Comparison of life cycles and morphology of *Cyanea nozakii* and other scyphozoans

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Abstract: Mass aggregations of the giant jellyfish *Cyanea nozakii* have occurred in China since the end of the 20th century. In particular, *C. nozakii* bloomed abnormally in Liaodong Bay during July and August of 2004 and the catch of edible *Rhopilema esculentum* was greatly reduced. In order to clarify the causes leading to mass occurrences of *C. nozakii*, the reproductive cycle and morphological characters of this species were compared with other common jellyfish species using data from both laboratory-rearing experiments and field investigations. The results showed that, in particular, settling of planulae and asexual reproductive strategies of scyphistomae made *C. nozakii* more capable of thriving under unfavorable physical conditions than *R. esculentum*. The ephyrae of *Nemopilema nomurai*, *R. esculentum*, *C. nozakii*, *Aurelia aurita*, *Rhopilema hispidum* and *Rhopilema asamushi* were differentiated by different shapes of lappets, rhopalar clefts, gastric filaments and nematocyst batteries. In addition, the life cycle of *C. nozakii* was compared with earlier reports on the life cycle of *Cyanea capillata*, *R. esculentum*, *Rhizostoma pulmo*, *Stomolophus meleagris* and *N. nomurai*, and the morphology of adult *C. nozakii* was compared and contrasted with species of the genus *Cyanea* (*C. capillata*, *C. ferruginea* and *C. purpurea*).

Key words: *Cyanea nozakii*, life cycles, morphological characters, scyphozoans

Introduction

Since the end of the 20th century, giant jellyfish have bloomed in the northeastern parts of the East China Sea, the Yellow Sea and the Bohai Sea. Such jellyfish blooms also occurred in Japan and Korea in 2003, and have caused damage and loss of fishing nets during the fishing season in all of the above waters. The giant jellyfish that bloomed along the coastal areas of Japan and Korea in 2003 was *Nemopilema nomurai* Kishinouye (Kawahara et al. 2006), but surveys suggested that different giant jellyfish may be blooming in Chinese waters. In addition to *N. nomurai*, *Cyanea nozakii* Kishinouye also bloomed (Chen et al. 2005). *Cyanea nozakii* in particular has caused ecological disasters (Chen et al. 2005). The giant jellyfish *C. nozakii* used to appear only sporadically in the past, but it is now widely distributed, abundant in quantity, and can spread over large areas within a short time. When blooming, it occurs in such large numbers that it can damage or break nets due to there being too many of them in a net, and it has be-

come trouble during the fishing season in the East China Sea, Yellow Sea and Bohai Sea. The harm to marine ecosystems caused by jellyfish blooms has exceeded that caused by red-tides in the coastal waters of China in recent years.

In the past, two other *Cyanea* species, *Cyanea capillata* Linneus (Haahtela & Lassig 1967, Dolmer & Svane 1993) and *Cyanea lamarckii* Péron & Lesueur (Gröndahl 1988, Brewer 1976, 1984, 1989, 1991) have mainly been studied. Morphological descriptions of the medusa of *C. nozakii* have been carried out with the aim of distinguishing species based on external structure (Uchida 1936, Hong 2004). Lu et al. (2003) studied the fisheries biology of *C. nozakii* in the waters of Dongshan Island. Zhong et al. (2004) investigated how environmental factors increased susceptibility to *C. nozakii* blooming. Ge (2005) reported that the catch of the edible jellyfish *Rhopilema esculentum* Kishinouye declined suddenly in Liaodong Bay in July 2004 due to the blooming of the jellyfish *C. nozakii*. The species of jellyfish blooming in Liaodong Bay, China, in July 2004 was identified as *C. nozakii* by Dong et al. (2005).

In order to clarify the causes of mass occurrences of *C.*

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nozakii, it is necessary to understand its reproduction and correctly characterize its morphology. Until now little attention has been paid to comparisons of the reproductive biological traits of bloom-forming species. In our laboratory, a large number of scyphistomae and ephyrae of *C. nozakii* were obtained under culture conditions for the first time in history and early developmental studies were carried out and reported (Dong et al. 2006a and b). In this paper, we report on mass occurrences of medusae in Chinese waters, in particular in Liaodong Bay. We also compare the morphological characteristics at different developmental stages and asexual reproductive strategies of *C. nozakii* and other species. The main aim of this research was to increase knowledge on the morphology of young stages of *C. nozakii* in the field in order to forecast its blooming.

