

Description of Feeding Apparatus and Mechanism in *Nemopilema nomurai* Kishinouye (Scyphozoa: Rhizostomeae)

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Abstract – Feeding apparatus, mechanism and passage of ingested prey were described for *Nemopilema nomurai* (Scyphozoa: Rhizostomeae). *N. nomurai* medusae without central mouths have developed complicated canal systems connecting the tip of the tentacle and oral arm to the gut cavity. The number of junctions in the canal system increases with the bell diameter. The prey is gathered by paralyzing nematocyst at the tentacles and by adhering cirri at the oral arms and scapulets. They are engulfed into the terminal pore located at the oral arms and scapulets, and entered into the gut cavity via the canal system. The estimated digestion time is 1 hour and 20 min. The diameter of terminal pore is always about 1 mm, implying that they could not eat prey larger than that pore size. On the other hand, ephyrae have central mouths and could swallow prey as large as adults could. Exploitation of the same size of food by adult and ephyra implies that *N. nomurai* can affect seriously the whole food web, massively ingesting micro- and mesozooplankton and cutting the energy transfer toward the higher level of carnivores.

Key words – *Nemopilema nomurai*, canal system, prey passage, medusa, ephyra

1. Introduction

Jellyfish rhizostomes with conspicuous eight oral arms (Larson 1991) comprise about 80 species (Kramp 1961). *Nemopilema nomurai* Kishinouye 1922 is one of the biggest jellyfish, reaching bell diameter of 160 cm, according to a specimen caught in the Yellow Sea in 2006 (Lee, unpublished data). This species is reported only in the far eastern north Pacific including the northern East China

Sea, Yellow Sea, and East Sea. Since the first appearance of *N. nomurai*, recorded about 200 years ago in Korea (Chong 1814), massive occurrences have been reported in 2003, 2005, 2006, and 2007 from late spring to the beginning of winter. Recent bloom of this species has also been reported in Japanese coastal waters (Kawahara *et al.* 2006). The jellyfish blooms are widely considered to be caused by combined factors of fisheries overexploitation, eutrophication and global warming (Arai 2001; Graham 2001; Parsons and Lalli 2002; Uye and Ueta 2004; Yasuda 2004). Their mass appearance has caused social and economic disturbances, so the Korean and Japanese governments launched scientific programs to elucidate the causes and consequences of the mass occurrences of the jellyfish.

Information on the biology and ecology of *N. nomurai* is extremely scarce due to the difficulties in sampling and rearing this giant jellyfish as well as its restricted distribution area. Recently biological and ecological studies on *N. nomurai* were undertaken by Kawahara *et al.* (2006); morphological characteristics described by Kishinouye (1922) and Omori and Kitamura (2004); the influence of ocean current on the distribution by Yoon *et al.* (2008).

We presumed that the mouth-like functioning terminal pores, as described by Larson (1991) have profound implication in the feeding behavior of rhizostomes, and that according to the diameter of the pore, a specific size of animal should be seriously affected, thus disturbing the whole food web. We, then, followed the passage of the ingested prey, measuring the diameters from the terminal pore of the oral arm to entrance of the gut cavity, in order to understand the internal connectivity and to show the

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potential prey size of *N. nomurai*. Additionally, the feeding mechanism and the prey size between medusa and ephyra were compared.

2. Materials and Methods

Nemopilema nomurai was sampled at Yorkji Island, Tongyoung, Korea in September, 2006 by SCUBA diving (Fig. 1). Four individuals of 33–70 cm in bell diameter were captured, transported to the laboratory and acclimated in a 100 L plastic tub for a day without prey. Seawater filtered onto 10 μm sieve was used and maintained at 26°C and 32 psu during the experiment. The photoperiod was 12 h light: 12 h dark. At the beginning newly hatched *Artemia* nauplii (< 24 hours; ca. 650 μm in length) were given for 15 minutes at a concentration of approximately 13,000 inds L^{-1} . The well fed jellyfish were transferred into the other tub without prey, and visually examined and photographed at every 5 minutes to follow the passage of the ingested items. Digestion time was estimated by ca. 45 cm in bell diameter of medusa at 24°C. Prey was newly hatched *Artemia* nauplii and observation was performed with the naked eyes. The digestion time was defined here as the time needed from the first ingestion to the complete disappearance in the gut cavity. The same individuals were reused in the experiment of describing the canal connection. Well fed *N. nomurai* was dissected and the canal connection in the whole body from the tentacle, scapulet, oral arm to the gut cavity was followed by staining with methylene blue. The diameters at each connection were measured under dissecting microscope (ZEISS, Stemi 2000C).

