

Occurrence of the Scyphomedusa *Parumbrosa polylobata* Kishinouye, 1910 in Suruga Bay, Japan

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Abstract: Aggregations of the scyphomedusa *Parumbrosa polylobata* were observed in the deep sea of Suruga Bay, Japan, using a crewed submersible and ROVs. This is the first record of *P. polylobata* off the Pacific coast of Japan. *Parumbrosa polylobata* was distributed in the benthopelagic layer (within 50 m of the seafloor) at 270–510 m bottom depth and was an active swimmer that was observed to feed on gelatinous zooplankton. Medium microbasic euryteles, one of four nematocyst types observed in the medusae, may play an important role in capturing gelatinous prey. Moribund individuals sank to the seafloor and became food for the benthos. *Parumbrosa polylobata*, which occurred in dense aggregations in the benthopelagic layer, seems to play an important role in matter transport from the pelagic to benthic communities.

Key words: scyphomedusa, *Parumbrosa polylobata*, Suruga Bay, nematocyst, benthopelagic layer

Introduction

The most well-known members of the ocean's gelatinous fauna are arguably the scyphomedusae. Mass occurrences of members of this group, including the moon jellyfish *Aurelia aurita* and the giant jellyfish *Nemopilema nomurai* (Omori & Kitamura 2004), can seriously interfere with man's economic activities, such as trawl fisheries, fixed-net fisheries, and electric power plants (Shimomura 1959; Matsueda 1969; Yasuda 1982, 1988). Over the last few decades, although many ecological studies concerning jellyfish blooms have been carried out, the species targeted in these studies are all shallow water species (Purcell et al. 2001). Studies on scyphomedusae (Youngbluth & Båmstedt 2001; Miyake et al. 2002; Matsumoto et al. 2003; Lindsay et al. 2004) and other gelatinous zooplankton (Larson et al. 1991; Larson et al. 1992; Mills et al. 1996; Toyokawa et al. 1998; Wrobel & Mills 1998; Hunt & Lindsay 1999; Miyake et al. 2001) using submersibles have increased in recent years. Mass occurrences of jellyfishes have been reported in deep waters off Hokkaido, Japan. Toyokawa et al. (2003) re-

ported dense aggregations of the lobate ctenophore *Bolinopsis infundibulum* at 1250 m depth, and Miyake et al. (2002) reported aggregations of *Aurelia limbata* at 250–450 m depths.

Parumbrosa polylobata Kishinouye, 1910 (Scyphozoa; Semaestomaeae; Umbrosinae) has been reported from relatively deep water in Toyama Bay, Sea of Japan, near the Goto Islands chain at the southernmost lip of the Sea of Japan and from Indochina (Kishinouye 1910; Bigelow 1913; Uchida 1936, 1954; Ranson 1945; Kramp 1961). This species was caught in a shrimp trawl net from deep water (>130 m depth) and has never been found at the surface in Japanese waters (Kishinouye 1910). Except for one example in Ranson (1945), the reported distribution of this species has until now been restricted to along the coast of the Sea of Japan. No ecological data are presently available for this species, and there have been no additional data concerning it since Uchida (1936).

In the present study, dense aggregations of *P. polylobata* were observed in the deep sea in Suruga Bay, along the Pacific coast of Japan. In Japanese waters, this is the first record of *P. polylobata* outside the Sea of Japan. Ecological data concerning *P. polylobata* (habitat environment, occurrence time, distribution pattern, swimming behavior *in situ*

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and feeding habits) are documented in the present study.

Materials and Methods

To clarify the occurrence, distribution, habitat environment and *in situ* behavior of *Parumbrosa polylobata*, investigations were carried out off Toi, off Mera and off Matsuzaki in Suruga Bay (Fig. 1) using the ROV *Dolphin-3K* (3K-Dives #541–543: NT01-10 Cruise), the ROV *Hyper-Dolphin* (HD-Dives #69 and #70: KY02-03 Cruise) and the crewed submersible *Shinkai 2000* (2K-Dives #1313–1316: NT01-11 Cruise, #1336 and #1337: NT02-06 Cruise)

