

Spatio-temporal structure of the jellyfish community in the transition zone of cold and warm currents in the northwest Pacific

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Abstract: Species composition, diversity and biomass of jellyfish (Cnidaria and Ctenophora), with their spatio-temporal distributions, were analyzed in the upper 1500 m of the Oyashio front, the Transition zone and the Kuroshio extension, off Tohoku, northeastern Japan, between May 2005 and March 2006. Species composition and abundance differed remarkably between the shallower layer and the deeper layer at the boundary of 300–500 m depth, where water density was within the range of the North Pacific Intermediate Water. In the deeper layer, diversity reached its peak with the appearance of 27 taxa common in all the regions throughout the year, though abundance was low. *Pantachogon haeckeli* and *Crossota rufobrunnea* were dominant in the deeper layer. The possibility of diel vertical migration was suggested in two midwater species: *Euphysa japonica* and *Atolla vanhoeffeni*. In the Oyashio waters, jellyfish abundance was much higher than in the Transition waters and Kuroshio-derived waters, but with low diversity, dominated by large numbers of *Aequorea victoria* and *Limnopsis arctica*. High values of diversity were found in the Kuroshio-derived waters with various tropical and warm-water species, especially calycophoran siphonophores being present. In the Transition waters, diversity was relatively high, with co-occurrence of warm-water species and cold-water species. Jellyfish biomass tended to be high in the midwater zone due to the occurrence of large species, particularly Scyphozoa. Carbon-based jellyfish biomass calibrated with other studies exceeded that of other organism groups.

Key words: biodiversity, gelatinous plankton, Kuroshio, midwater, Oyashio

Introduction

The oceanic environment is incredibly vast and its mid-water zone (we use the word to encompass the mesopelagic zone and the upper part of the bathypelagic zone) is the largest metazoan habitat on Earth (Widder et al. 1989; Webb et al. 2010). A lot of information exists concerning its larger and hard-bodied inhabitants, such as fish, squids, crustaceans and other organisms that are still recognizable after collection in trawl nets. Understanding of its fragile

gelatinous inhabitants has been gradually progressed by using modern survey technologies such as multiple opening/closing nets, crewed submersibles, remotely-operated vehicles (ROVs) and visual/video plankton recorders (VPRs), and it is now obvious that many kinds of gelatinous plankton inhabit the midwater zone in large numbers (Mackie 1985, Larson et al. 1991, Toyokawa et al. 1998, Miyake et al. 2004, Kitamura et al. 2008, Raskoff et al. 2010). This indicates that gelatinous organisms may play a significant role in marine food webs, material transfer and transformation (Bailey et al. 1995, González et al. 2004, Sweetman & Chapman 2011). Studies of the actual

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biomass, community structure and species diversity are crucial to the understanding of the dynamics of the global marine ecosystem.

In Japanese waters, information on gelatinous organisms has been accumulated by using ROVs (Lindsay et al. 2004, Lindsay et al. 2008, Lindsay & Miyake 2009). While video footage provided by ROVs is optimal for observing and counting larger creatures, smaller creatures with taxonomic characters of microscopic size are not surveyed effectively. The VPR towed from research vessels, is a powerful method for identifying and quantifying small, fragile particles and organisms that are hard to detect by other methods. However, purely visual methods do not collect actual specimens, so identification to taxonomic levels lower than family is not usually possible at current resolutions (Ichikawa et al. 2006, Ichikawa 2008), with notable exceptions (e.g. Lindsay et al. 2008). Physical specimens are still essential for checking taxonomic characters in detail and for identifying the majority of specimens to species level. The present study is intended to fill this knowledge gap by investigating the gelatinous fauna using samples collected by multiple layer opening/closing nets.

The area between the Oyashio front and the Kuroshio extension is called the Transition zone, where cold, low-salinity Oyashio waters encounter warm, high-salinity subtropical Kuroshio waters (Yasuda 2003), forming extremely complex oceanographic structures and a highly productive environment. The present study aims to reveal the species composition, abundance, biomass and diversity of pelagic cnidarians and ctenophores, as well as their spatio-temporal distribution in the upper 1500 m of the Oyashio front, the Kuroshio-Oyashio transition zone and the Kuroshio extension, off Tohoku, northeastern Japan.

Materials and Methods

Field sampling

Samples were collected by the R/V *Wakataka-Maru* of the Tohoku National Fisheries Research Institute, Fisheries Research Agency (TNFRI, FRA) and the R/V *Hokkoku-maru* of the Hokkaido National Fisheries Research Institute (HNFRI, FRA), at five stations (A4 [A3: only in July], A9, A13, A17 and A21) along the A-line transect (Saito et al. 2002) during both day and night, in May, July and September 2005 and March 2006 (Fig. 1, Table 1A), using a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS): 4 m² mouth area, 1/8 inch (3.175 mm) oval mesh (Wiebe et al. 1985). The following eight depth intervals were sampled: 1500–1000, 1000–750, 750–500, 500–300, 300–150, 150–100, 100–50 and 50–0 m. Ship speed was approximately 2 knots in order to keep the angle of the net mouth at 45°.

Fixation and identification

All samples were fixed on board in 10% formalin-sea-

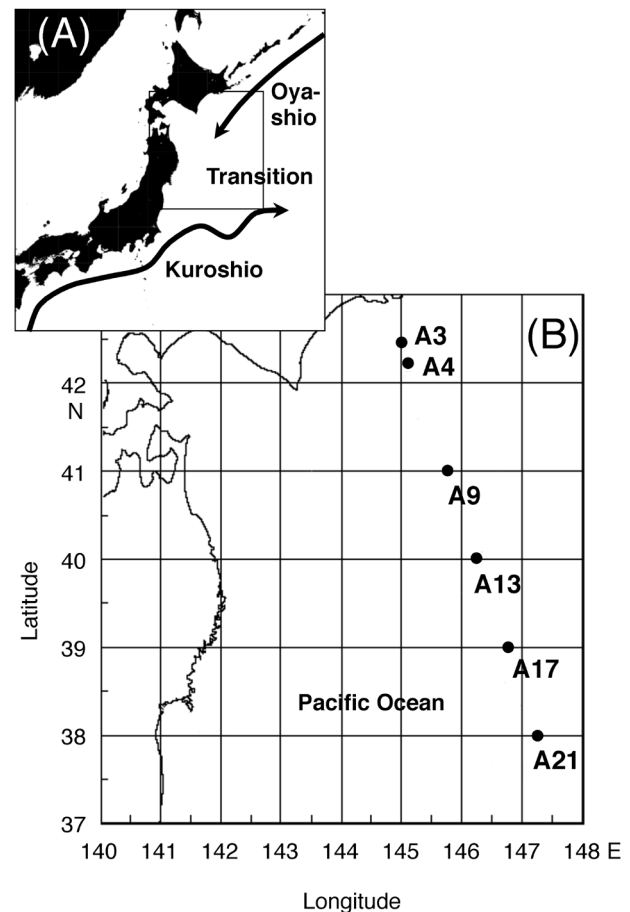


Fig. 1. (A) Oyashio, Kuroshio and Transition zone in the northwest Pacific; (B) locations of the sampling stations.

water buffered with borax. Cnidarians and Ctenophores, referred hereafter as 'Jellyfish,' were later sorted from the samples, transferred into 5% formalin-seawater buffered with borax and identified to the lowest taxonomic level possible under a dissecting microscope. Taxonomy followed Naumov (1960), Kramp (1968), Arai & Brinckmann-Voss (1980), Pagès & Gili (1992), Bouillon (1999), Bouillon et al. (2006), Collins et al. (2008) and Lindsay et al. (2008, 2017) for Hydromedusae; Totton (1965a, 1965b), Kirkpatrick & Pugh (1984), Pagès & Gili (1992), Pugh (1999, 2006), Bouillon et al. (2006) and Mapstone (2009) for Siphonophorae; Mianzan & Cornelius (1999) and Grossmann & Lindsay (2017) for Scyphomedusae; Mianzan (1999) and Mills & Haddock (2007) for Ctenophora.

Estimating abundance and biomass

All individuals were counted and the counts were converted to densities, being expressed as the number of individuals per unit volume (individuals m⁻³) according to the filtered volume, calculated from the numbers of revolutions of the flowmeter integrated on the MOCNESS. When necessary, the number of individuals per unit volume were converted to those per unit area, in the water column below one square meter (individuals m⁻²) for the

Table 1. Investigated stations.

(A) Locations and depths of the sampling stations.				
Station	Latitude	Longitude	Depth (m)	
A3	42°30'N	145°00'E	1780	
A4	42°15'N	145°07.5'E	2950	
A9	41°00'N	145°45'E	5580	
A13	40°00'N	146°15'E	4900	
A17	39°00'N	146°45'E	5210	
A21	38°00'N	147°15'E	5200	
(B) Stations were classified into O: Oyashio area, Tc: Transition zone of cold waters, Tw: Transition zone of warm waters and K: Kuroshio area.				
Month	O	Tc	Tw	K
May 2005	A4	A9, A13	A17	A21
July 2005	A3, A13	A9, A17	A21	—
Sep. 2005	A4, A9, A13	—	—	A17, A21
March 2006	A4, A9, A13	A17	A21	—

whole water column or for a given depth range according to the thickness of the stratum. To approximate the actual number of siphonophoran colonies present, specific protocols were adopted. The number of nectophores of Physonectae, Hippopodiidae and Prayidae was divided by 20, 10 and 2 respectively, and then rounded up to the next whole number (Grossmann & Lindsay 2013). The abundances of Diphyidae, Abylidae and Clausophyidae were estimated by taking the larger number of either anterior or posterior nectophores. Data on the eudoxid stages of siphonophores was used only for recognizing species composition and measuring wet-weight.

Wet weight of each taxon in each haul was measured to 0.01 g with an electronic balance, after blotting the specimen(s) on an absorbent paper towel until water was no longer absorbed onto the towel, and converted to carbon content. The following conversion factors were adopted: Hydromedusae (0.0039), Scyphomedusae (0.0091) (Larson 1986), and Ctenophora (0.0054) (Bailey et al. 1995). For Siphonophorae, the conversion factor for Hydromedusae was used. Biomass as wet-weight and carbon content was converted to the weight per unit volume (mg m^{-3}) according to the estimated filtered volumes.

Identification of the water masses

Temperature and salinity profiles were determined with a conductivity-temperature-depth (CTD) profiler (SBE 9plus, Sea-Bird Electronics) on each sampling occasion. Stations were classified into four regions based on the temperature at 100 m depth, according to Odate (1994) and Yokouchi et al. (1997), as the Oyashio area ($\leq 5^\circ\text{C}$), the Transition zone of cold waters ($>5^\circ\text{C}$, $\leq 10^\circ\text{C}$), the Transition zone of warm waters ($>10^\circ\text{C}$, $\leq 15^\circ\text{C}$), and the Kuroshio area ($>15^\circ\text{C}$).

Data analysis

A dissimilarity matrix between the species ($>0.3\%$ of the total number of catches) and between the net samples was constructed using the Bray-Curtis Index (Bray & Curtis 1957). Based on this matrix, clusters were resolved using the unweighted pair-group method with the arithmetic mean (UPGMA) (Sneath & Sokal 1973). Statistics were carried out using R version 3.4.1 (R Core Team 2012).

Vertical distribution profiles for each taxon were used to calculate the average values of abundance and biomass in each of the classified regions in each season. To determine the presence or absence of diel vertical migration (DVM) in each species ($>0.3\%$ of the total number of individuals), the weighted mean depth (WMD) of presence of a species was calculated as: $\text{WMD} = \sum(n_i z_i d_i) / \sum(n_i z_i)$, where d_i is the midpoint of the depth interval of sample i , z_i is the thickness of the stratum, and n_i is the number of individuals per unit volume (inds. m^{-3}) (Pearre 1973). Species diversity was determined using the Shannon index of diversity (H') (Shannon 1948).

Results

Hydrography of the regions

Stations were classified into the Oyashio area, the Transition zone of cold waters, the Transition zone of warm waters and the Kuroshio area as shown in Table 1B. In the Oyashio area, cold water below 5°C was present at all the layers except the shallowest layers, whereas in the Kuroshio area, Kuroshio-derived water, characterized by high temperature and high salinity, spread from the surface to 400–500 m depth (Fig. 2A). Transition zones contained mixtures of the Oyashio-derived waters and the Kuroshio-derived waters to various extents. In July, a warm core ring stayed around A9 (TNFRI, FRA 2005), making the oceanographic structure around this station extremely complex.

Up to 300 m depth at most stations (but deeper in the Kuroshio area), temperature and salinity decreased and then salinity gradually increased down to 1500 m depth, while temperature was relatively stable at $2.2\text{--}2.5^\circ\text{C}$.

Recorded taxa

Eighty-seven taxa of jellyfish were recorded in this study, as follows; Hydromedusae: 28 taxa, Siphonophorae: 52 taxa, Scyphomedusae: 5 taxa, and Ctenophora: 2 taxa (Table 2). Of the Hydromedusae, 9 Narcomedusan taxa, 9 Trachymedusan taxa, 7 Anthomedusan species, and 3 Leptomedusan taxa appeared. Of the Siphonophorae, 3 taxa of Physonectae and 49 taxa of Calycophorae were recognized.

