Wild polyps of the blooming jellyfish *Aurelia limbata* (Brandt, 1838) (Cnidaria: Scyphozoa) found on deep-sea debris off Sanriku, Japan

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**Abstract:** Mass aggregations of *Aurelia limbata* have been reported along the Pacific coast of northern Japan, from spring to fall. The polyp stage is important for understanding the factors leading to mass occurrences of jellyfish, because polyps reproduce asexually and are responsible for the release of many ephyrae. Until the present report, the polyps of *A. limbata* had not been found in the wild and their ecology remained unknown. We found 18 polyps of *A. limbata* attached to two pieces of deep-sea debris, an aluminum beverage can and a plastic bottle, collected by bottom trawl at depths of 296 m and 392 m, respectively. Strobilation of the polyps was observed at 4°C without temperature change stimulation. This raises the possibility that strobilation occurs in low-temperature environments throughout the year. A large quantity of debris had sunk to the seafloor off the coast because of the tsunami tidal wave after the Great East Japan Earthquake, increasing the available substrate for *A. limbata* polyps. Additional ecological research on polyps and medusae in deep waters is necessary to predict future blooms of *A. limbata*.

**Key words:** marine debris, sessile organisms, jellyfish bloom, strobilation, tsunami

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**Introduction**

*Aurelia limbata* (Brandt, 1838) belongs to the class Scyphozoa in the family Ulmaridae, and is characterized by having a maximum bell diameter of 30 cm, a reddish-brown bell margin, and a mesh-like gastrovascular system. This species is distributed in the boreal waters of the Pacific region of Tohoku and Hokkaido, northern Japan, the Okhotsk Sea, Bering Sea, and the northern part of the Sea of Japan (Uchida 1954, Kishinouye 1910, Kramp 1961, Larson 1990, Pogodin 1998, Wrobel & Mills 1998). Since 2008, dense aggregations of *A. limbata* have appeared on the Pacific coast of Iwate Prefecture from spring to summer (Goto 2012). *A. limbata* medusae bycatches clog and break set nets and bottom trawl nets, and downgrade the quality of the catch (Miyake et al. 2011b, Goto 2012).

It is important to understand the ecology of *A. limbata* polyps for a better understanding of the mechanisms of medusae blooms. Some studies have reported the life cycle of this species in captivity (Uchida & Nagao 1963, Straehler-Pohl 2009). However, polyps of *A. limbata* have never been found in the wild and their *in situ* ecology has never been studied. Medusae of *A. limbata* occur in coastal shallow water areas and large numbers have been collected with a bottom trawl net at a depth of 300 m (Miyake et al. 2011b). Additionally, *A. limbata* medusae, which had planulae in brooding pouches on their oral arms, have been observed at depths of 200–400 m off Kushiro, Hokkaido, Northern Japan by a remotely operated underwater vehicle (Miyake et al. 2002a). Miyake et al. (2002a) speculated that this species can reproduce in the deep sea and that the polyps can inhabit such depths.

Scyphopolyps have been collected from various substrates in the field. Miyake et al. (2004) reported polyps of *Sanderia malayensis* Goette, 1886 and *Aurelia aurita* (Linnaeus, 1758) attached on the tubes of the vestimentiferan tubeworm *Lamellibrachia satsuma* Miura, Tsukahara & Hashimoto, 1997 at depths of 80 to 110 m in Kagoshima Bay. This report suggested that the polyps of these epipe-
lagic species are able to inhabit depths of more than 100 m. Polyps require hard substrates for attachment. However, on the deep-sea floor off the Iwate coast, substrates are limited to soft sediments. Sessile organisms can use artificial substrates, such as marine debris, as habitats within an expanse of soft deep-sea sediments (Ammons & Daly 2008, Miyake & Lindsay 2003, Miyake et al. 2011a). Miyake et al. (2002b) observed polyps of *A. aurita* attached to a plastic cigarette package drifting in the water column. Holst & Jarms (2007) reported that artificial substrates offered a more attractive habitat to polyps than natural substrates.