(Table 1). All observations were carried out in the water column during the descent and ascent of the submersible or ROV in the benthopelagic layer (within 50 m of the bottom) in daylight hours. The number of medusae and occurrence depths were noted from dive videos. *P. polylobata* medusae were collected using a suction sampler (slurp gun) with a single large canister or six rotatable canister bottles and a gate sampler (Hunt et al. 1997; Lindsay 2003; Miyake et al. 2001). Environmental parameters (depth, temperature, salinity and dissolved oxygen concentration) were measured using a CTD-DO meter (SEABIRD: SBE-19+SBE-23). In addition to our dive data, the JAMSTEC video

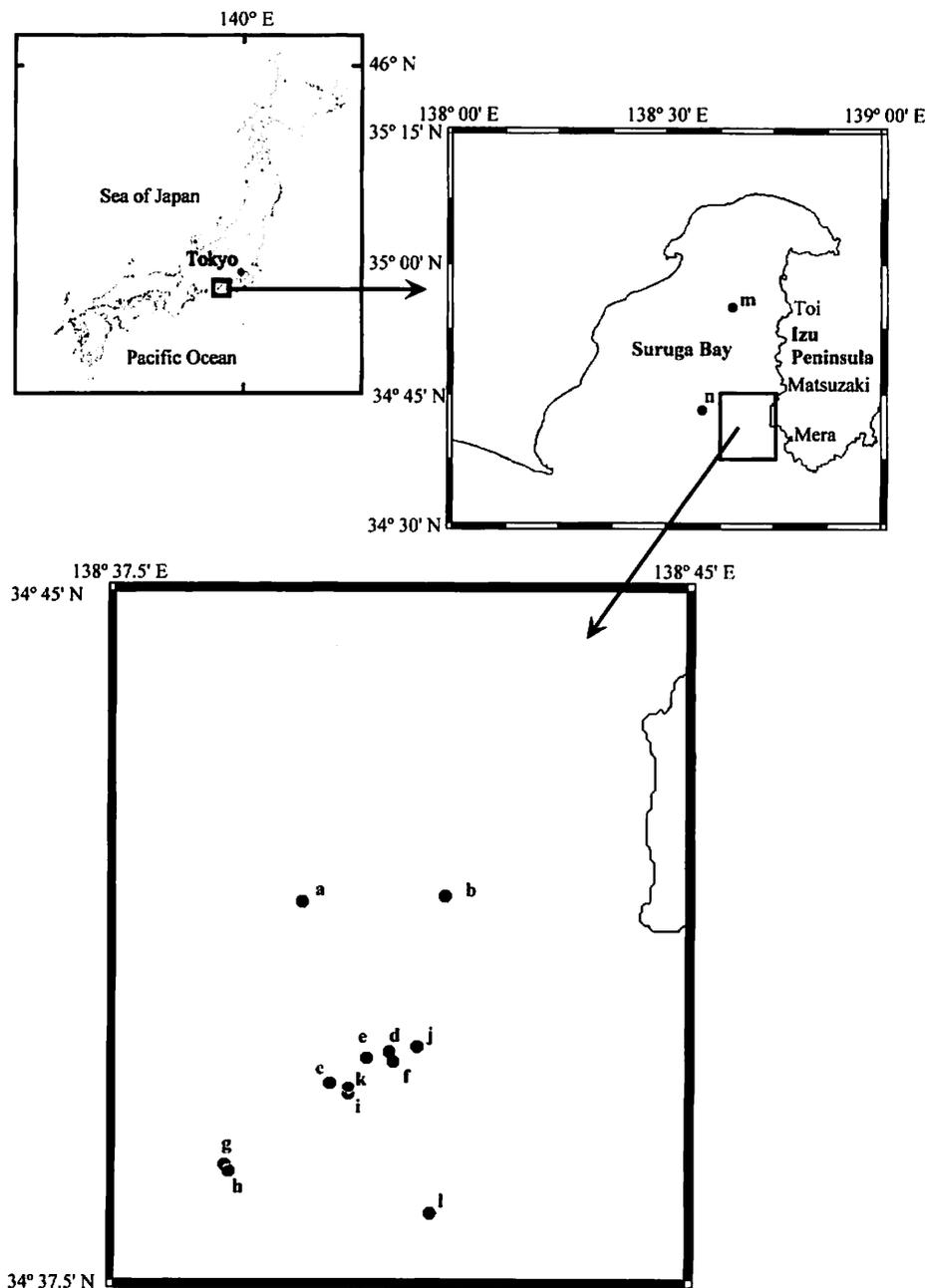


Fig. 1. Map of the investigation points in Suruga Bay, Japan. The coordinates and depth of each point are shown in Table 1.