Feeding of ephyra was also examined. Artificial fertilization was conducted with several female and male *N. nomurai* in September, 2005 and ephyrae developed from polyps after artificial fertilization in 2006. About 5 mm in bell diameter

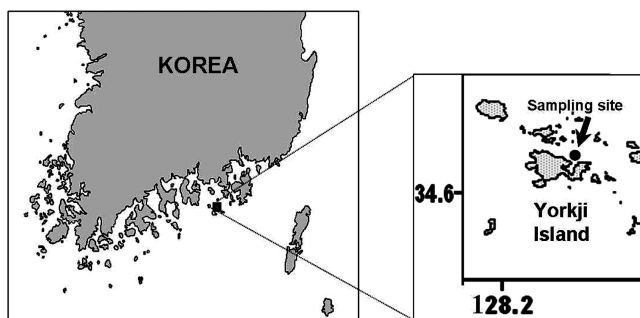


Fig. 1. Map of sampling site.

of ephyrae were used in this study. Newly hatched *Artemia* nauplii were given as prey at a concentration of approximately 500 inds L^{-1} . The experimental procedure was the same as for medusa.

3. Results

Nemopilema nomurai medusa used simultaneously nematocysts on the tentacles and cirri in the oral arms and scapulets for feeding. The nematocysts were about 100 μm size and located on the tentacles. The cirri were small (ca. 190 μm in length) and club-shaped, and located at the marginal parts of oral arms and scapulets (Fig. 2). The prey, *Artemia* nauplii, were immediately paralyzed by touching nematocyst or adhered to the cirri and transferred into the numerous tiny pores which were located at the end of the tentacle and around cirri. The pores merged into one main canal for each oral arm and scapulet. The canals in the oral arms and scapulets were well branched with number of connection increasing with the bell diameter of the specimen (Fig. 2A, 2B). The lips along the distal

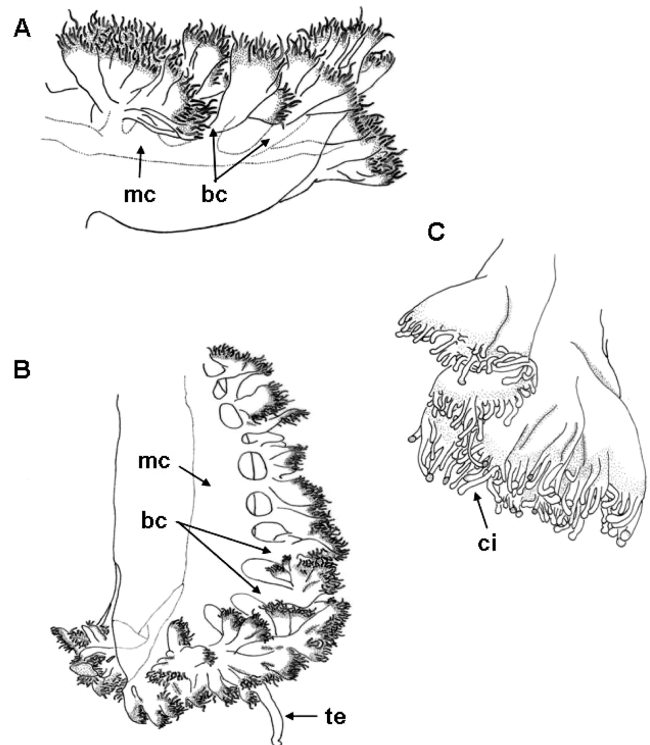


Fig. 2. Feeding apparatus in *Nemopilema nomurai*. Scapulet (A), oral arm (B), and enlarged marginal part of scapulet and oral arm (C). Abbreviations: mc main canal, bc branched canal, ci cirri, te tentacle.