This study is the first to discover *A. limbata* polyps in nature and to observe *A. limbata* polyps attached to deep-sea debris. We also discuss the environmental conditions for strobilation of *A. limbata* in the deep-sea and the influences of deep-sea debris on *A. limbata* blooming events.

**Materials and Methods**

**Collection of scyphopolyps**

We used scyphopolyps collected by bottom trawl surveys, using the R/V *Iwate-Maru*, from the continental slope off Iwate, Northern Japan. Forty-one tows were conducted on the upper continental slope at depths of 200 m to 500 m between 39°00'N and 40°00'N, 142°00'E and 142°20'E, from April 2010 to November 2011 (Fig. 1). Each tow lasted about 30 min. Vertical profiles of water temperature and salinity were measured using a CTD (SBE 9plus, Seabird Electronics, Bellevue, WA, USA).

**Cultivation of polyps and ephyrae**

Collected polyps were transferred to petri dishes (diameter 78 mm, height 45 mm) two weeks after collection. The polyps and ephyrae released from strobilae were maintained at 4°C, which was the same as the *in situ* temperature, in filtered (1.0 µm) seawater. *Artemia* nauplii were fed twice a week to polyps and thrice a week to ephyrae. Seawater was replaced regularly with freshly-filtered seawater, 4 h after feeding.

All polyps and ephyrae were identified using both morphological and molecular methods. Morphological identification of polyps and ephyrae followed Straehler-Pohl & Jarms (2010) and Straehler-Pohl et al. (2011). Standard measurements of lengths for polyps were used (Fig. 2A): total body length (TBL): length from hypostome tip to basal disc, and mouth disk diameter (MDD): widest diameter of the mouth disk (Straehler-Pohl et al. 2011). Measuring points and measurements in ephyrae were (Fig. 2B) as follows—total body diameter (TBD): 2×total length of marginal lappets+diameter of central disc, central disc diameter (CDD): adradial diameter of the central disc, and total marginal lappet length (TMLL): length of the lappet stem+length of rhopalial lappet (Straehler-Pohl & Jarms

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**Fig. 1.** Map of the sampling sites and the collection sites for scyphopolyps, off the coastline of Iwate Prefecture, Japan. White closed circles and gray closed circles denote sampling sites in 2010 and 2011, respectively. The large closed circle (aluminum can; April 15, 2010, 296 m) and closed triangle (plastic bottle; November 8, 2011, 392 m) show stations where scyphopolyps were collected.
To be sure of the morphological identifications, we observed the shape of the rhopalial lappets and gastric systems of some ephyrae of *Aurelia* sp.1 from Tokyo Bay that were bred in our laboratory and compared their morphological characters with *Aurelia aurita* from Helgoland, German (Straehler-Pohl & Jarms 2010, Straehler-Pohl et al. 2011).

**Molecular analyses**

Three polyps were used for extracting genomic DNA. A live clone polyp in a microfuge tube was resuspended in 100 μl of 10% Chelex100 (Bio-RAD, Hercules, CA, USA) and placed in a water bath at 100°C for 20 min with occasional vortexing at high speed for 10 s each time. We used the supernatant for PCR as a template.

The small subunit ribosomal RNA (18S rRNA) gene was amplified and sequenced using the primers and protocols outlined in Medlin et al. (1988). These sequences were compared against those in the GenBank database by using BLAST (http://blast.ncbi.nlm.nih.gov/Blast.cgi). Multiple alignments of these sequences were performed using MEGA 5 (Tamura et al. 2011) with built-in ClustalW (Larkin et al. 2007). Phylogenetic and molecular evolutionary analyses were performed using the neighbor-joining method with 1000 bootstrap replicates in MEGA 5.