Table 1. List of investigation points, occurrence ranges of depth and number of *P. polylobata* observed during dives. Altitude: depth above the seafloor.

Dive point in Fig. 1	Dive No.	Date	Locality	Landing point			Leaving point			Occurrence range of <i>P. polylobata</i> (m)	Number of <i>P. polylobata</i>
				Longitude (N)	Latitude (E)	Depth (m)	Longitude (N)	Latitude (E)	Depth (m)		
a	3K-Dive #542	07-Nov-01	Off Matsuzaki	34°41.625'	138°39.963'	484	34°41.940'	138°41.447'	317	272–362 (Altitude: 2.7–47.3)	9
b	2K-Dive #470	22-Apr-90	Off Matsuzaki	*	*	350	*	*	185	267–335	14
c	HD-Dive #69	23-Feb-02	Off Mera	34°39.666'	138°40.344'	623	34°40.251'	138°41.166'	460	390–416 (Altitude: 40–50)	6
d	HD-Dive #70	24-Feb-02	Off Mera	34°40.032'	138°41.083'	501	34°40.076'	138°41.739'	362	329–491 (Altitude: 0–43.5)	459
e	2K-Dive #1336	06-Apr-02	Off Mera	34°39.976'	138°40.796'	531	34°40.361'	138°40.555'	388	402–503	11
f	3K-Dive #543	07-Nov-01	Off Mera	34°39.914'	138°41.183'	442	34°40.539'	138°42.268'	303	363–360 (Altitude: 1.0–11.9)	14
g	2K-Dive #1313	14-Nov-01	Off Mera	34°38.733'	138°38.965'	859	34°39.930'	138°41.234'	435	423–478	4
h	3K-Dive #541	05-Nov-01	Off Mera	34°38.674'	138°38.974'	857	34°39.685'	138°40.380'	618	375–404 (Altitude: 2.1–2.2)	2
i	2K-Dive #1314	15-Nov-01	Off Mera	34°39.568'	138°40.548'	560	34°40.035'	138°41.431'	394	453	2
j	2K-Dive #1315	16-Nov-01	Off Mera	34°40.080'	138°41.455'	394	34°40.448'	138°42.151'	220	380–291	9
k	2K-Dive #1316	17-Nov-01	Off Mera	34°39.571'	138°40.570'	556	34°40.080'	138°41.455'	394	374–433	199
l	2K-Dive #1135	28-Sep-99	Off Mera	34°38.241'	138°41.655'	431	34°38.162'	138°42.830'	314	385–434	128
m	2K-Dive #1335	05-Apr-02	Off Toi	34°54.989'	138°39.081'	1526	34°54.953'	138°39.249'	1460	No occurrence	0
n	2K-Dive #1337	07-Apr-02	Off Matsuzaki	34°41.168'	138°35.007'	1970	34°43.240'	138°35.092'	1963	No occurrence	0

* Landing and leaving points were not able to be calculated from tracking chart (the center of the chart was 34°41.699'N, 138°41.813'E) of *Shinkai 2000*.

archive was consulted with respect to dives carried out in the same area (2K-Dives #470: 22nd April, 1990 and #1135: 28th September, 1999) and these tapes were also analyzed to elucidate the distribution and occurrence of *P. polylobata*.

During the KY02-03 cruise, long-term rearing of *P. polylobata* medusae that were collected in good condition was attempted in rectangular aquaria (L60–W27–H29 cm) with sponge filters (Tetra Japan: Tetra Brilliant Filter) on board. After the cruise the medusae were kept in planktonkreisels (Hamner 1990; Raskoff et al. 2003) in the laboratory. The rearing water was filtered natural seawater (50 μm mesh size) which was adjusted to the habitat salinity using artificial seawater salt, and the water temperature was kept at 7°C. The *P. polylobata* medusae were fed defrosted krill and the tissue from dead jellyfishes (*P. polylobata* and *A. aurita*). Other individuals were preserved in buffered 3% formalin-seawater solution. To clarify the relationship between the feeding habits of *P. polylobata* and its nematocyst signature, nematocysts in the tentacles and oral arms of fresh individuals and those of preserved individuals were observed by the squash preparation method using a phase

contrast microscope. The length, width, and cross sectional areas of nematocysts were analyzed from photo images using software, NIH Image ver. 1.6.2 (National Institute of Health).