Materials and Methods

Five quantitative surveys were conducted on fishing vessels of the Yingkou Fishery Company between May and October every year from 2004 to 2006. *Cyanea nozakii* was collected by drift nets and hand nets at 18 stations in Liaodong Bay of Bohai, China (Fig. 1). Medusae were counted and their umbrella diameters were measured. Samples for measurement of environmental parameters (such as surface water temperature, salinity, DO, crude oil, heavy metals, phytoplankton and pesticides etc.) were collected.

Fig. 1. Stations (·) for jellyfish surveys in Liaodong Bay. The circled region indicates jellyfish blooming area.

Mature medusae collected from Stns 17 and 18 by hand net on September 10, 2004, were cultured in a concrete tank (volume: 15 m³) at Huludao Breeding Center. Spawning and fertilization were achieved by holding 12 (umbrella diameter=200–360 mm) mature medusae (♀: ♂=1:1) in a 1 m³ aquarium. Planulae appeared 14 hours after fertilization at 20.8–21.4°C and settlement, metamorphosis and scyphistoma formation were observed. Young scyphistomae were fed with trochophorae of shellfish (*Crassostrea gigas* Thunberg) and blastulae of sea urchins (*Hemicentrotus pulcherrimus* Agassiz) twice or three times a week. Fully-developed scyphistomae were fed with *Artemia* nauplii once or twice a week. Ephyrae and young medusae were fed with *Artemia* nauplii and gelatinous prey (e.g., ephyrae of *Rhopilema esculentum*, *Aurelia aurita* Linneus) once or twice daily. Asexual reproduction, and morphology at different developmental stages were observed under an Olympus AX80TR-62E01 microscope with Canon camera.

Results

Mass occurrence and environmental factors

On June 20, 2004, the dominant species at Stns 17 and 18 was *Rhopilema esculentum*, as young medusae. However, on July 15 and July 24, 2004, the relative numbers of *Rhopilema esculentum* dropped rapidly while the numbers of *Cyanea nozakii* increased dramatically. On July 24, 2004, the number of *C. nozakii* was over 1000 times more than that of *R. esculentum*. The data is shown in Table 1.

On July 24, 2004, samples for measurement of environ-

Table 1. Number of *Rhopilema esculentum* and *Cyanea nozakii* from June 20 to July 24, 2004.

Date	Number (individuals/drift net)	
	<i>R. esculentum</i>	<i>C. nozakii</i>
20 June 2004	600	8
15 July 2004	104	870
24 July 2004	1	1250

Table 2. Environmental physicochemical parameters in different stations on July 24, 2004.

Parameters	Stn No.					Water Quality Standard for Fisheries
	12	11	17	18	10	
Temperature (°C)	26.4	26.8	26.4	26.5	26.8	
Salinity	34.12	33.64	34.09	33.90	33.80	
Diaphaneity	1.6	0.9	1.9	2.1	2.2	
pH	8.22	8.28	8.33	8.26	8.2	6.8–8.5
DO (mg/L)	6.01	7.86	5.78	5.01	4.3	≥3.0
Crude oil (mg/L)	0.381	0.387	0.237	0.233	0.229	≤0.05
Cu ²⁺ (μg/L)	3.66	4.15	5.13	2.56	4.39	
DDT (μg/L)		0.25		0.45		≤1.0

mental physicochemical parameters and analysis of phytoplankton were collected. The results are shown in Table 2. Salinity was 1.6 times higher than the mean value for salinity in past years in the same season, and the average concentration of crude oil in the surface water was 6.6 times as high as the allowable level according to the Water Quality Standard for Fisheries (GB11607-1989). Dead *Nitzschia pungens* Grunow occurred in large surface slicks in the areas where *C. nozakii* was blooming.