Three species were recorded for the first time from Japan: *Corymorpha furcata* (Kramp, 1948), *Zygocanna vagans* Bigelow, 1912 and *Melophysa melo* (Quoy & Gaimard, 1827).

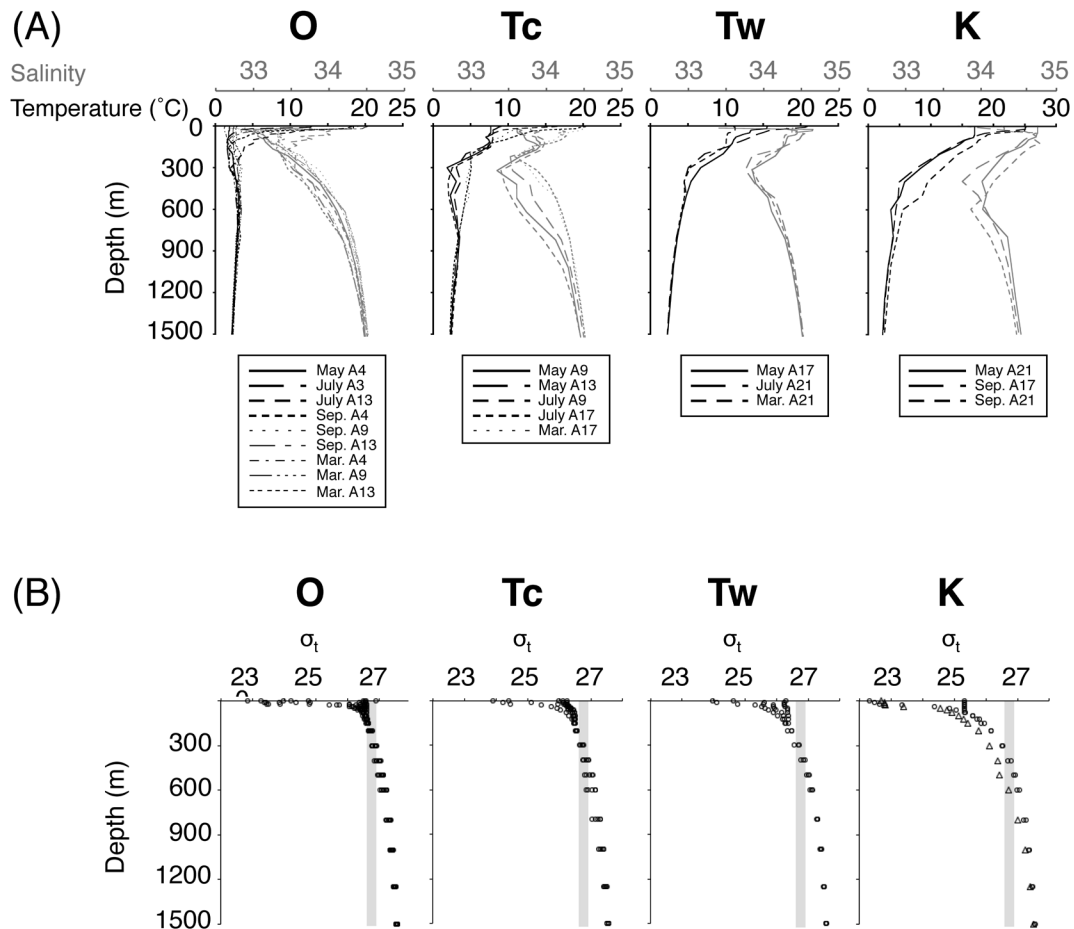


Fig. 2. Hydrography of all stations classified into four regions: the Oyashio area (O), the Transition zone of cold waters (Tc), the Transition zone of warm waters (Tw) and the Kuroshio area (K): (A) Vertical profiles of water temperature and salinity versus depth (Temperature in black, salinity in grey); (B) Vertical profiles of seawater density versus depth (grey range denotes $\sigma_t = 26.6-26.9$). Triangles: A21 in September where the depth of $\sigma_t = 26.6-26.9$ was around 600 m.

Phylum CNIDARIA Verrill, 1865

Class HYDROIDOMEDUSAE Claus, 1877

Subclass ANTHOMEDUSAE Haeckel, 1879

Family CORYMORPHIIDAE Allman, 1872

Corymorpha furcata (Kramp, 1948)

Material: Three specimens collected in the 500–750 m depth range at A17 in May 2005, in the 1000–1500 m depth range at A17 in July and in the 0–50 m depth range at A9 in September 2005. Specimens have been deposited in the Zooplankton Sample Collection of the Fisheries Research Agency (ZP-FRA), maintained at the Tohoku National Fisheries Research Institute, Fisheries Research Agency, as ZP-FRA 1510-1–3.

Description: Umbrella 5.0 to 5.4 mm high and 3.7 to 5.8 mm wide, with a pointed apex; stomach barrel-shaped, with conical apical cavity; four prominent radial canals; four tentacles of three types: longest tentacle in terminal part twice bifurcated, with four knobs, opposing tentacle shorter and filiform, remaining two still shorter and stockier.

Subclass LEPTOMEDUSAE Haeckel, 1866

Family AEQUOREIDAE Eschscholtz, 1829

Zygocanna vagans Bigelow, 1912

Material: One specimen collected in the 100–150 m depth range at A21 in May 2005. The specimen has been deposited at the ZP-FRA as ZP-FRA 1510-4.

Description: Umbrella flat, thin, hard, 50 mm in diameter; subumbrella with radial rows of gelatinous papillae; stomach almost 1/2 as wide as umbrella, mouth with crenulate lips; four primary canals from a cruciform structure in the center of stomach bifurcating, then branching to 37 single radial canals before reaching the stomach periphery.

Subclass SIPHONOPHORAE Eschscholtz, 1829

Order PHYSONECTAE Haeckel, 1888

Family ATHORYBIIDAE Huxley, 1859

Melophysa melo (Quoy & Gaimard, 1827)

Material: 3 detached nectophores, 12 bracts and 3 gastrozooids as well as a stem with a pneumatophore, 1 bract, 2 gastrozooids and 4 palpons collected in the 100–150 m depth range at A21 in May 2005. The specimen has been

Table 2. The recorded taxa with their relative abundance and the distribution in the Oyashio area (O), the Transition zone of cold waters (Tc), the Transition zone of warm waters (Tw), and the Kuroshio area (K).

Taxa		O	Tc	Tw	K	Relative abundance in total catch (%)
<i>Aegina citrea</i> Eschscholtz, 1829	h1	+	+	+	+	0.1
<i>Aeginopsis laurentii</i> Brandt, 1838	h1	+	—	—	—	≤0.05
<i>Aeginura grimaldii</i> Maas, 1904	h1	○	○	○	○	0.5
<i>Pseudaegina pentanema</i> (Kishinouye, 1910)	h1	—	—	—	+	≤0.05
<i>Solmundaegina nematophora</i> Lindsay, 2017	h1	●	●	○	○	2.6
<i>Solmundella bitentaculata</i> (Quoy & Gaimard, 1833)	h1	—	—	—	+	≤0.05
<i>Solmissus</i> spp. ^A	h1	○	○	○	○	0.7
<i>Tetraplatia volitans</i> (Busch, 1851)	h1	—	+	—	—	≤0.05
Narcomedusae spp. ^A	h1	+	+	+	+	0.2
<i>Liriope tetraphylla</i> (Chamisso & Eysenhardt, 1821)	h2	+	+	+	○	0.2
<i>Halicreas minimum</i> (Fewkes, 1882)	h2	○	○	○	○	0.7
Halicreatidae spp. ^B	h2	○	○	○	○	1.9
<i>Aglantha digitale</i> (O.F. Müller, 1776)	h2	★	★	●	●	41.9
<i>Colobonema sericeum</i> Vanhöffen, 1902	h2	+	+	○	○	0.2
<i>Crossota alba</i> Bigelow, 1913	h2	+	+	+	—	≤0.05
<i>Crossota rufobrunnea</i> (Kramp, 1913)	h2	●	●	○	○	6.7
<i>Pantachogon haeckeli</i> Maas, 1893	h2	●	●	●	○	8.2
Rhopalonematidae spp. ^B	h2	○	○	○	●	2.4
<i>Chiarella centripetalis</i> Maas, 1897	h3	+	+	—	—	≤0.05
<i>Bythotia depressa</i> Naumov, 1960	h3	○	○	○	○	0.7
<i>Calyropsis nematophora</i> Bigelow, 1913	h3	+	+	—	—	0.1
<i>Pandea rubra</i> Bigelow, 1913	h3	○	+	+	+	0.2
<i>Corymorpha furcata</i> (Kramp, 1948)	h3	+	+	+	—	≤0.05
<i>Euphysa japonica</i> (Maas, 1909)	h3	○	●	○	○	2
<i>Porpita porpita</i> (Linnaeus, 1758)	h3	+	—	—	+	≤0.05
Anthomedusae spp.; unident.	h3*	+	+	+	+	≤0.05
<i>Aequorea coerulescens</i> (Brandt, 1835)	h4	+	—	—	—	≤0.05
<i>Zygocanna vagans</i> Bigelow, 1912	h4	—	—	—	+	≤0.05
<i>Ptychogena lactea</i> Agassiz, 1865	h4	+	—	—	+	≤0.05
<i>Chromatonema</i> spp.	h4*	+	+	+	—	0.1
<i>Melophysa melo</i> (Quoy & Gaimard, 1827)	s1	—	—	—	+	≤0.05
<i>Bargmannia</i> spp.	s1	+	+	+	+	0.1
Physonectae spp. ^C	s1	○	○	○	○	0.6
<i>Abyla</i> spp.	s2	—	—	—	+	n.d.
<i>Ceratocymba leuckartii</i> (Huxley, 1859)	s2	—	—	—	+	≤0.05
<i>Ceratocymba sagittata</i> (Quoy & Gaimard, 1827)	s2	—	+	+	+	n.d.
<i>Abylopsis</i> spp. ^D	s2	+	—	○	●	1.5
<i>Bassia bassensis</i> (Quoy & Gaimard, 1833)	s2	—	—	—	○	0.1
<i>Enneagonum hyalinum</i> Quoy & Gaimard, 1827	s2	—	—	+	+	≤0.05
<i>Chuniphyes moserae</i> Totton, 1954	s2	—	+	—	+	≤0.05
<i>Chuniphyes multidentata</i> Lens & Van Riemsdijk, 1908	s2	+	○	○	○	0.4
<i>Chuniphyes</i> spp.; unident.	s2*	—	—	+	+	≤0.05
<i>Clausophyes galeata</i> Lens & Van Riemsdijk, 1908	s2	+	+	+	+	≤0.05
<i>Clausophyes moserae</i> Margulis, 1988	s2	○	○	○	○	0.7
<i>Clausophyes</i> spp.; unident.	s2*	—	+	—	—	≤0.05
<i>Kephyes</i> spp. ^D	s2	+	+	+	+	0.1
<i>Chelophyes appendiculata</i> (Eschscholtz, 1829)	s2	—	—	+	○	0.4
<i>Chelophyes contorta</i> (Lens & Van Riemsdijk, 1908)	s2	—	—	—	+	≤0.05
<i>Dimophyes arctica</i> (Chun, 1897) ^D	s2	●	●	○	○	9.2
<i>Diphyes bojani</i> (Eschscholtz, 1829)	s2	—	—	—	+	≤0.05
<i>Diphyes chamissonis</i> Huxley, 1859	s2	+	—	—	+	≤0.05
<i>Diphyes dispar</i> Chamisso & Eysenhardt, 1821	s2	+	—	○	●	1.3
<i>Eudoxoides mitra</i> (Huxley, 1859)	s2	—	—	—	+	≤0.05
<i>Eudoxoides spiralis</i> (Bigelow, 1911)	s2	—	+	—	+	≤0.05
<i>Lensia achilles</i> Totton, 1941	s2	○	○	○	○	1.5
<i>Lensia conoidea</i> (Keferstein & Ehlers, 1860)	s2	+	○	○	○	0.4
<i>Lensia cordata</i> Totton, 1965	s2	—	+	+	+	≤0.05
<i>Lensia cossack</i> Totton, 1941	s2	—	+	+	+	≤0.05
<i>Lensia fowleri</i> (Bigelow, 1911)	s2	—	—	—	○	0.1
<i>Lensia havock</i> Totton, 1941	s2	○	+	+	+	0.3
<i>Lensia leloupi</i> Totton, 1954	s2	—	—	○	—	≤0.05

Table 2. Continued.