**Results**

We investigated a total area of 0.996 km² of the upper continental slope from 200 m to 500 m depth, and collected 280 pieces of deep-sea debris. In 2010, 47 pieces of debris were collected in the survey area (0.418 km²). In 2011, 233 pieces of debris were collected in the survey area (0.578 km²). The average density of deep-sea debris was 112.4 pcs/km² in 2010 and 403.1 pcs/km² in 2011. From these pieces of deep-sea debris, we found 4 scyphopolyps...
attached to the inside wall of an aluminum beverage can, on April 15, 2010, at a water depth of 296 m, and 14 scyphopolyps attached to the inside wall of a plastic bottle, on November 8, 2011, at a water depth of 392 m (Fig. 1). On April 15, 2010, the temperature and salinity of the surface water was 7.0°C and 33.6, respectively (Fig. 3). The vertical temperature profile ranged from 5.2°C in the subsurface layer to 7.2°C at the bottom. There was a halocline in the upper 120 m of the water column, and salinity stabilized at 33.7 below the halocline. On November 8, 2011, the surface-water temperature and salinity was 16.2°C and 33.7, respectively (Fig. 3). From 70 m to 250 m depth, the salinity showed a drastic decrease caused by low salinity water derived from the Oyashio cold current, and the temperature dropped from 15°C to 2.7°C. Below 250 m depth, the temperature stabilized between 2.5 and 2.8°C and salinity gradually increased from 33.4 to 33.7 (Fig. 3).

The polyps were bowl-shaped with a very short stalk (Fig. 4). The TBL of the polyps was 0.91–2.47 mm (mean: 1.57 mm), the DMM of the polyps was 0.61–1.46 mm (mean: 1.00 mm), and polyps had 14–20 (mode: 16) filiform tentacles when they started asexual reproduction (Table 1). They reproduced asexually by budding. Polyps attached to the plastic bottle increased from 14 to 87 dur-

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**Table 1.** Comparison of morphological characters of scyphozoan polyps.

| Species                        | Culture temperature | Total body length (mm) | Mouth disk diameter (mm) | Number of tentacles | References                      |
|--------------------------------|---------------------|------------------------|--------------------------|--------------------|--------------------------------|
| Scyphopolyp on aluminum can   | 4°C                 | 1.21-2.47, mean: 1.83 | 0.69-1.13, mean: 0.95    | 14-18, mean: 16    | Present study                  |
| Scyphopolyp on plastic bottle | 4°C                 | 0.91-2.28, mean: 1.35 | 0.61-1.46, mean: 1.04    | 16-20, mean: 18    | Present study                  |
| *Cyanea capillata*             | 5-10°C              | 2.51-3.02, mean: 2.71 | 1.40-1.84, mean: 1.59    | 16-17, mean: 16    | Straehler-Pohl et al. (2011)   |
| *Aurelia aurita*               | 5-15°C              | 3.03-3.80, mean: 3.18 | 0.90-1.57, mean: 1.19    | 18-28, mean: 23    | Straehler-Pohl et al. (2011)   |
| *Aurelia limbata*              | 5-15°C              | 0.94-1.41, mean: 1.27 | 0.61-0.94, mean: 0.83    | 16                 | Straehler-Pohl et al. (2011)   |
| *Chrysaora melanaster*         | 20°C                | 2.0-3.2                | 1.8                      | 16-18              | Morandini et al. (2004)        |
| *Chrysaora pacifica*           | 20-25°C             | 2.0-3.0                | -                       | 16                 | Kakinuma (1967)                |
| *Nemopilema nomurai*           | 18°C                | -                      | 0.8-1.1                  | 16                 | Kawahara et al. (2006)         |
| *Rhopilema esculentum*         | 18-22°C             | 1.0-3.5                | -                       | 16                 | Ding & Chen (1981)            |
| *Phacellophora camtschatica*   | 14-15°C             | 4.85-11.0, mean: 7.62 | 1.25-3.5, mean: 2.45     | 30-44, mean: 38    | Straehler-Pohl et al. (2011)   |

- : no statement given in the publication
**Table 2.** Comparison of morphological characters of ephyrae.