Spawning

Fully developed oocytes of *C. nozakii* were released into open seawater. Fertilization and embryogenesis of *C. nozakii* occurred in open seawater too. Cleavage of the zygote was total and equal. A hollow blastula was formed 10 hours after fertilization at 20.8–21.4°C. Gastrulation occurs by invagination. Fourteen hours after fertilization, actively swimming planulae appeared.

Planulae and settlement

Planulae varied in outline from slipper-shaped to irregularly oval. Their lengths ranged from 90–180 μm and widths from 60–95 μm . They swam actively by means of cilia, and rotated counter-clockwise around their longer axis. Living planulae were milky in color with a ciliated ectoderm. Prior to settlement, the anterior-posterior axis shortened, swimming became slow, and they became encysted planulocysts. The planulocyst developed an elongated stalk and became flask-shaped in outline, they then gradually became newly metamorphosed scyphistomae (Fig. 2).

We found that the planulae of *C. nozakii* swam freely in the water for only 1.5 days at 21°C and settled quickly. In contrast, the planulae of *R. esculentum* metamorphosed into scyphistomae either at the settlement stage or already during the pelagic stage, where they could swim freely in the water for 5 days at 18–22°C (Ding & Chen 1981).

Scyphistomae

The color of newly-born scyphistomae was milky, and they varied between 90–200 μm in height from the pedal disk to the mouth, with the tentacles being 100–150 μm long. The four short tentacles were filiform with scattered nematocyst batteries and the slender stalk was sheathed in a thin cuticle. The color of young scyphistomae was also milky. The young scyphistomae were 170–400 μm high and bore eight contractile tentacles, which were 400–1200 μm long, filiform with scattered nematocyst batteries, and occurred in one whorl. The color of fully-developed scyphistomae was whitish, becoming light orange after feeding on *Artemia* nauplii. The scyphistomae attained 400–2000 μm in height. The 16 or more tentacles were contractile, in one whorl, 1000–3200 μm long, and had scattered nematocyst batteries.

Fig. 2. Planulae and settlement of *Cyanea nozakii*. A. Planula (view from above); B. Planulocyst (side view); C. Excystment (side view); D. Newly metamorphosed scyphistoma (side view).

Fig. 3. Scyphistomae and asexual reproduction of *Cyanea nozakii*. A: Intermediate scyphistoma. B: Fully-developed scyphistoma. C: Scyphistoma producing podocysts. D: A stolon formed and parent scyphistoma remained with the original pedal disk. Manubrium (m); podocysts (p); pedal disk (pd); stolon (s).

Strobilae

The earliest strobilation occurred within 2 months after settlement when scyphistomae were kept at 22–26°C. Stro-

Fig. 4. Strobilae and newly liberated ephyra of *Cyanea nozakii*. A: Strobila. B: Oral view of newly liberated ephyra. 8 marginal lobes (ml); 8 rhopalia (r); 8 pairs of blunt-shaped lappets (l); manubrium (m) with by 4 lips (li).

bilation was typically monodiscous in *C. nozakii* (Fig. 4A). Expansion at the base of future rhopalar tentacles occurred first. A clear external indication of strobilation was the development of a small marginal lobe at the base of each rhopalar tentacle. Segmentation began as a faint circular incision proximal to the tentacular ring. This incision gradually became deeper and more distinct. After about 1.5–2.0 days the eight rhopalar tentacles began to undergo regression and were finally resorbed. At the same time, rhopalia with statoliths became apparent, lappets elongated, and incisions constricting the segments deepened.

Ephyrae

Newly released ephyra (Fig. 4B) were 2–3 mm wide from lappet-tip to lappet-tip when extended. They typically had 16 blunt-shaped lappets, 8 marginal lobes and 8 rhopalia. Rhopalar clefts were U-shaped and about half the depth of the large ocular clefts separating the marginal lobes. The exumbrella was marked by numerous scattered nematocyst batteries. The manubrium was large and quadrangular, with four lips often present at the mouth. The stomach portion of the gastrovascular cavity was nearly circular, and 1 gastric filament was present in each quadrant. The radial muscles were visible, extending into each lappet from the marginal lobes (Fig. 4B).