Taxa		O	Tc	Tw	K	Relative abundance in total catch (%)
<i>Lensia multicristata</i> (Moser, 1925)	s2	○	○	○	○	1.2
<i>Lensia subtiloides</i> (Lens & Van Riemsdijk, 1908)	s2	+	—	+	+	≤0.05
<i>Lensia</i> spp.; unident.	s2*	+	+	+	○	0.2
<i>Muggiaea atlantica</i> Cunningham, 1892	s2	○	●	○	○	2.5
<i>Sulculeolaria chuni</i> (Lens & Van Riemsdijk, 1908)	s2	—	—	+	+	≤0.05
<i>Sulculeolaria monoica</i> (Chun, 1888)	s2	—	—	—	+	≤0.05
<i>Sulculeolaria quadrivalvis</i> de Blainville, 1834	s2	—	—	—	○	0.1
<i>Sulculeolaria turgida</i> (Gegenbaur, 1854)	s2	—	—	+	+	≤0.05
<i>Hippopodius hippopus</i> (Forsskal, 1776)	s2	—	—	+	○	0.1
<i>Vogtia glabra</i> Bigelow, 1918	s2	+	+	+	○	0.1
<i>Vogtia pentacantha</i> Kölliker, 1853	s2	—	+	+	+	≤0.05
<i>Vogtia serrata</i> (Moser, 1925)	s2	○	○	○	○	1.2
<i>Vogtia spinosa</i> Keferstein & Ehlers, 1861	s2	+	—	+	—	≤0.05
Hippopodiidae spp.; unident.	s2*	+	+	—	—	≤0.05
<i>Amphicaryon acaule</i> Chun, 1888	s2	+	—	—	+	≤0.05
<i>Amphicaryon ernesti</i> Totton, 1954	s2	—	—	—	+	≤0.05
<i>Amphicaryon</i> spp.; unident.	s2*	—	—	—	+	≤0.05
<i>Nectadamas diomedea</i> (Bigelow, 1911)	s2	+	+	+	+	n.d.
<i>Nectopyramis natans</i> (Bigelow, 1911)	s2	+	—	—	—	≤0.05
<i>Nectopyramis thetis</i> Bigelow, 1911	s2	+	—	—	+	n.d.
<i>Nectopyramis</i> spp.; unident.	s2*	—	+	+	—	≤0.05
<i>Desmophyes</i> spp.	s2	+	○	+	+	0.2
<i>Maresearsia praeclara</i> Totton, 1954	s2	+	—	—	+	≤0.05
<i>Praya reticulata</i> (Bigelow, 1911)	s2	—	+	—	—	≤0.05
<i>Praya dubia</i> (Quoy & Gaimard, 1833)	s2	—	—	—	+	≤0.05
<i>Rosacea</i> spp. ^D	s2	●	●	○	○	4.4
<i>Stephanophyes superba</i> Chun, 1888	s2	—	—	—	+	n.d.
Prayidae spp.; unident.	s2*	—	+	+	—	≤0.05
<i>Atolla chuni</i> (Vanhöffen, 1902)	sc	—	+	—	—	≤0.05
<i>Atolla vanhoeffeni</i> Russell, 1957	sc	+	+	○	○	0.3
<i>Atolla wyvillei</i> Haeckel, 1880	sc	○	○	○	○	0.4
<i>Atolla</i> spp.; unident.	sc*	+	+	+	+	0.1
<i>Periphylla periphylla</i> (Péron & Lesueur, 1810)	sc	○	○	○	○	0.5
<i>Periphyllopsis braueri</i> Vanhöffen, 1902	sc	+	+	+	+	0.1
Scyphozoa sp. ephyra	sc	—	+	—	—	≤0.05
Tentaculata spp.	c	+	+	○	○	0.5
<i>Beroe</i> spp. ^E	c	○	○	+	○	1.1

★: >10 inds. m⁻², ●: 1–10 inds. m⁻², ○: 0.1–1 inds. m⁻², +: <0.1 inds. m⁻², —: 0 inds. m⁻², n.d.: not determined as only eudoxids appeared. h1: Narcomedusae, h2: Trachymedusae, h3: Anthomedusae, h4: Leptomedusae, s1: Physonectae, s2: Calycophorae, sc: Scyphozoa, c: Ctenophora. *Excluded from taxa counting and diversity analysis. ^A *Solmissus incisa* (Fewkes, 1886) and *Solmissus marshali* Agassiz & Mayer, 1902 both occur in this area, but we were unable to distinguish them from each other by morphological characters of fixed specimens. For the same reason, *Cunina* spp., *Pegantha* spp., and *Solmaris* spp. were treated as Narcomedusae spp.. ^B *Botrynema* sp. and *Haliscera* sp. are characterized by the thick flat umbrella with apical projection without perradial gelatinous papillae on exumbrella. As apex was often squashed and tentacles were lost in most cases, therefore the two genera were treated as Halicreatidae spp.. Midwater species *Arctapodema* spp. and shallower layers species (*Amphogona* spp. and *Rhopalonema* spp.) occurred in these areas. Because there were not enough characters remaining evident in the damaged specimens to distinguish them, we treated these species as Rhopalonematidae spp.. ^C In this study, several species of Physonectae were present, but further identification was not possible due to the damage to the specimens, with the exception of the characteristically-shaped *Bargmannia* spp. and *Melophysa melo*. ^D The majority of *Abylopsis* spp. was *Abylopsis tetragonna* (Otto, 1823), but *A. eschscholtzi* (Huxley, 1859) was also found sometimes. Further identification was impossible because of the damaged condition of the specimens. In most cases the characteristic canal on the nectosac of the anterior nectophore was invisible, and it was difficult to distinguish the two species. Therefore, they were treated as *Abylopsis* spp. Because we could not distinguish the recently described species *Kephyes hiulcus* Grossmann & Lindsay, 2017 from *K. ovata* (Keferstein & Ehlers, 1860) because of the damaged condition of the specimens, we treated them as *Kephyes* spp.. *Dimophyes arctica* and *Muggiaea bargmannae* are morphologically very similar. We treated these calycophoran siphonophores as *D. arctica* after a recheck of every specimen in the 300–500 m depth range (230 inds.) found 100% of specimens were *D. arctica*. The greater part of *Rosacea* spp. was *Rosacea plicata* Bigelow, 1911, but *R. cymbiformis* Delle Chiaje, 1830 was found in the 50–100 m depth range at A21 in May and the 100–150 m depth range at A21 in July. Further identification was impossible because of the damaged condition of the specimens. ^E The majority of *Beroe* spp. was *B. abyssiicola* Mortensen, 1927 with densely anastomosing branches of meridional canals and with long ctene rows, however, a small number of specimens were thought to be *B. cucumis* Fabricius, 1780 but could not be positively distinguished from *B. abyssiicola*.

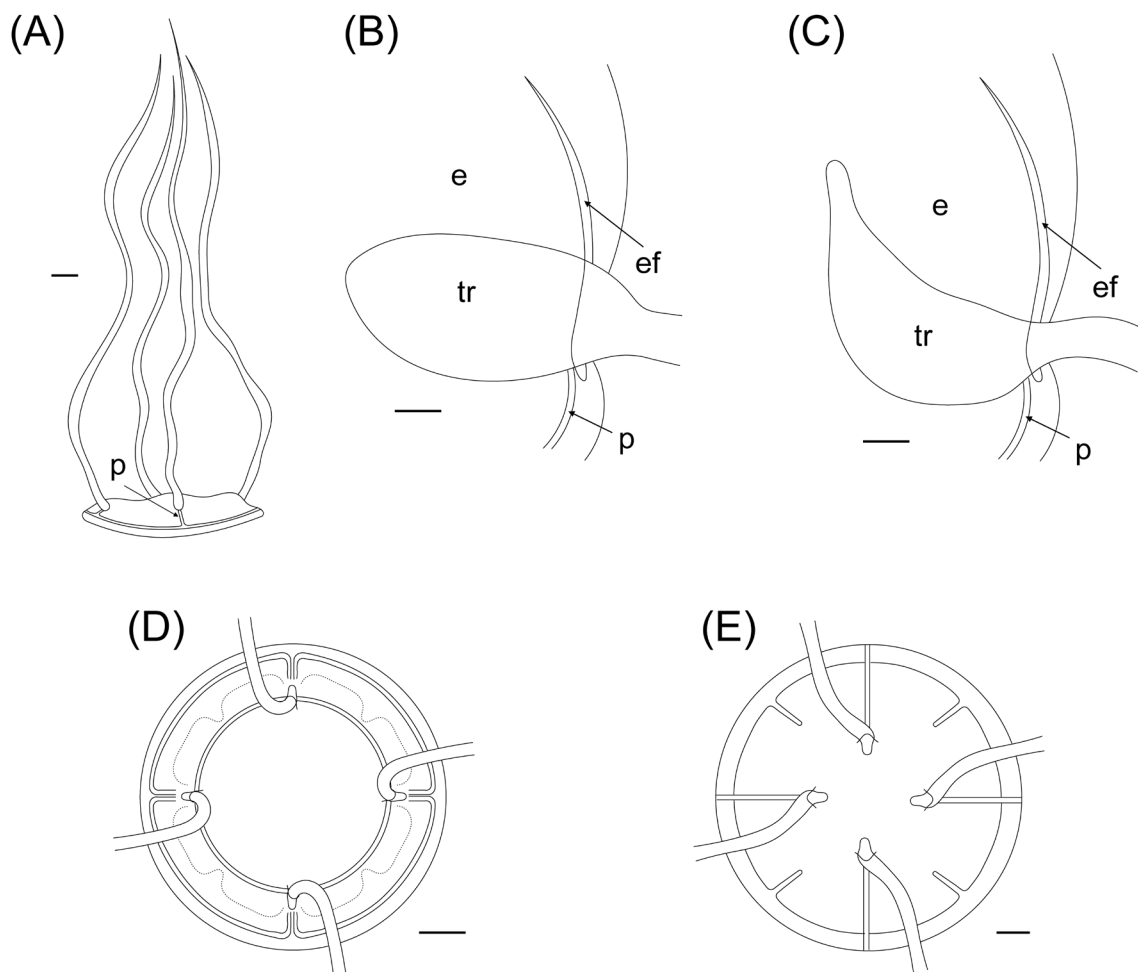


Fig. 3. Key characters of 4 species of Aeginidae sensu lato: (A) *Solmundaegina nematophora*. With small tentacle roots and with a nesselring and no peripheral canal system; (B) *Aegina citrea*. With enormous, stout roots on the tentacles and a deep exumbrellar furrow above each root; (C) *Aegina citrea*. With a long, sharply-pointed root like a hawk's claw and a deep exumbrellar furrow above the root; (D) Aboral view of *Pseudaequina pentanema*. With an obvious peripheral canal system; (E) Aboral view of *Aeginopsis laurentii*. With tentacles issuing at a very high level and with 4 perradial and 4 interradian peronia. e: exumbrella; ef: exumbrellar furrow; p: peronia; tr: tentacle root. Scale bars=1 mm.

deposited at the ZP-FRA as ZP-FRA 1510-5.

Description: Nectophores 3 to 5 mm high and 2.5 to 3.5 mm wide, mostly occupied by the nectosac, the upper radial canal straight, the lower radial canal with several curves, the lateral radial canals looped; Bracts 6 to 11 mm high and 2.5 to 4.5 mm wide, thick and gelatinous with a proximal keel for attachment, upper surface with several rows of prominent papillae.

Notes on Aeginidae sensu lato

We identified four species in the family formerly identified as Aeginidae, other than *Aeginura grimaldii* Maas, 1904 and *Solmundella bitentaculata* (Quoy & Gaimard, 1833), according to the new taxonomy (Lindsay et al. 2017).

1) *Solmundaegina nematophora* Lindsay, 2017

With thin jelly, 4 long tentacles (length up to more than

four times diameter of umbrella diameter), quite small endodermal roots of the marginal tentacles and with a nesselring and no peripheral canal system (Fig. 3A). Umbrella 3–11 mm in diameter. The size of a tentacle root was up to 1 mm in length and 0.8 mm in width in the largest specimen. Specimens of this species were collected from all the regions (total abundance: 36.2 inds. m⁻²), with abundances high in the Transition zone of cold waters (49%) and the Oyashio area (39%). Vertically, they occurred in all the layers and the abundance was high in the depth ranges of 300–500 m (35%), 500–750 m (24%), 150–300 m (16%) and 0–50 m (11%).