| Species                              | Total body diameter (mm) | Central disc diameter (mm) | Number of marginal lappets | Shape of rhopalial lappets / Distinctions                                                                 | Gastric system                                      | Color                        | References                      |
|--------------------------------------|--------------------------|----------------------------|-----------------------------|----------------------------------------------------------------------------------------------------------|-----------------------------------------------------|------------------------------|--------------------------------|
| Scyphopolyps on plastic bottle       | 3.8-4.0, mean: 3.94      | 1.51-1.57, mean: 1.54      | 8                           | Bread knife-shaped / 1 gastric filament per quadrant                                                    | Spade-like, unforked radial canals                  | Pale yellow                  | Present study                  |
| *Aurelia aurita*                     | 3.86-4.5, mean: 4.19     | 1.44-1.81, mean: 1.66      | 8                           | Broad lancet-like / 1-2 gastric filaments per quadrant                                                  | Spade-like to slightly forked rhopalial canals, rhombic velar canals | Milky to bluish              | Strahpler-Pohl & Jarms (2010) |
| *Aurelia limbata*                    | 3.0-4.5                  | -                          | 8                           | Lappets with rather narrow tips overlapped inside / statocyst bright yellowish, 1-2 gastric filaments per quadrant | Rather wide radial canals, larger velar canals than *A. aurita* | Pale yellow or greyish yellow | Uchida & Nagao (1963)          |
| *Aurelia limbata*                    | 2.62-5.33, mean: 3.66    | 1.07-1.71, mean: 1.26      | 8                           | Bread knife-shaped / 1 gastric filament per quadrant                                                    | Spade-like, unforked radial canals                  | Greenish yellow with reddish brown | Strahpler-Pohl & Jarms (2010) |
| *Cyanea capillata*                   | 5.97-9.54, mean: 8.55    | 2.43-3.79, mean: 3.34      | 8                           | Lancet-like / 2-8 tentacle buds                                                                       | Forked rhopalial canals, tips reach far into the rhopalial lappets, forked velar canals, tips reach to tip level of rhopalial in the marginal lappets | Red orange                   | Strahpler-Pohl & Jarms (2010) |
| *Chrysaora pacifica*                 | 2.0-3.0                  | -                          | 8                           | Lancet-like, rhopalial lappets parallel to each other / *Chrysaora*-typical nematocyst clusters        | Forked radial canals with pointed tips, velar canal tips very long | Light pink                   | Kakinuma (1967), Morandini & Marques (2010) |
| *Nemopilema nomurai*                 | 2.2-3.8                  | -                          | 8                           | Hand-shaped / nematocyst batteries                                                                    | Unforked rhopalial canals, U-shaped velar canals    | -                           | Kawahara et al. (2006)          |
| *Rhopilema esculentum*               | 2.11                     | 9.91                       | 8                           | Hand-shaped / 1 gastric filament per quadrant                                                          | Unforked, spatula-shaped rhopalial canals, unforked triangular velar canals | Milky to transparent        | Strahpler-Pohl & Jarms (2010) |
| *Phacellophora camtschatica*          | 10.0-10.8, mean: 10.23   | 5.64-6.46, mean: 5.85      | 14-16, mean: 15             | Pointed flame-shaped / 1-2 gastric filaments per quadrant                                               | Arrow shaped rhopalial canals, arrowhead-shaped velar canals | Yellowish, gastric system: yellowish orange | Strahpler-Pohl & Jarms (2010) |

- : no statement given in the publication
ing a year in captivity. The three polyps that were attached to the plastic bottle strobilated at 4°C, 550–568 days after the initial incubation. The calyx became elongated and segmented. The tentacles of the uppermost disc regressed with the progress of strobilation and then polyp tentacles developed on the distal-most residuum. Four to five ephyrae were produced from a single strobila. The residuum developed into a polyp after strobilation. Strobilation was not observed in polyps that were attached to the aluminum can.

Newly released ephyrae were pale yellow in color and had one gastric filament per quadrant, eight rays with short lappet stems (47% of the TMLL), bread knife-shaped rhopalial lappets, and eight marginal lappets (53% of TMLL). Statolith tips projected beyond the lappet rim. Radial canals did not reach the rim of the central disc. The TBD of the ephyrae was 3.8–4.0 mm (mean: 3.94 mm) and the CDD was 1.51–1.57 mm (mean: 1.54 mm) (Table 2). The exumbrella was scattered with nematocysts. No marginal tentacle buds were observed.