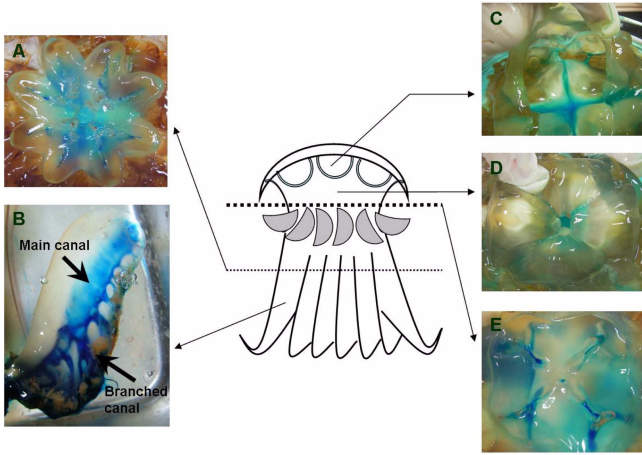


Fig. 3. The detailed pictures of each part in *Nemopilema nomurai*. A: cross section of whole oral arm; B: oral arm; C: gut cavity; D: upper part of manubrium; E: lower part of manubrium.

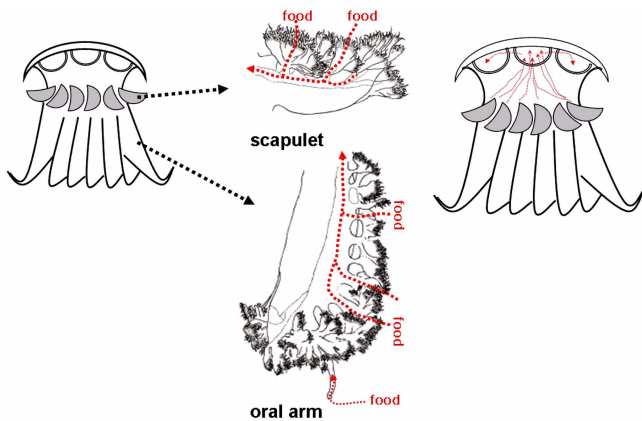


Fig. 4. The diagram of the prey passage in *Nemopilema nomurai* adult.

margin of the oral arms and scapulets were frilled, thus increasing the surface area and the number of terminal pores (Fig. 2C). Each main canal of the oral arms and scapulets joined at manubrium and connected to the gut cavity (Fig. 3).

After 10 minutes with food, terminal parts on canals of the oral arm and scapulet were full of prey. About 15 minutes later, the prey was found in the main canals of oral arm and scapulet, and 20 minutes later, the preys were observed in the manubrium and gut cavity. After that, the prey filled the whole of the canals from tentacles and cirri to the gut cavity (Fig. 4). Finally, after about 1 hour and 20 minutes, the prey in the gut cavity had completely disappeared, and the setae and carapaces of the prey were found in the radial canal.

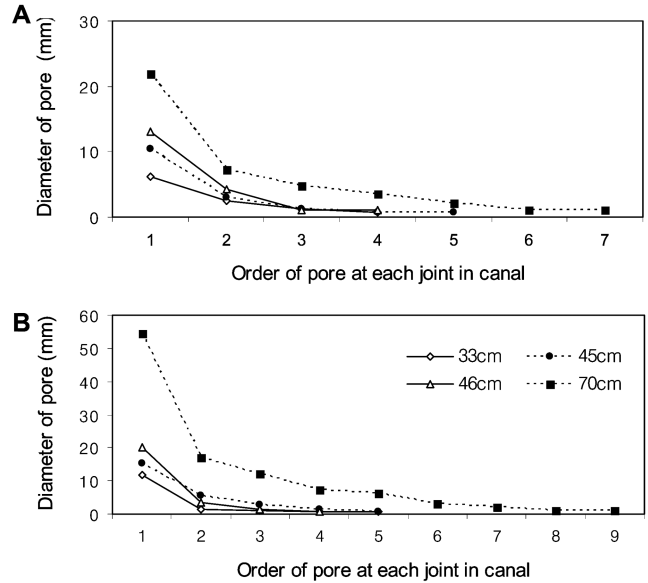


Fig. 5. The diameter of the branched canals and the main canal of the scapulets (A) and oral arms (B). Last number means terminal pore of canal.