Results

Many *Parumbrosa polylobata* medusae were observed on every dive off Mera and off Matsuzaki (a–l in Fig. 1 and Table 1) in February, April, September and November (Fig. 2). On the other hand, *P. polylobata* was not observed off Toi (m in Fig. 1 and Table 1) where the bottom depth was 1526 m or off Matsuzaki (n in Fig. 1 and Table 1) where the bottom depth was 1970 m. Occurrence ranges and numbers of individuals observed during each dive are outlined in Table 1. On HD-Dive #70, a total of 459 individuals were observed and the maximum population density was 18 individuals per video frame. The average bell diameter was 15–20 cm during all dives. Small individuals (<10 cm) were not observed. *P. polylobata* medusae were observed at depths of 267–509 m in the benthopelagic layers at 270–510 m bottom depth, with a peak in population density occurring at 370–450 m depths (Fig. 3a). *P. polylobata* was

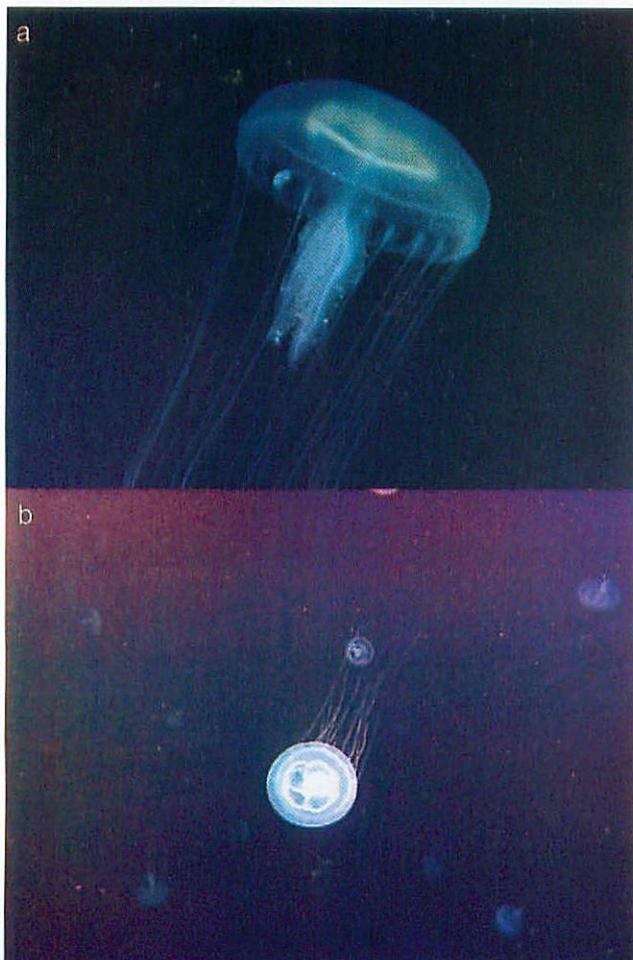


Fig. 2. *Parumbrosa polylobata*. a: Close up video frame, b: aggregation of *P. polylobata* at 415 m depth.