A sequence of 1800 base pairs was characterized from a fragment of the 18S rRNA gene for each of the five polyps selected from among the specimens used in this study. These sequences were compared to the sequences of 19 scyphozoan species, including *Aurelia limbata*, in GenBank (http://www.ncbi.nlm.nih.gov). The maximum likelihood (ML) phylogenetic tree, including the present samples and *A. limbata* (JX393277) within the monophyletic clade containing all *Aurelia* species showed this was a monophyletic sister clade to *Aurelia* sp.1 (Fig. 5).

Discussion

The shape and size of the polyps and ephyrae collected from the aluminum can and the plastic bottle differentiate them from previously described polyps and ephyrae of other Scyphozoa (Tables 1, 2). Common scyphomedusae observed off Sanriku are *Aurelia aurita*, *A. limbata*, *Cyanea capillata* (Linnaeus, 1758), *Chrysaora pacifica* (Goette, 1836), Ch. melanaster Brandt, 1838, Phacelophora camtschatica Brandt, 1835, Rhopilema esculentum Kishinouye, 1891, and Nemopilema nomurai Kishinouye, 1922 (Uchida 1936, Uchida 1954, Kakinuma 1967). The eight lappet stems of the ephyrae have been reported for these species, with *P. camtschatica* as an exception (Uchi-
Strobilation in *A. limbata* was induced at 4°C without stimulation from a temperature change. In contrast, strobilation of *A. limbata* has been observed with a temperature decrease from 15°C to 5–10°C (Strahler-Pohl & Jarms 2010) and from 13–20°C to 4°C (Miyake et al. 2011b). On the deep-sea floor, where the polyps were collected, the water temperature and salinity remained within the range of 2.2–6.3°C and 33.4–33.9, respectively, throughout the year (data provided by Iwate Fisheries Technology Center). Strobilation of *A. aurita* is caused by a decrease in water temperature (Watanabe & Ishii 2001, Miyake et al. 2002b, Ishii & Katsukoshi 2010). Fuchs et al. (2014) reported that the gene CL390 was induced at 4°C without stimulation from a temperature change. In contrast, strobilation of *A. aurita* has been observed with a temperature decrease from 15°C to 5–10°C (Strahler-Pohl & Jarms 2010) and from 13–20°C to 4°C (Miyake et al. 2011b). In this study, *A. limbata* strobilated at a non-fluctuating low temperature, which may be due to the continuous activation of the temperature-dependent “timer”. Strobilation of *A. limbata* can be induced by the length of the low-temperature period and *A. limbata* may strobilate throughout the year in constant low-temperature conditions. The *A. limbata* polyps collected in this study could have attached to the debris in three ways: 1) planulae attached to drifting debris in the surface layer and then the polyps sank to the bottom of the sea with the debris, 2) planulae, which were released from medusae in the deep-sea, attached to deep-sea debris, 3) planulae that bred in the surface layer sank to the bottom of the sea and attached to deep-sea debris. In this study, polyps attached to only two of the 280 pieces of collected debris. If the medusae bred many planulae near the deep sea floor, the percentage of the debris with polyps attached should be higher. Moreover, the polyps of *A. limbata* were attached to the inside wall of both the aluminum beverage can and the plastic bottle. The aluminum beverage can and the plastic bottle, to which the polyps of *A. limbata* were attached, could easily float at the sea surface. Seawater including planulae could easily find its way into a beverage can or bottle debris while they were drifting at the surface. It may be difficult for planulae to enter the inside of an aluminum beverage can or bottle at the sea floor by virtue of their own swimming behavior. This suggests that as for the *A. limbata* polyps collected in this study, the planulae most likely attached to the drifting debris in the surface layer and then the polyps sank to the sea floor along with the debris.

On the other hand, Iwate Prefecture suffered badly from the tsunami tidal wave caused by the Great East Japan Earthquake on March 11, 2011. The tsunami washed away large quantities of debris, which sank to the seafloor off the coast. Mature medusae of *A. limbata*, brooding planulae, were also observed near the bottom in the deep-sea benthopelagic layer between 200 and 400 m off Kushiro, Hokkaido, Japan (Miyake et al. 2002a). This suggests that debris may be used as a substrate for the attachment of the planulae of *A. limbata* into the future. Additional research into the seasonal occurrence of medusae and the distribution of polyps in deep and shallow waters is required to predict future blooms of *A. limbata*.

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