For an individual of 70 cm in bell diameter, the terminal pore, which is the entrance of canal, was connected with the gut cavity after 7 joints in the scapulet and 9 joints in the oral arm. The diameter of each joint on canal decreased toward terminal pore. And the diameter of terminal pore was always less than 1 mm (Fig. 5), suggesting that the food of *N. nomurai* should be less than that size, irrespective of the medusa size.

Ephyrae of *N. nomurai* had central mouth of approximately 1 mm (Fig. 6). The prey was engulfed by that mouth and

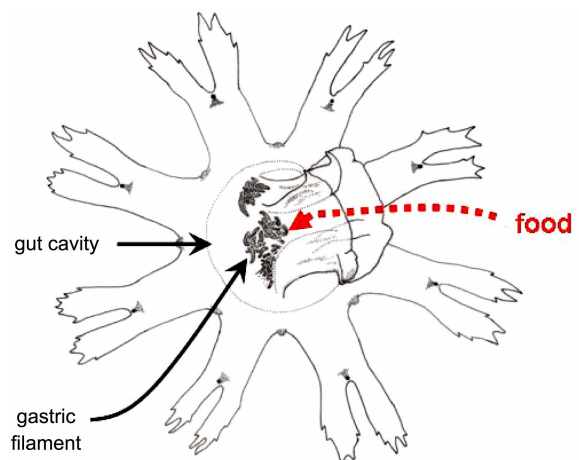


Fig. 6. The diagram of the prey passage in *Nemopilema nomurai* ephyra.

Table 1. Digestion time of jellyfish

Species	Prey	Digestion time (h)	Temp. (°C)	References
<i>Aurelia aurita</i>	Herring larvae	3.8	22	Heeger and Möller, 1987
	Mixed prey	0.95	22	Ishii and Tanaka, 2001
<i>Chrysaora quinquecirrha</i>	Ctenophora	< 10	26-29	Larson, 1986
	Fish egg	4	26	Purcell et al. 1994
<i>Pelagia noctiluca</i>	Medusae	8-10	27-29	Larson, 1987
<i>Stomolopus meleagris</i>	Barnacle larvae	2	28-30	Larson, 1991
	Copepods	1.5-2	"	"
<i>Nemopilema nomurai</i>	<i>Artemia</i> nauplii	1.2	22-25	This study

digested in the gut cavity. The cirri and tentacles with nematocyst were increased with somatic growth.

4. Discussion

With the following biological and ecological characteristics, *N. nomurai* could proliferate and affect -- in a fundamental manner -- the bottom of the food web. The characteristics are i) medusa possess huge number of tiny pores which are properly sized for feeding on micro- and mesozooplankton, ii) the whole body, except exumbrella, is covered with paralyzing and adhering feeding apparatus, and iii) the short digestion time (Table 1). These characteristics also imply that they could survive only in areas where prey species are abundant, i.e. coastal and neritic areas. Although some jellyfishes are reported to feed on phytoplankton (Mironov 1967; Båmstedt 1990; Matsakis and Conover 1991), the amount is negligible compared to zooplankton prey (Arai, 1997). From a classical viewpoint, the impact of a predator on the marine food web depends on the prey items, quantitative and qualitative, the abundance of predators and their ingestion rate. Generally, rhizostomes, including *N. nomurai* are believed to have profound effect on the marine ecosystem due to their high abundance, highly non-selective feeding habits on zooplankton and ichthyoplankton (Smith 1934; Thiel 1964; Kikinger 1983; Fancett 1988; Larson 1991), and quasi non-existence of predators on them. For rhizostomes, the success of non-selective feeding should be determined by the size of the prey since they do not have a mouth. This implies that other part of the body should take the mouth function, which is, after Larson (1991) for rhizostomes in general, the terminal pores. He described that the pore diameter was less than 3 mm. This should restrict the potential to feed on the prey.

So far no description on the canal system has been made

for *N. nomurai*. Our study showed huge numbers of pores of a diameter less than 1 mm, an efficient conveyer system from the tip of the tentacle to the gut cavity, and a fast digestion time. Considering a lack of conspicuous natural predators, negligible human consumption, and voracious feeding habit on various preys, *N. nomurai* medusae and ephyrae could restructure the local planktonic food web to an extreme simplicity, compete with other zooplanktivorous fishes, cut the energy transfer toward the higher level of consumer, and exert fundamental disturbance on the local fisheries.

Acknowledgments

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