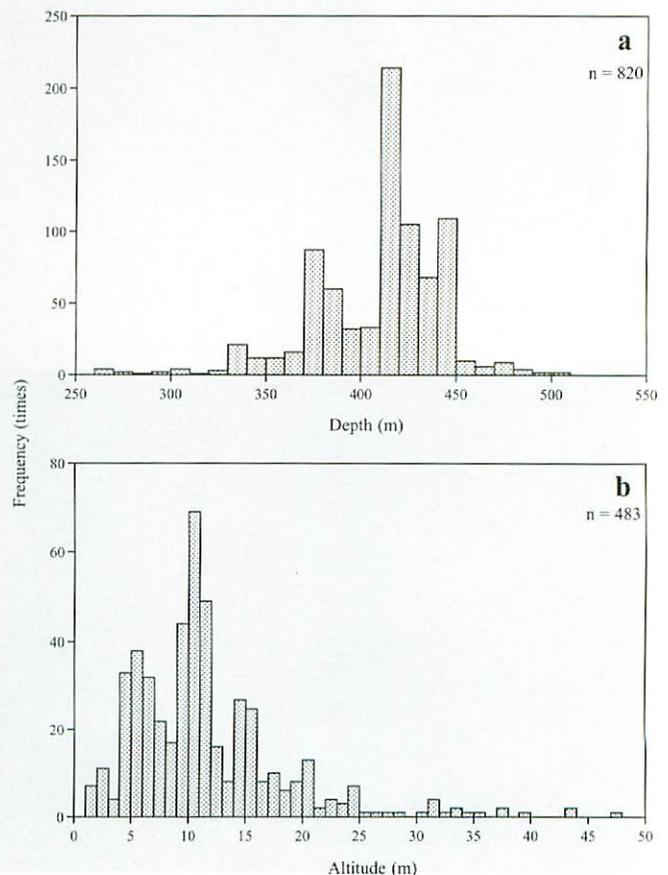


Fig. 3. Occurrence frequency of *Parumbrosa polylobata*. a: Relationship between frequency and depth of occurrence. b: Relationship between frequency and altitude (depth above the seafloor) of occurrence.

distributed in the benthopelagic layer within 50 m from the bottom, with highest densities occurring mainly 5–20 m above the bottom (Fig. 3b). No medusae were observed in the 267–509 m depth layer above bottom depth of 600–1970 m. Temperature, salinity, density ($\sigma-t$) and dissolved oxygen concentrations in the layers where *P. polylobata* occurred were 6.6–9.2°C, 34.2–34.4 PSU, 26.7–26.9 and 2.1–2.4 ml/l, respectively. Other animals observed in the same water mass as *P. polylobata* were gelatinous zooplankters [Hydromedusae: *Aegina* sp., *Cuninidae* sp., *Halicreas minimum*, *Aequorea* sp. and *Solmissus* sp.; Scyphomedusae: *Periphylla periphylla*; Ctenophores: *Bolinopsis* spp., *Bathocyroe* sp., the “Two spot” bathyctenid cydippid (Fig. 5f, Hunt & Lindsay 1999) and a mertensid cydippid; Siphonophores: *Prayinae* sp.; Salpidae: *Salpa fusiformis*; larvaceans], crustacean zooplankters [copepods, krill (*Euphausia* sp.) and sergestid shrimps], and fishes (*Maurollicus muelleri* and *Trichiurus lepturus*).

Parumbrosa polylobata swam vigorously with strong bell

contractions at pulsation rates of 9–20 times/minute (mean \pm S.D. = 12.3 ± 2.4 , $N=31$) *in situ*. Almost all the medusae in the same area swam in the same direction, mainly obliquely upwards. However, all medusae 14 m off the bottom swam downwards (Bottom depth 416 m; HD-Dive #70). The four oral arms were closed together, and the tentacles trailed, extending 8–10 times the length of the bell diameter while swimming. Individuals were observed to capture several gelatinous zooplankton species: *Salpa fusiformis*, siphonophores (Fig. 4a), and *Solmissus* sp. On one occasion, two medusae had caught zooids of *Salpa fusiformis*, and five zooids were observed in the gastric pouch of one of these medusae (Fig. 4b, c). Crustacean zooplanktons were not observed in the gut contents of *P. polylobata*. On Dive #1135 of the *Shinkai 2000* in September, a moribund individual of *P. polylobata* had sunk to the seafloor at 453 m depth and was being manipulated by ophiuroids (Fig. 4d).

