two morphologically similar species, *Lensia leloupi* Totton 1954 and *L. subtiloides*, might compete for the same resources and be mutually exclusive. Indeed, in March, *L. leloupi* was one of the most abundant forms in the upper 200 m, and was one of the forms contributing the most to cluster B (Table 5), while the only previous records of this species from Sagami Bay were of a single individual in February and a single individual in June, from 0 to 150 m vertical NORPAC net tows (Kitamura 1997).

However, the influence of the surface Kuroshio Current was not enough to explain the presence of all warm-water species. Indeed, the presence of *Lensia cordata* between 500 and 700 m, a species only previously recorded from the Indian Ocean (Totton 1965b) and the South China Sea (Gao et al. 2002; Zhang 2005; Zhang and Lin 1997), might point to a transport of waters in the mesopelagic zone from the tropical Pacific to Sagami Bay, possibly following a similar path to that of the Kuroshio Current. Similarly, *Lensia panikkari*, found between 200 and 400 m, has only previously been recorded in the Indian (Daniel 1985; Gibbons and Thibault-Botha 2002; Thibault-Botha and Gibbons 2005) and Atlantic Oceans (Pugh 1984).

The diversity of the Siphonophora matched that of a study of the scolecitrichid copepods of Sagami Bay (Kuriyama and Nishida 2006) obtained using similar sampling methods, and of the calanoid copepod community sampled at the same station in Sagami Bay using smaller stratified net systems (Shimode et al. 2006), both in terms of Shannon–Wiener index values and of the profile of this index over the water column, except for the important decrease observed around 400 m in the present study. This decrease in diversity could be directly linked to the decrease in evenness caused by the single species *Dimophyes arctica*, the large increase in abundance of which coincided with the lowest salinity values. Although this species has a worldwide distribution, it is primarily found in cold, polar waters, and is believed to spawn only in such water masses (Stepanjants et al. 2006). Indeed, the small *D. arctica* polygastric stages were concentrated within the LSW, associated with the much larger eudoxid stages, while larger polygastric stages were collected both in the LSW and in the warmer upper-mesopelagic layers (Fig. 4). The numerical dominance of the polygastric stage over the eudoxid one, and the extremely small size of the anterior nectophores would indicate the generation succession occurring in May in the waters of British Columbia (Mapstone 2009; Mills 1982) and in Norwegian fjords (Hosia and Båmstedt 2008) happened earlier, possibly at the start of March, in the present study area. This difference in timing between latitudes of 50–60°N and Sagami Bay might be due to the Oyashio origin of the LSW. The Oyashio Current flows at up to 0.4 m s⁻¹ southwards along the north-eastern coast of Japan (Ohshima et al. 2005), and the observed animals were probably produced in northern waters and transported into the mesopelagic depths of Sagami Bay by subduction of Oyashio waters at the Oyashio–Kuroshio convergence zone. Indeed, the maximum abundance of both eudoxid and polygastric stages of *D. arctica* were found around 400 m, much deeper than the upper-mesopelagic records of this species from Canadian (Mapstone 2009; Mills 1982) and Norwegian (Hosia and Båmstedt 2008) waters. The presence of large numbers of

eudoxids and very small, young, polygastric stages at depths greater than they are normally found in more northern waters (Table 3), could therefore resemble the pathway described for *Neocalanus cristatus* copepodite V stages by Oh et al. (1991). Similarly, it is not known whether the physico-chemical parameters of the Bay would allow active reproduction of the polar *D. arctica*.

The presence of midwater, subarctic-derived water intrusion events in the Bay could also be confirmed by the presence of *Muggiaea bargmannae*, a species found exclusively in Arctic and Antarctic waters. Margulis (1978) notes that in the western North Atlantic, mixing with 'tropical water' (the North Atlantic Drift) did not appear to affect the distribution of *M. bargmannae*. A similar phenomenon could be observed in Sagami Bay, where the water temperatures at the sampling area approximated 6 °C, 2 °C more than the upper temperature limit reported for this species by Stepanjants (1967).

Also found in the LSW waters was the eudoxid form herein referred to as *Eudoxia cf. galathea* Moser (1925). Although their vertical distribution ranged from 78 m at night to 1,000 m during the day in Sagami Bay, their peak of maximal abundance was found between 350 and 450 m during the day, and between 400 and 450 m at night. This is in agreement with the 300- to 500-m depth distribution of this eudoxid recorded by von Leloup and Hentschel (1935) in the Southern Atlantic. The samples described by Moser (1925) from the Southern and Atlantic Oceans were collected in non-closing vertical nets, but the majority of the samples were collected in nets towed from 400 m to the surface. The bracts of these eudoxids did show some similarity with the bracts of *Muggiaea bargmannae* illustrated in Stepanjants (1967) and Zang and Lin (2001). However, this species is primarily bipolar and appeared only twice in the present data series, in contrast to *E. cf. galathea*, one of the most abundant forms in the lower 600 m (not shown). This eudoxid stage, the eudoxids of *Dimophyes arctica* and *Eudoxoides spiralis*, those of the genera *Chuniphyes* and *Kephyes*, as well as 3 others of unknown polygastric stages (Eudoxids A and B, and Bract C), were found to contribute greatly to the community structure (Table 5), and eudoxid stages were the most abundant form in 65 % of the net samples. A brief description of these new eudoxid forms is provided, but considering the great diversity of diphyid siphonophores in Japanese waters, the application of DNA barcoding techniques may be necessary to definitively assign these eudoxid stages to known polygastric ones, and thereby obtain a better understanding of the niche partitioning between polygastric and eudoxid stages of calyphoran siphonophores.

The lower mesopelagic cluster was characterized by deep-water species such as *Gilia reticulata*, *Lensia asymmetrica*, *L. havock* and *L. quadriculata*. These species are

commonly found below 700 m at all latitudes in all oceanic basins, and may represent a cold-, deep-water signature, as they have yet to be recorded from warm deep seas such as the Mediterranean (Table 3) or the Sulu Seas (D.J.L., personal observation). However, it is not known whether the high temperatures at depth, or the shallow sills controlling the water flow to these seas limit the access of these species, which are rarely recorded shallower than 200 m (Table 3).

Despite the wide or worldwide distribution of most siphonophore species (Alvarino 1971; Mapstone 2009; Margulis 1980), the stratified IONESS samples collected in Sagami Bay in March 2006 showed water mass-specific community structure within the Siphonophora. The presence of lateral transport of some key siphonophore species into Sagami Bay following both the Kuroshio and Oyashio paths could be confirmed. Several eudoxids of unknown polygastric stage were found to play important roles in the community structure. Although it is one of the most well-studied bays in Japan, the complex oceanographic structure of Sagami Bay means the biodiversity it houses has yet to be fully assessed. Indeed, 11 siphonophore species and 2 previously described eudoxids of unknown parentage were recorded for the first time from the Bay in this study, bringing the total number of siphonophores species known from Sagami Bay to 118, more than 60 % of the total 191 valid siphonophore species (WoRMS 2013).

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