2) *Aegina citrea* Eschscholtz, 1829

With thick jelly, peripheral canal system, 4–7 tentacles (length 1–2 times diameter of umbrella), enormous, stout, sometimes long sharply-pointed endodermal roots of the marginal tentacles and deep exumbrellar furrows

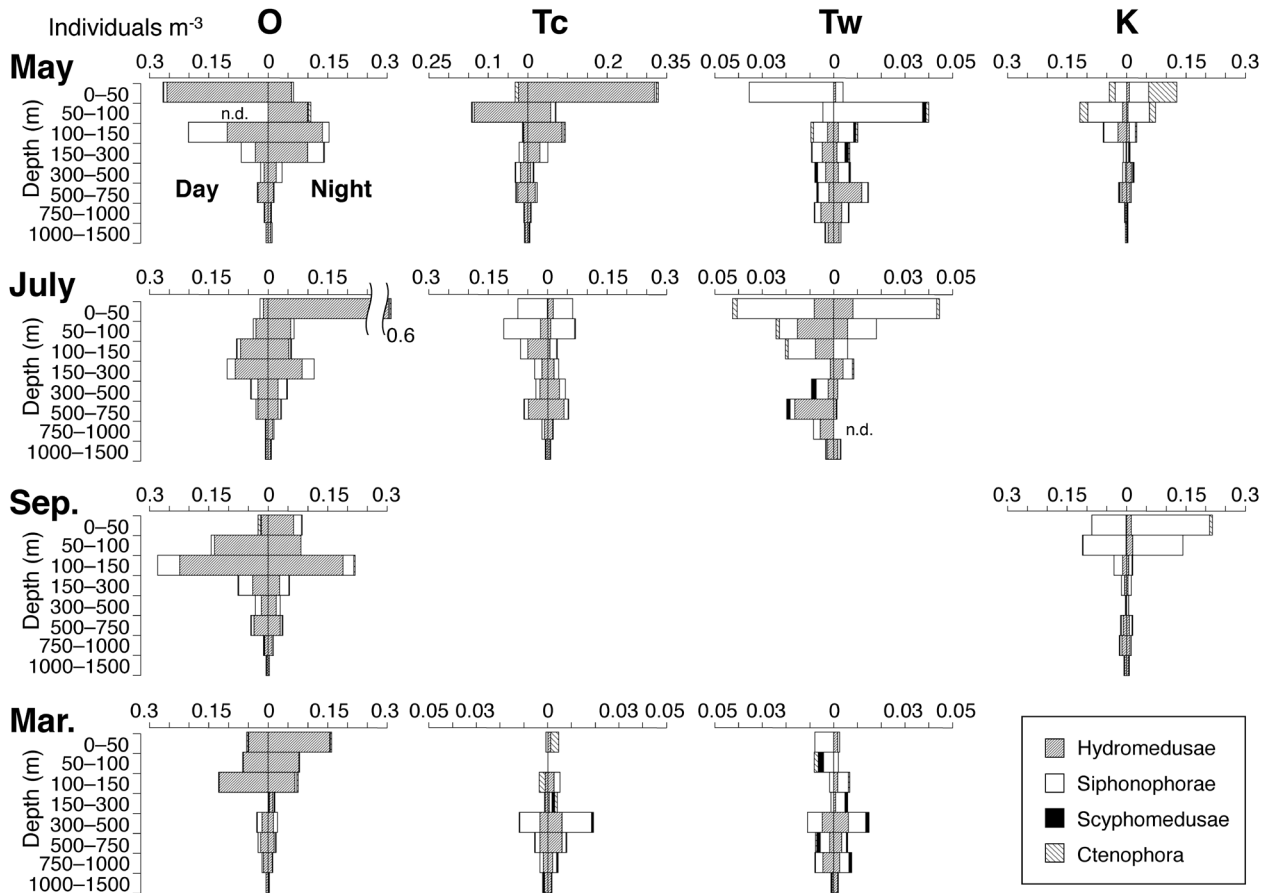


Fig. 4. The day (left) and night (right) depth distributions of jellyfish abundances in the Oyashio area (O), the Transition zone of cold waters (Tc), the Transition zone of warm waters (Tw) and the Kuroshio area (K), seasonally in terms of population density (Individuals m^{-3}). "n.d.": no data. Note that scale bars of Tw differ.

above the roots (Figs. 3B & C). Long sharply-pointed roots looked like hawk's claws projecting upwards in the jelly and reaching nearly to the summit of the umbrella. Umbrella 8–40 mm in diameter. Specimens of the species were collected from all the regions (total abundance: 0.8 inds. m^{-2}), with the abundance high in the Transition zone of warm waters (36%), the Kuroshio area (29%) and the Oyashio area (25%). Vertically, they occurred in the 100–150 m and 500–1500 m depth range, being most abundant in the 1000–1500 m depth range (72%).

3) *Pseudaegina pentanema* (Kishinouye, 1910)

Very similar to the sketch of *Aegina citrea* adopted by Kramp (1968), with relatively thin jelly, 4 short marginal tentacles (length 1.3 times diameter of umbrella), and an obvious peripheral canal system (Fig. 3D). The endodermal roots of the marginal tentacles were thin and long, but not projecting upwards into the jelly. Only one specimen was collected in the 50–100 m depth range at A21 in September. Umbrella 5.5 mm in diameter. The size of a tentacle root was 0.8 mm in length and 0.4 mm in width.

4) *Aeginopsis laurentii* Brandt, 1838

With relatively thin jelly, peripheral canal system ab-

sent, 4 tentacles (length 2 times diameter of umbrella) and 8 peronia (Fig. 3E). Only one specimen was collected in the 150–300 m depth range at A3 in July. Umbrella 9 mm in diameter. The tentacles issued at a very high level and the size of a tentacle root was 1.7 mm in length and 0.8 mm in width.

Abundance of jellyfishes

Abundance peaked in the 0–150 m depth range whereas the maximum number of taxa occurred below 300 m depth (Figs. 4 & 5). Abundance was highest in the Oyashio area with $5 \pm 1.9 \times 10$ inds. m^{-2} (average \pm SD) and was a little lower in the Transition zone of cold waters ($3 \pm 1.6 \times 10$). Abundance was lowest in the Transition zone of warm waters ($1 \pm 0.3 \times 10$) and increased in the Kuroshio area ($3 \pm 0.7 \times 10$). Abundance in the Oyashio area was relatively stable throughout the year, whereas in the Transition zones it decreased dramatically in March.

Vertical distribution

In the Oyashio area, the net samples were vertically divided at 300 m depth at the 70% dissimilarity level according to the Bray-Curtis Index (Fig. 6). Because we could not divide the net samples successfully in the Transition zones

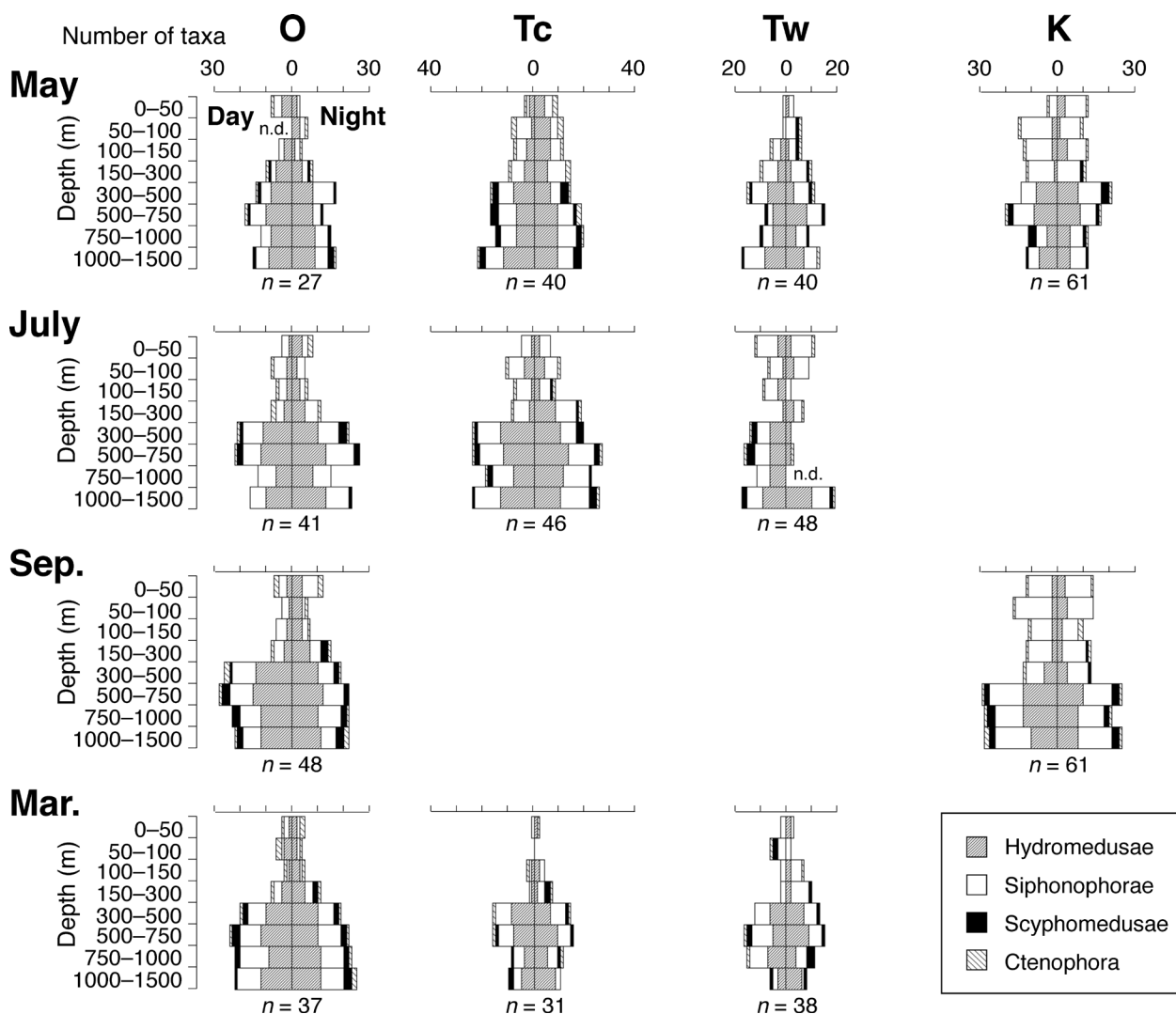


Fig. 5. The day (left) and night (right) depth distributions of jellyfish diversity in the Oyashio area (O), the Transition zone of cold waters (Tc), the Transition zone of warm waters (Tw) and the Kuroshio area (K), seasonally in terms of the number of taxa ("n" below each figure is the total number of taxa that occurred). "n.d.": no data.

and the Kuroshio area by the Bray-Curtis Index, we divided each water column based on the depth at which there was a salinity minimum within seawater density $\sigma_t=26.6-26.9$, which defines the North Pacific Intermediate Water (NPIW), formed by the merging of Oyashio and Kuroshio current waters (Talley 1993), into 2 layers as follows: The shallower layer, above the stratum that includes the depth of a salinity minimum within $\sigma_t=26.6-26.9$; the deeper layer, being the stratum including the depth of a salinity minimum within $\sigma_t=26.6-26.9$ and below that stratum. As the result of this re-division, the water columns in the regions, excluding the Oyashio area, were vertically divided at 300 m depth, except for A21 in September where the depth of the salinity minimum within $\sigma_t=26.6-26.9$ was around 600 m (Figs. 2A & B). We divided the water columns of A21 in September at 500 m depth. Thus, we divided the water columns into "the shallower layer" and "the deeper layer" for the vertical analyses.

Biodiversity of jellyfishes

The number of taxa increased from May to September and decreased in March at every station. Species composition differed remarkably between the shallower layer and the deeper layer (Table 3).

In the shallower layer, the Shannon index of diversity (H') in the Transition zone of cold waters was higher than in the Oyashio area, in the Transition zone of warm waters it was higher than in the Transition zone of cold waters, and in the Kuroshio area it was higher than in the Transition zone of warm waters (Fig. 7). H' increased as the depth increased. In the deeper layers of all stations, down to 1500 m depth, H' remained high throughout the year.

Community structure

Twenty-two species (>0.3% of the total number of individuals) were classified into the following 2 groups at

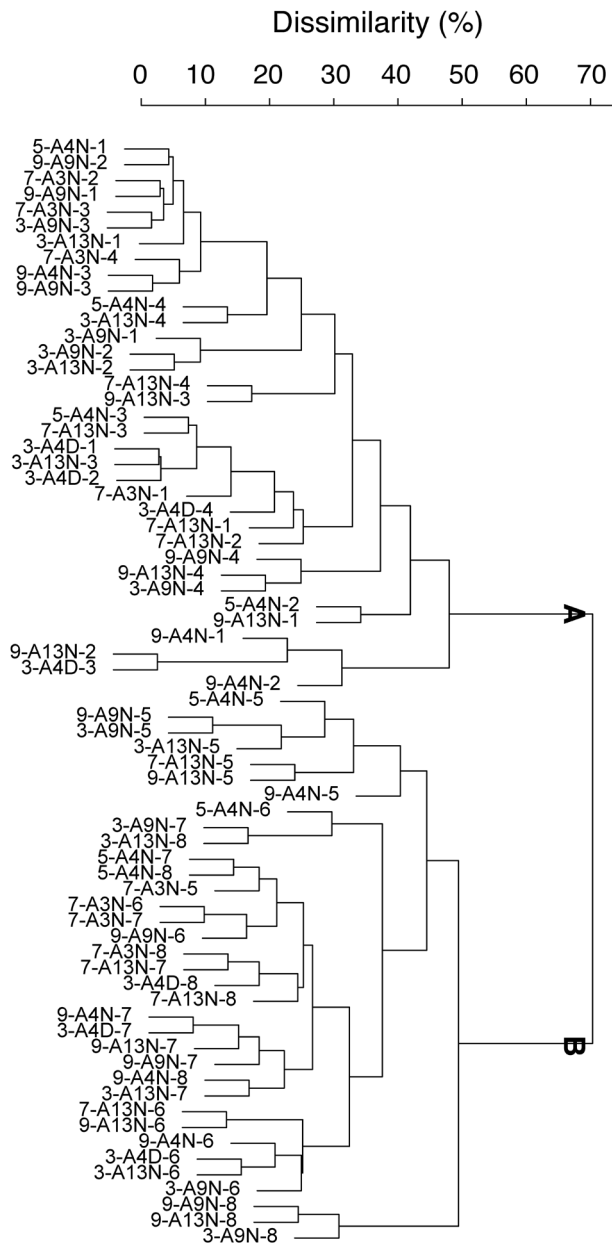


Fig. 6. Inter-sample cluster analysis dendrogram in the Oyashio area. The name of the sample is as Month-Station-Layer (Layer 1: 0–50, 2: 50–100, 3: 100–150, 4: 150–300, 5: 300–500, 6: 500–750, 7: 750–1000, 8: 1000–1500 m depth range). In the Oyashio area, the samples were divided at 300 m depth at the 70% dissimilarity level. A: 0–300 m depth range; B: 300–1500 m depth range.

the 95% dissimilarity level, according to the Bray-Curtis Index (Fig. 8):

A) warm-water species occurring only in the Kuroshio area and the Transition zone of warm waters: *Diphyes dispar* Chamisso & Eysenhardt, 1821 and *Chelophyes appendiculata* (Eschscholtz, 1829), and

B) species commonly occurring in all the regions.