Three *Parumbrosa polylobata* individuals measuring

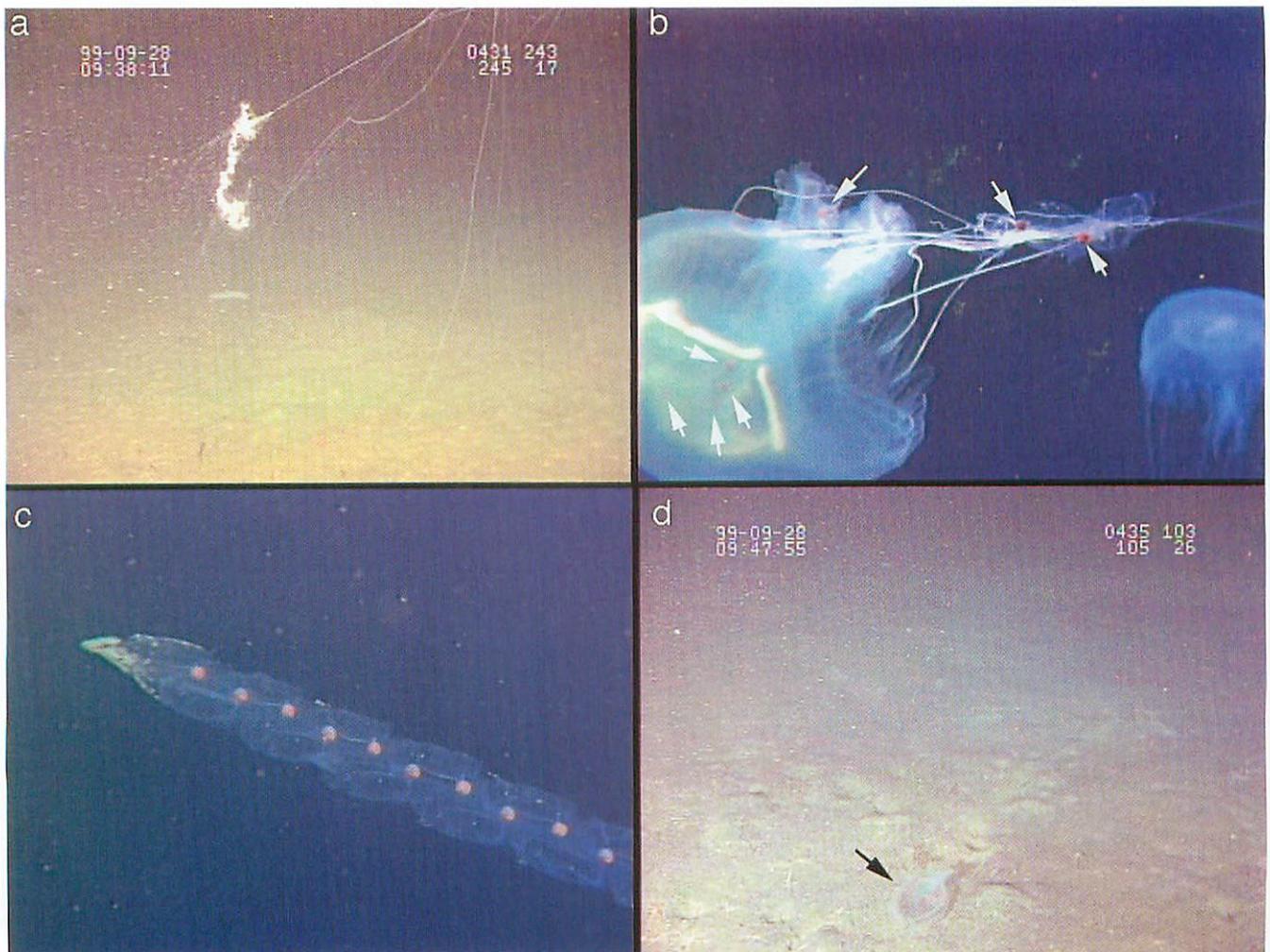


Fig. 4. Predatory behaviors and trophic consequence of *Parumbrosa polylobata*. a: *Parumbrosa polylobata* caught a siphonophore with its tentacles. b: Two medusae caught the same zooids of *Salpa fusiformis*. Zooids were observed in the gastric pouch, on the oral arm, and on the tentacles of the medusae (arrows). c: *Salpa fusiformis*, which was preyed on by *P. polylobata*, in the benthopelagic zone at 447 m depth. d: Moribund medusa sank to the seafloor (arrow).

10–15 cm in diameter were kept in an aquarium. When fed defrosted krill, they were unable to digest them completely, and the undigested krill decayed in the gut cavity. As a result, one of the medusae, which weakened, died due to rotting out of its gelatinous matrix. The other two *P. polylobata* were kept in the same tank and were not fed for two days to allow them to egest the undigested krill. One of them caught the other one with its oral arm, and cannibalism was observed. Subsequently, when some tissue from a dead *P. polylobata* and a dead *A. aurita* came in contact with the oral arm of *P. polylobata*, it quickly captured the tissue pieces with its oral arm and ingested them. *Parumbrosa polylobata* medusae caught and ate all jellyfish tissues they came in contact with. However, they did not catch all the defrosted krill that were placed on their oral arms or tentacles, and most of the krill that were captured were soon released. In addition, when the tissues of jellyfishes were fed to them, *P. polylobata* remained in good condition without the gelatinous matrix around their gastric cavity rotting out.