Medusae

Adult medusae of *C. nozakii* are about 200–300 mm, in diameter with a maximum size of over 500 mm. The middle of the smooth exumbrella is marked by numerous scattered nematocyst batteries. They have 8 marginal lobes, 8 rhopalia, a strong oral canalis carpi, and many long tentacles. The length of the oral canalis carpi is longer than the diameter of the umbrella, and the roots were combined together. The most striking feature is perhaps that *C. nozakii* has many long tentacles (about 1–2 m), 8 groups of tentacles were in a U-type arrangement on the umbrella. *C. nozakii* is dioecious with four stacks of gonads hid in the 4 subgenital pits.

Discussion

Mass occurrence of *Cyanea nozakii* and salinity

In the present investigation, the salinity in those areas where jellyfish blooming occurred was 33 to 35. Under experimental conditions, the author found that the salinity survival range was 12–35 for scyphistoma of *Cyanea nozakii*, with the salinity suitable for growth being 15–32, while optimal salinity was 20–30. However, the salinity survival range was 15–35 for ephyrae, and the most suitable salinity for growth was 20–35. Lu et al. (1989) reported the lowest salinity for scyphistoma survival *Rhopilema esculentum* to be 10, and the most suitable salinity for growth was 14–20. Chen et al. (2005) found that *C. nozakii* preferred warm, high salinity environments with a suitable surface salinity range being 28–32 with a bottom salinity range of 32–34. According to the above study, the following characters may be recognized: (1) Adults of *C. nozakii* prefer high salinity environments and mainly occur in high-salinity areas; (2) Origin of larvae of *R. esculentum* lies in estuaries with lower salinity and abundant food. *Rhopilema esculentum* inhabits coastal sea waters during its entire life cycle.

Asexual reproduction

Some aspects of asexual reproduction specific to scyphistomae of *C. nozakii* can be compared with those of *R. esculentum*. Scyphistomae of *C. nozakii* could produce podocysts and tendrils and develop new scyphistomae. Tendrils attached to new attachment points near the base of the scyphistoma, and then formed a cyst. Meanwhile, the parent scyphistoma retained the original pedal disk. Scyphistomae of *R. esculentum* only produced one kind of cysts: podocysts (Fig. 3C). When a podocyst formed, parent scyphistomae migrated to new attachment points and left behind the podocysts, which remained on the original substrate sites (Ding & Chen 1981).

Morphological distinction of ephyrae

The main aim of the morphological study of the ephyrae was to offer taxonomic evidence helpful in forecasting jellyfish blooms. Based on the different morphology of the ephyral lappets, 2 groups of ephyrae can be recognized: the first group (such as *R. esculentum*, *Rhopilema asamushi* Uchida and *Nemopilema nomurai*) has ungula-shaped lappets, while the second (such as *C. nozakii*) has almost blunt lappets. There is also another kind of lappet in *Rhopilema hispidum* VanhÖffen, and *Aurelia aurita*, which are sharp-angled, but do not have branched tips. This means that the ephyrae of *N. nomurai* and *R. asamushi*, which often co-occur in Japanese coastal waters, can not be morphologically distinguished based only on the morphology of the lappets. However, we also found that the lobes of *N. nomurai* have 3–4 branched tips while the lobes of *R. asamushi* have 4–6 shorter branched tips. A similar situation occurs

Table 3. Morphological differences between ephyrae of 6 common species of scyphozoans in China.

Morphological character	Lappet	Rhopalar cleft	Nematocyst batteries	Gastric cavity	Sources
<i>Rhopilema esculentum</i>	longer, ungula-shaped, 4 branched tips	<1/2 marginal lobe	8	eight-square	Ding & Chen (1981)
<i>Cyanea nozakii</i>	shorter, blunt-shaped, no branched tips	>1/2 marginal lobe	scattered	rotund	Dong et al. (2006a & b)
<i>Nemopilema nomurai</i>	longer, ungula-shaped, 3–4 branched tips	<1/2 marginal lobe	unconspicuous	rotund	Observed by author
<i>Rhopilema hispidum</i>	longer, sharp-angled, no branched tips	>1/2 marginal lobe	16	rotund	Observed by author
<i>Rhopilema asamushi</i>	ungula-shaped, 4–6 shorter branched tips	<1/2 marginal lobe	unconspicuous	rotund	Observed by author
<i>Aurelia aurita</i>	longer, sharp-angled, no branched tips	>1/2 marginal lobe	scattered	rotund	Observed by author

Table 4. Life cycle comparison of 6 species of scyphozoans.