Group B was further divided into the following 2 groups at the 90% dissimilarity level.

B-I) the warm water species *Muggiaea atlantica* Cun-

ningham, 1892 and *Lensia conoidea* (Keferstein & Ehlers, 1860),

B-II) all other species commonly occurring in all the regions (i.e. excluding the warm water species: *M. atlantica* and *L. conoidea*).

Group B-II was further divided into the following 2 groups at the 82% dissimilarity level:

B-II-a) midwater species,

B-II-b) abundant species in the shallower layer that clustered together - *Aglantha digitale* (O. F. Müller, 1776) and *Dimophyes arctica* (Chun, 1897).

Species composition in the shallower layer

Seasonally, abundance was high in May, July and September, and low in March at every station.

In the Oyashio area, abundance was high due to the occurrence of the extremely dominant medusa *Aglantha digitale* (70–90% of total no. individuals sampled), though only a small number of taxa were present. The calycophoran siphonophore *Dimophyes arctica* was secondarily dominant (11–21%) except in March when *Solmundaegina nematophora* (3%) became more abundant than *D. arctica* (2%). At night in July in the 0–50 m depth range at A3, *A. digitale* occurred at the maximum abundance recorded in this study: 1.2 inds. m⁻³ (99% of the total abundance of jellyfish individuals in the stratum). In September, the abundance of jellyfish was secondarily highest in this study in the 100–150 m depth range with the deeper appearance of *A. digitale*. In July and September, neritic warm-water species, such as *Muggiaea atlantica* and *Liriope tetraphylla* (Chamisso & Eysenhardt, 1821), occurred.

In the Transition zone of cold waters, *A. digitale* (77%) and *D. arctica* (9%) were dominant in May, similar to the trend in the Oyashio waters. However, in July, when a warm core ring stayed around A9, *M. atlantica* was most dominant (33%), followed by *A. digitale* (30%) and *D. arctica* (29%). In March, abundance decreased remarkably when warm-water species disappeared and the most dominant taxon became *Beroe* spp. (32%), followed by *A. digitale* (14%).

In the Transition zone of warm waters, abundance was the lowest among the four classified regions. *M. atlantica* was most dominant (50%) in May. In July *Abylopsis* spp. (17%), *A. digitale* (13%) and *Diphyes dispar* (13%) were dominant and warm-water calycophoran siphonophores such as *Chelophyes appendiculata*, *Sulculeolaria turgida* (Gegenbaur, 1854), *Sulculeolaria chuni* (Lens & van Riemsdijk, 1908) and *Enneagonum hyalinum* Quoy & Gaimard, 1827 appeared. In March (A21) the lowest abundance in this study was recorded when warm-water species disappeared, *A. digitale* was scarce, and *D. arctica* was not observed. *Lensia conoidea* (Keferstein & Ehlers, 1860) (16%) and *Lensia multicristata* (Moser, 1925) (10%) replaced them in abundance.

In the Kuroshio area, observed only in May and September in this study, various calycophoran siphonophores in-

Table 3. Relative abundance of jellyfish taxa (>5% of the total abundance) in the Oyashio area (O), the Transition zone of cold waters (Tc), the Transition zone of warm waters (Tw) and the Kuroshio area (K), in each season. The shallower layer (shallow) is 0–300 m depth except A21 in September: 0–500 m and the deeper layer (deep) is 300–1500 m depth except A21 in September: 500–1500 m.

	May (%)	July (%)	September (%)	March (%)
O shallow	<i>A. digitale</i> (69.5) <i>D. arctica</i> (20.8)	<i>A. digitale</i> (86.4) <i>D. arctica</i> (11.1)	<i>A. digitale</i> (72.4) <i>D. arctica</i> (21.0)	<i>A. digitale</i> (90.3)
O deep	<i>C. rufobrunnea</i> (24.3) <i>P. haeckeli</i> (20.6) Halicreatidae spp. (10.9) <i>Rosacea</i> spp. (10.1) <i>A. digitale</i> (6.8) <i>L. achilles</i> (5.2)	<i>P. haeckeli</i> (20.1) <i>C. rufobrunnea</i> (15.3) <i>A. digitale</i> (12.0) <i>D. arctica</i> (10.3) <i>E. japonica</i> (9.4) <i>Rosacea</i> spp. (7.8)	<i>P. haeckeli</i> (22.2) <i>A. digitale</i> (17.6) <i>C. rufobrunnea</i> (16.8) <i>Rosacea</i> spp. (7.9) <i>D. arctica</i> (6.3)	<i>C. rufobrunnea</i> (17.8) <i>P. haeckeli</i> (17.2) Rhopalonematidae spp. (9.8) <i>Rosacea</i> spp. (9.5) <i>A. digitale</i> (9.0)
Tc shallow	<i>A. digitale</i> (77.2) <i>D. arctica</i> (8.7) <i>S. nematophora</i> (5.3)	<i>M. atlantica</i> (33.4) <i>A. digitale</i> (29.9) <i>D. arctica</i> (28.9)	no data	<i>Beroe</i> spp. (31.5) <i>A. digitale</i> (14.4) <i>A. vanhoeffeni</i> (9.3) <i>Desmophyes</i> spp. (7.2) <i>Solmissus</i> spp. (6.2)
Tc deep	<i>P. haeckeli</i> (23.3) <i>C. rufobrunnea</i> (13.8) <i>Rosacea</i> spp. (12.0) <i>A. digitale</i> (9.5) <i>S. nematophora</i> (7.8)	<i>A. digitale</i> (17.3) <i>P. haeckeli</i> (14.5) <i>C. rufobrunnea</i> (14.2) <i>E. japonica</i> (9.9) <i>Rosacea</i> spp. (6.9) Rhopalonematidae spp. (6.1)	no data	<i>Rosacea</i> spp. (16.1) <i>L. multicrostata</i> (10.5) <i>P. haeckeli</i> (9.1) <i>C. rufobrunnea</i> (7.3) <i>H. minimum</i> (6.8) Rhopalonematidae spp. (5.1)
Tw shallow	<i>M. atlantica</i> (49.5) Rhopalonematidae spp. (10.4) <i>L. multicrostata</i> (5.1)	<i>Abylopsis</i> spp. (17.0) <i>A. digitale</i> (13.4) <i>Diphyes dispar</i> (13.3) <i>P. haeckeli</i> (7.2) <i>L. conoidea</i> (5.9) <i>D. arctica</i> (5.7)	no data	<i>L. conoidea</i> (16.1) <i>L. multicrostata</i> (10.5) <i>P. periphylla</i> (8.7) <i>Rosacea</i> spp. (7.6) Physonectae spp. (6.9) <i>V. pentacantha</i> (5.8) <i>V. glabra</i> (5.1) <i>Desmophyes</i> spp. (5.0)
Tw deep	<i>P. haeckeli</i> (21.5) Halicreatidae spp. (8.8) <i>V. serrata</i> (8.5) <i>C. rufobrunnea</i> (8.4) <i>Cl. moserae</i> (7.6) <i>H. minimum</i> (6.6) <i>Rosacea</i> spp. (5.2)	<i>A. digitale</i> (35.7) <i>P. haeckeli</i> (9.6) <i>Rosacea</i> spp. (7.1)	no data	<i>P. haeckeli</i> (11.5) <i>Rosacea</i> spp. (9.7) <i>L. multicrostata</i> (8.1) Rhopalonematidae spp. (7.6) <i>Cl. moserae</i> (7.3) <i>V. serrata</i> (5.0)
K shallow	<i>M. atlantica</i> (23.3) <i>Beroe</i> spp. (15.3) Tentaculata gen. et spp. (10.8) <i>Abylopsis</i> spp. (7.7) Rhopalonematidae spp. (7.4) <i>Che. appendiculata</i> (5.4)	no data	<i>Abylopsis</i> spp. (35.0) <i>Diphyes dispar</i> (29.9) <i>Che. appendiculata</i> (7.3) Rhopalonematidae spp. (6.7)	no data
K deep	<i>P. haeckeli</i> (18.2) <i>C. rufobrunnea</i> (13.1) Halicreatidae spp. (6.6) <i>L. conoidea</i> (5.8) <i>Solmissus</i> spp. (5.5) <i>L. multicrostata</i> (5.3) <i>H. minimum</i> (5.1)	no data	<i>A. digitale</i> (29.2) <i>L. multicrostata</i> (6.6) <i>C. rufobrunnea</i> (6.0) Halicreatidae spp. (5.7) Rhopalonematidae spp. (5.2)	no data

cluding tropical species such as *Bassia bassensis* (Quoy & Gaimard, 1833), *Sulculeolaria quadrivalvis* de Blainville, 1830, *Lensia fowleri* (Bigelow, 1911), *Chelophyes contorta* (Lens & van Riemsdijk, 1908), *Sulculeolaria monoica*

(Chun, 1888) etc., occurred in this layer. Both *A. digitale* and *D. arctica* were absent in the shallower layers of this area. The dominant taxa (>10%) in May: *M. atlantica* (23%), *Beroe* spp. (15%) and Tentaculata spp. (11%) were

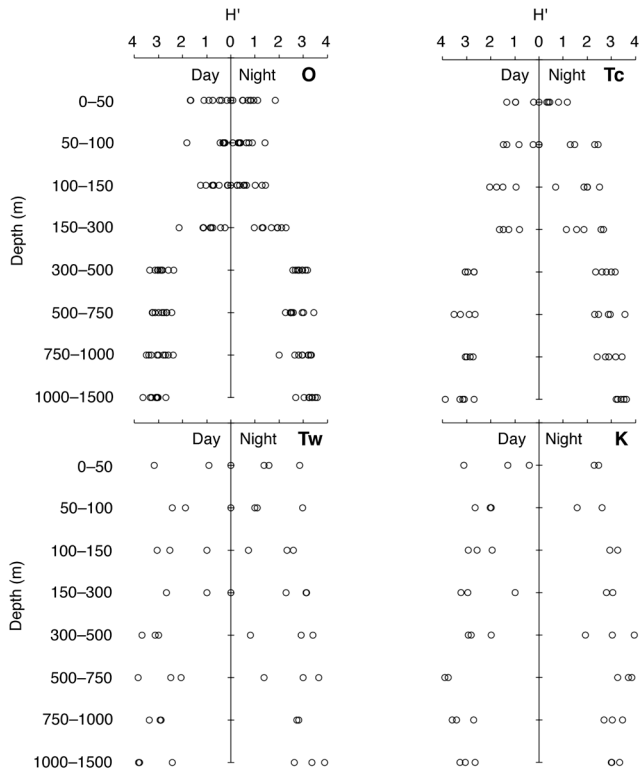


Fig. 7. Biodiversity (H') of jellyfish from each net sample in the Oyashio area (O), the Transition zone of cold waters (Tc), the Transition zone of warm waters (Tw) and the Kuroshio area (K), in the day (left) and night (right).

replaced with *Abylopsis* spp. (35%) and *D. dispar* (30%) in September. Specifically many tropical species were present at A21 in May, including *Zygocanna vagans* and *Melophysa melo*, both collected from the 100–150 m depth range.

Species composition in the deeper layer

At all stations throughout the year, abundance was lower in the deeper layer than the shallower layer, whereas the number of taxa was higher. Thirteen taxa (11 identified species) appeared commonly at all stations throughout the year. Not less than 27 taxa (24 identified species) appeared commonly in the deeper layer of the Oyashio area, the Transition zone of cold waters, the Transition zone of warm waters and the Kuroshio area throughout the year (Table 4). The dominant species (>10%) were *Pantachogon haeckeli* (Maas, 1893) (18%), *Crossota rufobrunnea* (Kramp, 1913) (15%) and *Aglantha digitale* (14%). The maximum number of taxa (26) was collected at A21 in the 1000–1500 m depth range, below Kuroshio-derived waters during daytime in September.

Individual species occurred over wide depth ranges but several species had a restricted distribution in the meso- and bathypelagic realm. *Clausophyes moserae* Margulis, 1988, *Chuniphyes multidentata* Lens & van Riemsdijk, 1908, *Atolla wyvillei* Haeckel, 1880 and *Lensia havock* Totton, 1941 appeared only below 300 m depth. *Colobonema*

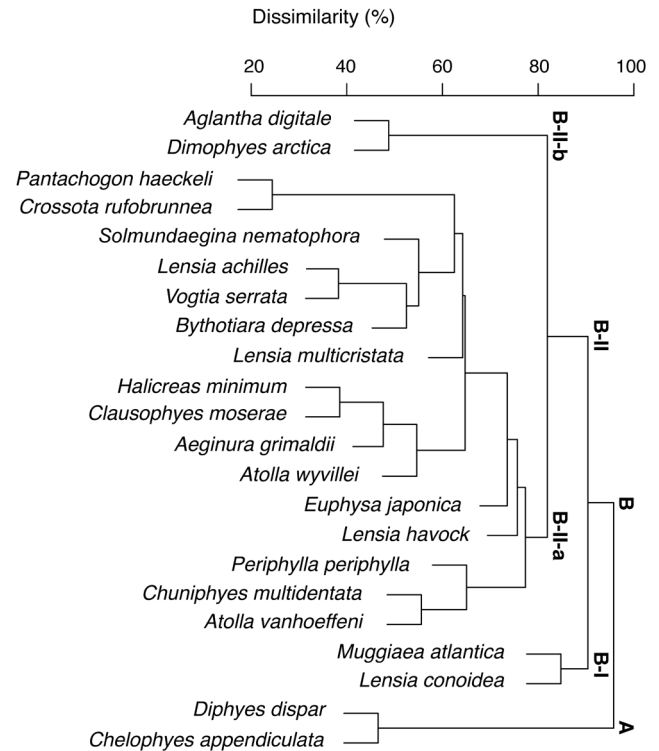


Fig. 8. Inter-species cluster analysis dendrogram of 22 species (>0.3% of the total number of individuals caught).

sericeum Vanhöffen, 1902 mainly occurred below 300 m depth. *C. rufobrunnea*, *Halicreas minimum* Fewkes, 1882, *Cl. moserae*, *Aeginura grimaldii* Maas, 1904, *A. wyvillei* and *L. havock* mainly occurred below 500 m depth.