Four types of nematocysts (atrachous isorhizas, small microbasic euryteles, medium microbasic euryteles and large microbasic euryteles) were observed (Fig. 5). Atrichous isorhizas, small microbasic euryteles and medium microbasic euryteles were found in the tentacles and minute brachial filaments at the margins of the oral arms. The large microbasic euryteles were found only on the oral arms, and they were very rare. The dominant type of nematocyst was the small microbasic eurytele. The dimensions of each nematocyst type are given in Table 2. The lengths (average \pm S.D. μ m) of the atrichous isorhizas, small microbasic euryteles, medium microbasic euryteles and large microbasic euryteles were 7.60 ± 0.68 , 14.89 ± 1.32 , 20.94 ± 1.23 , 30.22 ± 3.12 , respectively.

Discussion

This report is the first record of *Parumbrosa polylobata* off the Pacific coast of Japan and the first original report concerning this species in almost 70 years. *P. polylobata* formed swarms in the benthopelagic layer between 0–40 m altitude from the bottom at 300–500 m depth, indicating it may be a benthopelagic species. It did not occur in the 300–500 m depth layer at stations where the bottom depth was greater than 600 m. The distribution of *P. polylobata*, therefore, depended on the absolute depth and, more importantly, on the relative depth compared to the seafloor.

Suruga Bay is located along the Pacific coast of central mainland Japan. The width of the bay is about 55 km and the length is 60 km. The deepest part is on the eastern side of the bay mouth and reaches about 2500 m. There is a submarine trough (>1000 m depth) from the bay head to the eastern part of the bay mouth. An offshoot from the Kuroshio current enters the eastern part of the bay mouth. Suruga Bay contains four water masses vertically. These are coastal water (0–100 m), Kuroshio oceanic

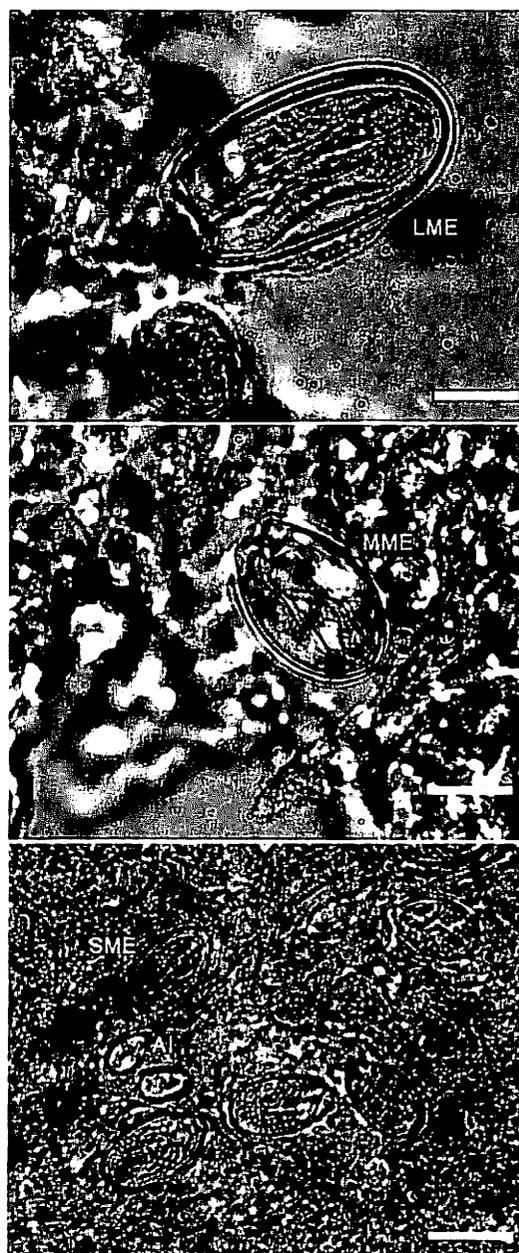


Fig. 5. Nematocysts of *Parumbrosa polylobata*. LME: large microbasic eurytele, MME: medium microbasic eurytele, SME: small microbasic eurytele, AI: atrichous isorhiza. Scale bar 10 μ m.

water (100–200 m), North Pacific Intermediate Water (200–1200 m) and Pacific deep water (>1200 m) (Inaba et al. 2001; Nakamura & Muranaka 1979; Yasuda 2002). North Pacific Intermediate Water is characterized by a minimum density layer (26.7–26.9) at depths of 300–800 m (Talley 1993; Yasuda et al. 1996). The physico-chemical water mass parameters where *Parumbrosa polylobata* occurred correspond to those of North Pacific Intermediate Water. The zone around 400 m depth is a zone where some species that exhibit diel vertical migration may come into contact with the bottom during the daylight hours. The ben-

Table 2. Dimensions of each type of nematocyst (μm).

		Microbasic eurytele			Atrichous isorhiza
		Large (9)	Medium (15)	Small (23)	(23)
Length	Average	30.22	20.94	14.89	7.60
	Range	26.56–35.85	19.33–23.62	12.72–17.30	6.29–9.47
	S.D.	3.12	1.23	1.32	0.68
Width	Average	16.95	20.94	9.32	4.39
	Range	14.74–19.09	12.24–15.75	7.38–10.97	3.38–7.12
	S.D.	1.36	0.98	0.75	0.98
Cross sectional area	Average	412.47	225.96	108.68	24.63
	Range	340.32–571.09	197.61–291.48	81.88–156.30	18.23–35.42
	S.D.	81.89	24.18	17.38	4.02

Numbers examined are given in parenthesis.

thopelagic zone at these depths may be an ecotone where two communities overlap, resulting in high biomass and high diversity. Off Mera, the mesopelagic community (*Maurolicus*, jellies and krill) and the benthic community overlapped with each other. *P. polylobata* aggregated at this zone. Although Kishinouye (1910) reported *P. polylobata* occurred from more than 130 m depth, we were unable to investigate shallower areas (<185 m) or the nighttime distributions due to operational constraints. Data concerning the diel vertical migration and distribution of *P. polylobata* in the benthopelagic layer at shallower depths need to be accumulated in the future.

Parumbrosa polylobata preferred soft-bodied gelatinous zooplankton to hard-bodied crustaceans as their principal food source. Gelatinous zooplankton were good foods for maintaining *P. polylobata* in laboratory tanks, as is also the case with *Sanderia malayensis* (Scyphozoa: Semaestomae: Pelagiidae), which may have similar feeding habits to *P. polylobata*. *S. malayensis* thrives more on gelatinous zooplankton than on crustaceans such as *Artemia* nauplii (personal observation). Purcell and Mills (1988) reported on the relationship between nematocyst types and diets. Hydromedusae that exclusively consume soft-bodied prey have microbasic mastigophores, euryteles, basitrichous isorhizas or apotrichous isorhizas which penetrate soft-bodied organisms, but lack the adhesive rhopaloneme nematocysts that enable ready capture of crustaceans. Scyphomedusae have four types of nematocysts: atrichous isorhizas, holotrichous isorhizas, homotrichous microbasic euryteles and heterotrichous microbasic euryteles (Kass-Simon and Scappaticci 2002; Mariscal 1974). *Parumbrosa polylobata* ate krill and jellyfishes in the laboratory, and salps, siphonophores, and medusae *in situ*. The medusa has atrichous isorhizas and three size classes of microbasic euryteles. Microbasic euryteles, which were the predominant type, may be for catching gelatinous zooplankton, while atrichous isorhizas which are glutinant (i.e. sticky surfaces used to stick to prey) may be

for catching hard-bodied prey. In particular, it is thought that medium microbasic euryteles may play an important role in capturing gelatinous prey due to their longer penetrative threads.

Parumbrosa polylobata occurred in dense aggregations in deep benthopelagic areas as reported for *Aurelia limbata* (Miyake et al. 2002) and *Bolinopsis infundibulum* (Toyokawa et al. 2003). Moribund medusae were observed being manipulated and probably ingested by ophiuroids. The same phenomenon was observed for *A. limbata* (Miyake et al. 2002). Moribund individuals sink to the seafloor and become food for the benthos. Thus, *P. polylobata*, which occurs in dense aggregations, seems to occupy an important position in terms of benthic-pelagic coupling.

Parumbrosa polylobata medusae were found from February to November, and the moribund individual was observed in September. This suggests that if this species has a polyp stage, strobilation would occur in December–January as it does in the life cycle of *Aurelia aurita* and that the medusae grow during spring to summer. Some potted-plant markers (Miyake & Lindsay 2003) were deployed as possible settling sites for *P. polylobata* polyps on the ROV *Hyper-Dolphin* Dives #69 and #70 at the sites where the largest concentrations of this species occurred. We would like to investigate the settlement of polyps on these markers, try to maintain these polyps and medusae throughout the year, and clarify the life cycle of this species.

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