Populations of *Euphysa japonica* (Maas, 1909) were frequently concentrated in narrow depth ranges. A high density (>0.006 inds. m⁻³) of *E. japonica* was observed in the 300–750 m depth range in the Oyashio area and the Transition zone of cold waters in July and the 300–500 m depth range in the Oyashio area in September.

The vertical distributions of *A. digitale*, *Dimophyes arctica*, *Solmundaegina nematophora* and *E. japonica* tended to become deeper in the order of the Oyashio area, the Transition zones, and the Kuroshio area, with the population density decreasing gradually from north to south (Fig. 9).

Weighted mean depth (WMD)

The WMDs of 22 species (>0.3% of the total number of individuals caught) were compared between day and night in the same month and the same station (Table 5). Means of WMDs at night were deeper than during the day in 6 species, and shallower in 16 species. Among the 16 species, the WMDs were significantly different between day and night in *Euphysa japonica* and *Atolla vanhoeffeni* Russell, 1957 (t-test, $P < 0.05$).

Biomass

Biomass of jellyfish was highest in the Oyashio area

Table 4. Twenty-seven taxa (24 identified species) that appeared commonly in the deeper layer of the Oyashio area, the Transition zone of cold waters, the Transition zone of warm waters and the Kuroshio area in this study, with their distributions worldwide.

	Sagami Bay ¹	Northeast Pacific ²	Atlantic ³	Indian Ocean ⁴	Southern Ocean ⁵	Arctic Ocean ⁶	Mediterranean Sea ⁷
<i>P. haeckeli</i> *	+	+	+	+	+	—	+
<i>C. rufobrunnea</i> *	+	+	+	—	—	—	—
<i>A. digitale</i> *	—	+	+	—	—	+	—
<i>Rosacea</i> spp.*							
<i>R. plicata</i>	+	+	+	+	+	—	+
<i>R. cymbiformis</i>	—	+	+	—	—	—	+
<i>D. arctica</i>	+	+	+	+	+	+	—
<i>E. japonica</i> [#]	—	+	—	—	—	—	—
<i>S. nematophora</i> *	—	—	—	—	—	—	—
<i>L. achilles</i> *	+	+	+	+	+	—	—
<i>V. serrata</i> *	+	+	+	+	+	—	+
<i>L. multicristata</i>	+	+	+	+	—	—	+
<i>H. minimum</i> *	+	+	+	+	+	—	—
<i>B. depressa</i> ^{##}	—	+	—	—	—	—	—
<i>Cl. moserae</i>	+	+	+	+	+	—	—
<i>A. grimaldii</i> *	+	+	+	+	—	—	—
<i>A. wyvillei</i> *	+	+	+	+	+	—	—
<i>P. periphylla</i> *	+	+	+	+	+	—	+
<i>Chu. multidentata</i>	+	+	+	+	+	—	—
<i>Beroe</i> spp.*	+	+	+	+	+	+	+
<i>L. havock</i>	+	+	+	+	+	—	+
<i>A. vanhoeffeni</i>	+	+	+	—	—	—	—
<i>P. rubra</i>	+	—	+	+	+	—	—
<i>C. sericeum</i>	+	+	+	+	+	—	—
<i>L. conoidea</i>	+	+	+	+	—	—	+
<i>M. atlantica</i>	+	+	+	+	—	—	+
<i>Kephyes</i> spp.	+	+	+	+	—	—	+
<i>Periphyllopsis braueri</i>	+	—	+	+	—	—	—
<i>Cl. galeata</i>	+	+	+	—	+	—	—

* Appearance from all stations throughout the year. [#] Endemic species in Pacific area (Kramp, 1968). ¹Lindsay & Hunt, 2005; Lindsay, 2006; Kitamura *et al.*, 2008; Kitamura, 2009; Grossmann & Lindsay, 2013. ²Alvariño 1967; Kramp, 1968; Haddock & Case, 1999; Raskoff, 2001; Osborn *et al.*, 2007; Mapstone, 2009. ³Pugh, 1990; Bouillon, 1999; Mianzan, 1999; Mianzan & Cornelius, 1999; Pugh, 1999. ⁴Kramp, 1968; Alvariño, 1971. ⁵O'Sullivan, 1982, 1986; Pagès *et al.*, 1996; Pugh *et al.*, 1997; Toda *et al.*, 2014. ⁶Kramp, 1968; Raskoff *et al.*, 2010. ⁷Alvariño, 1971; Pagès & Gili, 1992; Bouillon *et al.*, 2004.

with $69 \pm 5.5 \times 10 \text{ mgC m}^{-2}$ (average \pm SD) and low in the Transition zone of cold waters ($34 \pm 3.4 \times 10 \text{ mgC m}^{-2}$). In the Transition zone of warm waters, it was a little higher ($38 \pm 4.2 \times 10 \text{ mgC m}^{-2}$) in spite of the abundance being lowest. In the Kuroshio area, biomass was lowest at $31 \pm 1.4 \times 10 \text{ mgC m}^{-2}$. Biomass of jellyfish frequently tended to be high in the deeper layer (Fig. 10) due to the occurrence of large species, especially Scyphozoa: *Periphylla periphylla* (Péron & Lesueur, 1810), *Periphyllopsis braueri* Vanhöffen, 1902, *Atolla chuni* (Vanhöffen, 1902) and *Atolla wyvillei*, and Hydromedusae: *Solmissus* spp.. For example, an individual of *P. periphylla* (diameter of bell: 12.5 cm, 185 gWW), collected from the 500–750 m depth range of A17 during the day in May, caused the maximum observed wet-weight and the sudden high value of biomass (47 mgWW m^{-3}) in that range. And in March, fragments

of *P. braueri* were collected from the 750–1000 m depth range of A4 at night and in the 750–1500 m depth range of A17 during the day: 43 mgWW m^{-3} and 32 mgWW m^{-3} , respectively, and led to the high biomass value for jellyfish though the abundance was low.

Discussion

Cosmopolitan species in the midwater zone

There was a striking change in the abundance and species composition of the jellyfish population between the shallower layer (0–300 m depth except A21 in September: 0–500 m) and the deeper layer (300–1500 m depth except A21 in September: 500–1500 m) (Table 3). Not less than 24 species appeared commonly in the deeper layer of all

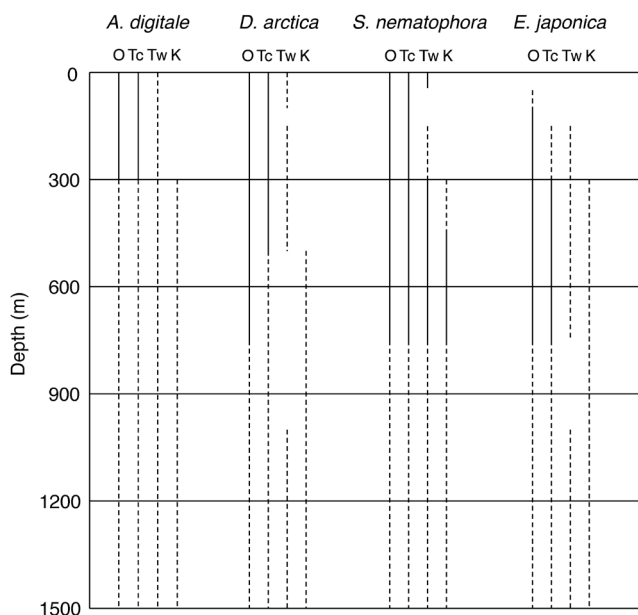


Fig. 9. Vertical distribution ranges of the 4 species that tended to move deeper from the Oyashio area through the Transition zone into the Kuroshio area, with population densities. Solid bold lines show the depth ranges where population densities were of the same order as where they were at their maximum or were only smaller by 1 order. Dashed lines show the depth ranges where population densities had decreased by >2 orders of magnitude.

the regions. Most of them are common with species reported from Sagami Bay, the northeast Pacific, the Atlantic and the Indian Ocean (Table 4). Many of them are also common in the Southern Ocean and the Mediterranean Sea. These facts suggest the possibility that these common species found in the midwater zone can occur at almost any latitude in the open ocean, since the temperature and the salinity do not vary largely at these depths (Kitamura 2009). It is also possible that, because of the scarceness of studies on the deep-water jellyfish fauna, we still do not recognize differences among similar species, as in the case of Aeginidae *sensu lato* (Lindsay et al. 2017).

Diversity in the Transition zones

In the shallower layers of the Transition zones, complicated mixing of Oyashio-derived cold water and Kuroshio-derived warm water led to the formation of a variety of water masses. Species diversity was higher than in the Oyashio area throughout the year, though member species changed seasonally. This was probably due to the effect of expatriate species because endemic species were not found in the Transition zone.

Trends in species distributions

The vertical distributions of 4 species (*Aglantha digitale*, *Dimophyes arctica*, *Solmundaegina nematophora* and *Euphysa japonica*) tended to get deeper moving from the Oyashio area through the Transition zones to the Kuroshio area (Fig. 9). It is known that the core of the intermediate

water in the Kuroshio region originates from the Oyashio area and the Oyashio waters sink gradually at about 42°N and flow southward underneath the warm Kuroshio waters (Talley et al. 1995). Omori (1967) and Shimizu et al. (2009) suggested that Oyashio water sinks and transports its inhabitants southward. Considering these reports, it is possible that these jellyfish species are entrained in the southward flow of the Oyashio undercurrent and are gradually transported to greater depths below the Kuroshio-derived water, as previously pointed out for *E. japonica* (Lindsay et al. 2008) and *D. arctica* (Grossmann & Lindsay 2013). The decreasing gradient in population densities from north to south suggests their reproduction in the Oyashio area (Lindsay et al. 2008, Grossmann & Lindsay 2013). More information on the dynamics of the water masses and the life cycles/histories of these species are needed to confirm this.

In July and September, frequent patches of high abundance were found for *Euphysa japonica* in the shallower midwater zone of the Oyashio area and the Transition zone of cold waters. In summer, the species has been observed in situ to have patchiness in their distributions in the neighboring areas (Toyokawa et al. 2003, Lindsay et al. 2008, Yamakita et al. 2015). It suggested that its reproduction may follow an annual cycle in this area.

Diel vertical migration of jellyfish

In *Euphysa japonica* and *Atolla vanhoeffeni*, the possibility of diel vertical migration (DVM) was suggested by the present data. *A. vanhoeffeni* has already been reported to possibly carry out DVM (Roe et al. 1984), but this is the first report in *E. japonica*. In *Periphylla periphylla*, it is possible that the number of specimens was not enough to detect the difference between day and night (i.e. DVM). There are previous studies that report DVM in *P. periphylla* to be triggered by light intensity (Dupont et al. 2009, Dupont & Aksnes 2010).

Actual biomass

Ichikawa (2008) and Ichikawa et al. (2006) recorded the biomass of jellyfish in the 25–500 m depth range at A4 and A13 in the Oyashio area in June and July in 2004 by a combination of VPR observations calibrated with net-sampling by MOCNESS and a Remodeled NORPAC net (LNP) (both 0.35 mm mesh). Ichikawa (2008) estimated greater carbon biomass than found in this study (A3 and A13 in the Oyashio area in July in 2005, 0–500 m depth range) by 15–46 times in Hydromedusae, 5–15 times in Siphonophora, by 189–2621 times in Ctenophora and for total jellyfish by 20–77 times. The main reason for this difference might be attributable to loss of samples during sampling and preservation. First, there were many small jellyfishes that could not be collected by the 1/8 inch (3.175 mm) mesh used in this study. Secondly, most ctenophores, except *Beroe* spp. and several species of Tentaculata are impossible to fix in formalin-seawater (Purcell

Table 5. Range of WMD at day/night of 22 species with means and 95% confidence intervals (c.i.) of the difference between day and night, number of day/night pairs compared, and *P*-value of t-test if the difference was significantly different from zero.

Species	WMD (m)		Difference mean (95% c.i.) (m)	<i>N.</i> of pairs	<i>P</i>	Previous report of DVM
	Day	Night				
<i>E. japonica</i>	432–877	318–626	186 (61–312)	8	0.00976	
<i>A. vanhoeffeni</i>	399–766	225–626	141 (24–257)	8	0.0245	Roe <i>et al.</i> , 1984
<i>A. wyvillei</i>	625–1248	572–1252	131 (–19–281)	16	0.0823	Roe <i>et al.</i> , 1984
<i>P. periphylla</i>	317–962	94–874	120 (–5–244)	16	0.0587	Dupont <i>et al.</i> , 2009
<i>S. nematophora</i>	278–1016	85–1252	102 (–43–247)	20	0.156	
<i>Che. appendiculata</i>	83–383	24–258	88 (–530–706)	3	0.604	Mackie <i>et al.</i> , 1987
<i>Cl. moserae</i>	804–1252	651–1257	64 (–42–169)	17	0.219	
<i>L. conoidea</i>	120–625	142–626	30 (–58–119)	7	0.432	Pugh, 1984; Mackie <i>et al.</i> , 1987; Lučić <i>et al.</i> , 2011
<i>H. minimum</i>	702–1250	577–1257	29 (–91–148)	19	0.620	
<i>D. arctica</i>	174–1255	207–1005	25 (–46–96)	16	0.466	Kitamura, 2009
<i>A. digitale</i>	95–1049	24–1036	24 (–52–100)	19	0.517	Kitamura, 2009
<i>A. grimaldii</i>	620–1250	398–1246	23 (–48–94)	18	0.510	
<i>C. rufobrunnea</i>	675–1250	606–1246	17 (–71–106)	20	0.691	
<i>V. serrata</i>	448–1040	430–1111	12 (–86–110)	19	0.794	
<i>P. haeckeli</i>	551–1255	586–1252	9 (–38–57)	20	0.685	Kitamura, 2009
<i>L. achilles</i>	494–1250	400–1251	5 (–123–133)	19	0.930	
<i>M. atlantica</i>	24–309	35–350	–4 (–148–141)	7	0.951	
<i>L. multicristata</i>	376–876	397–873	–14 (–120–91)	14	0.774	
<i>Chu. multidentata</i>	397–1256	399–1033	–45 (–150–60)	11	0.360	
<i>B. depressa</i>	397–750	400–859	–72 (–161–17)	16	0.104	
<i>L. havock</i>	533–1255	872–1246	–99 (–233–34)	9	0.125	
<i>D. dispar</i>	24–400	45–616	–165 (–630–300)	4	0.342	

1988), and they therefore don't usually occur in net samples. Ichikawa (2008) and Ichikawa *et al.* (2006) did not identify taxa lower than Hydromedusae, Siphonophora and Ctenophora (no Scyphozoa), but their data suggest that the actual biomass of jellyfish at the stations investigated in this study is most probably at least 1 order greater than the presently estimated biomass in the present study.

Comparison of biomass and biodiversity between jellyfish and other organisms

The biomass of other organisms collected by the same net hauls was compared with that of jellyfish (Fig. 11). When all the hauls were combined, the wet-weight of jellyfish was higher than both squids ($\times 2.3$) and shrimps ($\times 2.1$), while it was 0.9 times that of krill and 0.5 times that of fish. Jellyfish sometimes exceeded fish in terms of biomass in the deeper layer and near the surface. In spite of the high wet-weight value, the high water content of jellyfish (91 to 96.5%) (Larson 1986, Clarke *et al.* 1992) makes their estimated biomass in terms of carbon as low as 1/4 times, 1/6 times, 1/10 times and 1/23 times those of squids, shrimps, krill and fish respectively. However, the jellyfish biomass calibrated with the estimated biomass according to Ichikawa (2008) exceeds that of other organisms, even in terms of carbon biomass.

In terms of biodiversity, *H'* of jellyfish was higher than

fish ($\times 1.9$) and shrimps ($\times 2.0$). The diversity of fish and shrimps was high in the mesopelagic zone, but decreased in the 1000–1500 m depth layer, while that of jellyfish remained high.

The life cycle of midwater jellyfishes

Both in the shallower and deeper layers, the dominant species were holoplanktonic, i.e. they undergo direct development from a pelagic planula or larval stage to a pelagic adult (Jarms *et al.* 1999, Bouillon *et al.* 2006). Nevertheless, species that include a polyp stage in their life cycles were present even in the deeper layers (e.g. Anthomedusae and Leptomedusae), although the midwater zone lacks substrates for sessile forms. It has been reported that polyps of *Pandea* sp. were found attached to a euthecosome pteropod, while *Pandea rubra* Bigelow, 1913 itself is a host to pycnogonids, hyperiid amphipods, and larval narcomedusae (Pagès *et al.* 2007, Lindsay *et al.* 2008). However, the details of life cycles are still unknown for most midwater jellyfish.

The present study is one of extremely few that describe the abundances and vertical distributions of a midwater jellyfish community over a seasonal cycle. Unfortunately, perhaps because of the extensive water mass mixing in this area, it was not possible to elucidate the life history strategies of the gelatinous fauna, with the possible exception of

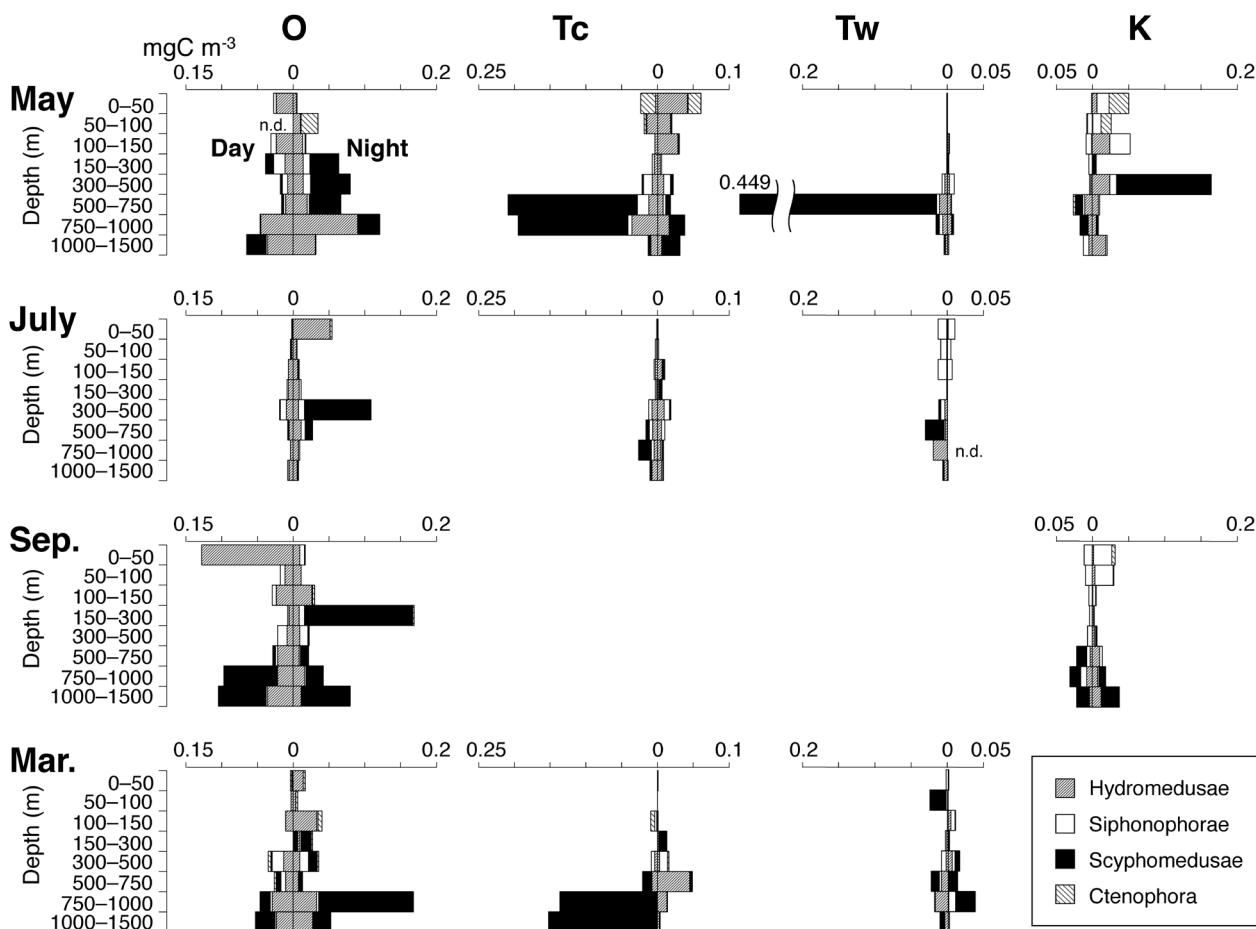


Fig. 10. The day (left) and night (right) depth distributions of jellyfish biomass in the Oyashio area (O), the Transition zone of cold waters (Tc), the Transition zone of warm waters (Tw) and the Kuroshio area (K), seasonally in terms of carbon (mgC m^{-3}). "n.d.": no data.

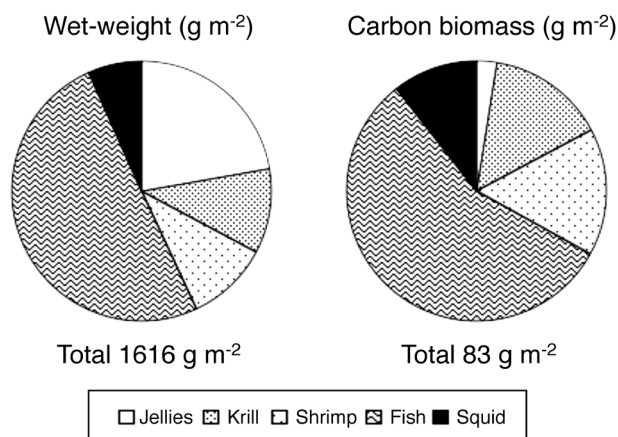


Fig. 11. Relative biomass (left: wet-weight; right: carbon biomass) of jellyfish, krill, shrimp, fish and squid collected by the same hauls.

Euphysa japonica. More studies of this type are needed.

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References

- Alvariño A (1967) Bathymetric distribution of Chaetognatha, Siphonophorae, Medusae, Ctenophorae off San Diego, California. *Pac Sci* 21: 474–485.
- Alvariño A (1971) Siphonophores of the Pacific with a review of the world distribution. *Bull Scripps Inst Oceanogr Univ Calif* 16: 1–432.
- Arai MN, Brinckmann-Voss A (1980) Hydromedusae of British Columbia and Puget Sound. *Can Bull Fish Aquat Sci* 204: 1–192.
- Bailey TG, Youngbluth MJ, Owen GP (1995) Chemical composition and metabolic rates of gelatinous zooplankton from mid-water and benthic boundary layer environments off Cape Hatteras, North Carolina, USA. *Mar Ecol Prog Ser* 122: 121–134.
- Bouillon J (1999) Hydromedusae. In: *South Atlantic Zooplankton* (ed Boltovskoy D). Backhuys Publishers, Leiden, pp. 385–465.
- Bouillon J, Medel MD, Pagès F, Gili JM, Boero F, Gravili C (2004) Fauna of Mediterranean Hydrozoa. *Sci Mar* 68 (Suppl.2): 5–438.
- Bouillon J, Gravili C, Pagès F, Gili JM, Boero F (2006) An introduction to Hydrozoa. *Mémoires du Muséum National d'Histoire Naturelle*, Tome 194. Publications Scientifiques du Muséum, Paris, 591 pp.
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of Southern Wisconsin. *Ecol Monogr* 27(4): 325–349.
- Clarke A, Holmes LJ, Gore DJ (1992) Proximate and elemental composition of gelatinous zooplankton from the Southern Ocean. *J Exp Mar Biol Ecol* 155: 55–68.
- Collins AG, Bentlage B, Lindner A, Lindsay D, Haddock SHD, Jarms G, Norenburg JL, Jankowski T, Cartwright P (2008) Phylogenetics of Trachylina (Cnidaria: Hydrozoa) with new insights on the evolution of some problematical taxa. *J Mar Biol Assoc UK* 88(8): 1673–1685.
- Dupont N, Klevjer TA, Kaartvedt S, Aksnes DL (2009) Diel vertical migration of the deep-water jellyfish *Periphylla periphylla* simulated as individual responses to absolute light intensity. *Limnol Oceanogr* 54(5): 1765–1775.
- Dupont N, Aksnes DL (2010) Simulation of optically conditioned retention and mass occurrences of *Periphylla periphylla*. *J Plankton Res* 32(6): 773–783.
- González HE, Giesecke R, Vargas CA, Pavez M, Iriarte J, Santibañez P, Castro L, Escribano R, Pagès F (2004) Carbon cycling through the pelagic foodweb in the northern Humboldt Current off Chile (23°S). *ICES J Mar Sci* 61(4): 572–584.
- Grossmann MM, Lindsay DJ (2013) Diversity and distribution of the Siphonophora (Cnidaria) in Sagami Bay, Japan, and their association with tropical and subarctic water masses. *J Oceanogr* 69: 395–411.
- Grossmann MM, Lindsay DJ (2017) A new species of clausophiid calycophoran siphonophore (Cnidaria: Hydrozoa), *Kephyes hiulcus* sp. nov., widely distributed throughout the world's oceans. *Zootaxa* 4250(1): 43–54.
- Haddock SHD, Case JF (1999) Bioluminescence spectra of shallow and deep-sea gelatinous zooplankton: ctenophores, medusae and siphonophores. *Mar Biol* 133: 571–582.
- Ichikawa T (2008) Analysis of the community structure of mesozooplankton in the Oyashio and Transition Zone using Video Plankton Recorder (VPR II). *Bull Fish Res Agen* 24: 23–104. (in Japanese with English abstract)
- Ichikawa T, Segawa K, Terazaki M (2006) Estimation of Cnidaria and Ctenophora biomass and vertical distribution using the Video Plankton Recorder II (VPR II) in the meso- and epipelagic layers of the Oyashio and Transition zone off eastern Japan. *Bull Jpn Soc Fish Oceanogr* 70: 240–248. (in Japanese with English abstract)
- Jarms G, Båmstedt U, Tiemann H, Martinussen MB, Fosså JH (1999) The holopelagic cycle of the deep-sea medusa *Periphylla periphylla* (Scyphozoa, Coronatae). *Sarsia* 84: 55–65.
- Kirkpatrick PA, Pugh PR (1984) Siphonophores and Velellids. *Synopsis of the British Fauna (New Series)* 29. Linnean Society of London, London, 154 pp.
- Kitamura M (2009) Hokusei-bu Taiheiyō 3 kaiiki ni okeru kurage-rui no enchoku-bunpu [Vertical distribution of planktonic Cnidaria in three sites of northwestern Pacific]. *Kaiyo Monthly* 41(7): 382–392. (in Japanese)
- Kitamura M, Miyake H, Lindsay D (2008) Chapter 24. Cnidaria. In: *Deep-sea Life-Biological observations using research submersibles*. (eds Fujikura K, Okutani T, Maruyama T). Tokai University Press, Kanagawa, pp. 295–320. (in Japanese)
- Kramp PL (1968) The Hydromedusae of the Pacific and Indian Oceans, Sections II and III. *Dana-Report No. 72*. Carlsberg Foundation, Copenhagen, 200 pp.
- Larson RJ (1986) Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific. *J Exp Mar Biol Ecol* 99: 107–120.
- Larson RJ, Mills CE, Harbison GR (1991) Western Atlantic hydrozoan and scyphozoan medusae: in situ studies using manned submersibles. *Hydrobiologia* 216/217: 311–317.
- Lindsay DJ (2006) A checklist of midwater cnidarians and ctenophores from Sagami Bay-species sampled during submersible surveys from 1993–2004. *Bull Plankton Soc Jpn* 53(2): 104–110. (in Japanese with English abstract)
- Lindsay DJ, Hunt JC (2005) Biodiversity in midwater cnidarians and ctenophores: submersible-based results from deep-water bays in the Japan Sea and north-western Pacific. *J Mar Biol Assoc UK* 85: 503–517.
- Lindsay D, Miyake H (2009) A checklist of midwater cnidarians and ctenophores from Japanese waters: species sampled during submersible surveys from 1993–2008 with notes on their taxonomy. *Kaiyo Monthly* 41(8): 417–437. (in Japanese)
- Lindsay DJ, Furushima Y, Miyake H, Kitamura M, Hunt JC (2004) The scyphomedusan fauna of the Japan Trench: preliminary results from a remotely-operated vehicle. *Hydrobiologia* 530/531: 537–547.
- Lindsay D, Pagès F, Corbera J, Miyake H, Hunt JC, Ichikawa T, Segawa K, Yoshida H (2008) The anthomedusan fauna of the Japan Trench: preliminary results from *in situ* surveys with

- manned and unmanned vehicles. *J Mar Biol Assoc UK* 88(8): 1519–1539.
- Lindsay DJ, Grossmann MM, Bentlage B, Collins AG, Minemizu R, Hopcroft RR, Miyake H, Hidaka-Umetsu M, Nishikawa J (2017) The perils of online biogeographic databases: a case study with the 'monospecific' genus *Aegina* (Cnidaria, Hydrozoa, Narcomedusae). *Mar Biol Res*: 13(5): 494–512, DOI: 10.1080/17451000.2016.1268261.
- Lučić D, Benović A, Batistić M, Morović M, Onofri I, Molinero J-C, Kogovšek T, Gangai B, Miloslavić M (2011) A short-term investigation of diel vertical migrations of the calyphoran Siphonophora in the open south Adriatic Sea (July 2003). *Acta Adriatica* 52(2): 159–172.
- Mackie GO (1985) Midwater macroplankton of British Columbia studied by submersible PISCES IV. *J Plankton Res* 7: 753–777.
- Mackie GO, Pugh PR, Purcell JE (1987) Siphonophore biology. *Adv Mar Biol* 24: 97–262.
- Mapstone GM (2009) Siphonophora (Cnidaria, Hydrozoa) of Canadian Pacific Waters. National Research Council Research Press, Ottawa, 302 pp.
- Mianzan HW (1999) Ctenophora. In: South Atlantic Zooplankton (ed Boltovskoy D). Backhuys Publishers, Leiden, pp. 561–573.
- Mianzan HW, Cornelius PFS (1999) Cubomedusae and Scyphomedusae. In: South Atlantic Zooplankton (ed Boltovskoy D). Backhuys Publishers, Leiden, pp. 513–559.
- Mills CE, Haddock SHD (2007) Ctenophora. In: The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon (ed Carlton JT). University of California Press, Berkeley and Los Angeles, pp. 189–199.
- Miyake H, Lindsay D, Kubota S (2004) Midwater and benthopelagic animals on the south slope of Shiribeshi Seamount off the west coast of Hokkaido. *JAMSTEC J Deep Sea Res* 24: 37–42.
- Naumov DV (1960) Hydroids and Hydromedusae of the U.S.S.R. Translated from Russian (1969). Israel Program for Scientific Translations, Jerusalem, 660 pp.
- Odate K (1994) Zooplankton biomass and its long-term variation in the Western North Pacific Ocean, Tohoku sea area, Japan. *Bull Tohoku Nat Fish Res Inst* 56: 115–173. (in Japanese with English abstract)
- Omori M (1967) *Calanus cristatus* and submergence of the Oyashio water. *Deep Sea Res* 14: 525–532.
- Osborn DA, Silver MW, Castro CG, Bros SM, Chavez FP (2007) The habitat of mesopelagic scyphomedusae in Monterey Bay, California. *Deep-Sea Res I* 54: 1241–1255.
- O'Sullivan D (1982) A guide to the hydromedusae of the Southern Ocean and adjacent waters. Department of Science and Technology, Antarctic Division [ANARE Research Notes, no. 5], Kingston, 136 pp.
- O'Sullivan D. (1986) A guide to the ctenophores of the Southern Ocean and adjacent waters. Department of Science and Technology, Antarctic Division [ANARE Research Notes, no. 36], Kingston, 43 pp.
- Page F, Gili JM (1992) Planktonic Cnidarians of the Benguela Current. *Scientia Marina* 56 (Suppl.1): 1–112.
- Page F, White MG, Rodhouse PG (1996) Abundance of gelatinous carnivores in the nekton community of the Antarctic Polar Frontal Zone in summer 1994. *Mar Ecol Prog Ser* 141: 139–147.
- Page F, Corbera J, Lindsay DJ (2007) Piggybacking pycnogonoids and parasitic narcomedusae on *Pandea rubra* (Anthomedusae, Pandeidae). *Plankton Benthos Res* 2: 83–90.
- Pearre S Jr (1973) Vertical migration and feeding in *Sagitta elegans* Verrill. *Ecology* 54: 300–314.
- Pugh PR (1984) The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 7. Siphonophores. *Prog Oceanogr* 13: 461–489.
- Pugh PR (1990) Biological collections made during Discovery CR 175 to BIOTRANS CR 175 (47°N, 20°W). Report 277. Institute of Oceanographic Sciences Deacon Laboratory, Wormley, 78 pp.
- Pugh P.R. (1999) Siphonophorae. In: South Atlantic Zooplankton (ed Boltovskoy D). Backhuys Publishers, Leiden, pp. 467–551.
- Pugh PR (2006) Reclassification of the clausophyid siphonophore *Clausophyes ovata* into the genus *Kephyes* gen. nov. *J Mar Biol Assoc UK* 86: 997–1004.
- Pugh PR, Page F, Boorman B (1997) Vertical distribution and abundance of pelagic cnidarians in the Eastern Weddell Sea, Antarctica. *J Mar Biol Assoc UK* 77: 341–360.
- Purcell JE (1988) Quantification of *Mnemiopsis leidyi* (Ctenophora, Lobata) from formalin-preserved plankton samples. *Mar Ecol Prog Ser* 45: 197–200.
- R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Raskoff KA (2001) The ecology of the mesopelagic hydromedusae in Monterey Bay, California. PhD thesis. University of California, Los Angeles, USA.
- Raskoff KA, Hopcroft RR, Kosobokova KN, Purcell JE, Youngbluth M (2010) Jellies under ice: ROV observations from the Arctic 2005 hidden ocean expedition. *Deep-Sea Res Pt II* 57: 111–126.
- Roe HSJ, James PT, Thurston MH (1984) The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 6. Medusae, Ctenophores, Amphipods and Euphausiids. *Prog Oceanogr* 13: 425–460.
- Saito H, Tsuda A, Kasai H (2002) Nutrient and plankton dynamics in the Oyashio region of the western subarctic Pacific Ocean. *Deep-Sea Res Pt II* 49: 5463–5486.
- Shannon CE (1948) A mathematical theory of communication. *Bell System Technical Journal* 27: 379–423, 623–656.
- Shimizu Y, Takahashi K, Kakehi S, Tatabe H, Yasuda I, Kusaka A, Nakayama T (2009) Transport of subarctic large copepods from the Oyashio area to the mixed water region by the coastal Oyashio intrusion. *Fish Oceanogr* 18(5): 312–327.
- Sneath PHA, Sokal PR (1973) Numerical Taxonomy. The principles and practice of numerical classification. Freeman, San Francisco, 573 pp.
- Sweetman AK, Chapman A (2011) First observations of jellyfalls at the seafloor in a deep-sea fjord. *Deep-Sea Res Pt I* 58: 1206–1211.
- Talley LD (1993) Distribution and formation of North Pacific Intermediate Water. *J Phys Oceanogr* 23: 517–537.
- Talley LD, Nagata Y, Fujimura M, Iwao T, Kono T, Inagake D, Hirai M, Okuda K (1995) North Pacific intermediate water in

- the Kuroshio/Oyashio mixed water region. *J Phys Oceanogr* 25: 475–501.
- TNFRI, FRA <http://tnfri.fra.affrc.go.jp/kaiyo/kaiyoubu/predict/pdf/200508fig.pdf>
- Toda R, Lindsay D, Fuentes VL, Moteki M (2014) Community structure of pelagic cnidarians off Adélie Land, East Antarctica, during austral summer 2008. *Polar Biol* 37: 269–289.
- Totton AK (1965a) A synopsis of the Siphonophora. British Museum (Natural History), London, 232 pp.
- Totton AK (1965b) A new species of *Lensia* (Siphonophora: Diiphyidae) from the coastal waters of Vancouver, B.C.; and its comparison with *Lensia achilles* Totton and another new species *Lensia cordata*. *Ann Mag Nat Hist* 13(8(85–86)): 71–76.
- Toyokawa M, Toda T, Kikuchi T, Nishida S (1998) Cnidarians and ctenophores observed from the manned submersible Shinkai 2000 in the midwater of Sagami Bay, Pacific coast of Japan. *Plankton Biol Ecol* 45: 61–74.
- Toyokawa M, Toda T, Kikuchi T, Miyake H, Hashimoto J (2003) Direct observations of a dense occurrence of *Bolinopsis infundibulum* (Ctenophora) near the seafloor under the Oyashio and notes on their feeding behavior. *Deep-Sea Res Pt I* 50: 809–813.
- Webb TJ, van den Berghe E., O'Dor R (2010) Biodiversity's big wet secret: the global distribution of marine biological records reveals chronic under-exploration of the deep pelagic ocean. *PLoS ONE* DOI:10.1371/journal.pone.0010223.
- Widder EA, Bernstein SA, Bracher DF, Case JF, Reisenbichler KR, Torres JJ, Robison BH (1989) Bioluminescence in the Monterey Submarine Canyon: image analysis of video recordings from a midwater submersible. *Mar Biol* 100: 541–551.
- Wiebe PH, Morton AW, Bradley AM, Bachus RH, Craddock JE, Barber V, Cowles TJ, Flierl GR (1985) New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Mar Biol* 87: 313–323.
- Yamakita T, Yamamoto H, Yokoyama Y, Sakamoto I, Tsuchida S, Lindsay D, Fujiwara Y, Kawato M, Kasaya T, Kitazato H (2015) Distribution of the marine debris on seafloor from the primary report of five cruises after the Great East Japan Earthquake 2011. In: *Proceedings of the 15th French-Japanese Oceanography Symposium. Marine Productivity: Perturbations and Resilience of Socio-ecosystems* (eds Ceccaldi HJ, Henocque Y, Koike Y, Komatsu T, Stora G, Tusseau-Vuillemin M-H). pp. 101–109.
- Yasuda I (2003) Hydrographic structure and variability of the Kuroshio-Oyashio Transition Area. *J Oceanogr* 59: 389–402.
- Yokouchi K, Tomosada A, Matsuo Y (1997) Photosynthesis-light response curves in Kuroshio, Oyashio and the transition area off Tohoku. *Bull Tohoku Nat Fish Res Inst* 59: 127–138.