Species	Fertilization	Planulocyst/Podocyst or new column	Strobilation type	Sources
<i>Cyanea nozakii</i>	external	planulocyst, podocyst, stolon	monodiscous	Dong et al. (2006a & b), present study
<i>Cyanea capillata</i>	internal	planulocyst, podocyst	polydiscous	Widersten (1968), Brewer (1976, 1984, 1989, 1991)
<i>Rhopilema esculentum</i>	external	podocyst	polydiscous	Ding & Chen (1981)
<i>Stomolophus meleagris</i>	—	podocyst	polydiscous	Calder (1982)
<i>Nemopilema nomurai</i>	—	podocyst	polydiscous	Kawahara et al. (2006)
<i>Rhizostoma pulmo</i>	—	podocyst, planuloid, polyp bud, stolon	polydiscous	Paspaleff (1938), Russell (1970)

between *R. esculentum* and *N. nomurai*, which usually co-occur in Chinese coastal waters. According to our observations, the ephyrae of *N. nomurai* and *R. asamushi* can not be differentiated by the number and length of branched tips in the ephyrae (Table 3). *Rhopilema esculentum* and *N. nomurai* differ in the shape of the gastric cavity, and in the arrangement of the nematocyst batteries. In *R. esculentum*, they are aggregated into 8 spots of nematocyst batteries, but they are unconspicuous in *N. nomurai*.

Life cycle comparison

The life cycle of *C. nozakii* was compared with earlier descriptions of the life cycles of *C. capillata* (Widersten 1968, Brewer 1976, 1984, 1989, 1991), *R. esculentum* (Ding & Chen 1981), *Rhizostoma pulmo* Agass (Paspaleff 1938, Russell 1970) and *Stomolophus meleagris* L. Agassiz (Calder 1982). Kawahara et al. (2006) described the life cycle of *N. nomurai*. The comparison is shown in Table 4. According to our observations, because the embryogenesis from a fertilized egg, and cleavage of the zygote to a blastula and planula being in open sea water, the situation in *C. nozakii* is like in *R. esculentum* (Ding & Chen 1981). Planulae of *C. nozakii* could form planulocysts prior to forming

a scyphistoma, *C. nozakii* also could produce podocysts and a stolon, which could also be involved in the formation of new cysts and development of new polyps. Widersten (1965) showed that planulae of *C. capillata* could also form planulocysts prior to forming a scyphistoma, and that scyphistomae could produce podocysts. However, *R. esculentum* (Ding & Chen 1981), *S. meleagris* (Calder 1982), and *N. nomura* (Kawahara et al. 2006) only produced one kind of cysts: podocysts. The numbers of ephyrae released from a strobila varied among species, Dale (1982), Ding & Chen (1981), and Kawahara et al. (2006) found that *S. meleagris*, *R. esculentum* and *N. nomurai* all were polydiscous. Strobilation in semaeostomes such as *C. capillata* and *A. aurita* were usually of the polydisk type (Brewer 1976, 1984, 1989, 1991), but in the semaeostome *C. nozakii* was typically monodiscous.

Key to species of the genus *Cyanea*

Four species of the genus *Cyanea* have been reported from Chinese waters. They are *C. nozakii*, *C. capillata*, *C. ferruginea* Eschscholtz and *C. purpurea* Kishinouye (Hong 2002). These species all share the common characteristics of 8 marginal lobes, 8 rhopalia, strong oral canalis carpi,

Table 5. Characteristics of species of the genus *Cyanea*.

Species	Differentia				
	Tentacular pouches and gastric pouches	Peripheral canals	nematocyst batteries in the centre of exumbrella	Umbrella diameter (mm)	Color of umbrella
<i>Cyanea nozakii</i>	connected by transverse tubes	with numerous anastomoses	present	200–300, max 1200	translucent-whitish, light-brown
<i>Cyanea capillata</i>	separated absolutely	with anastomoses, curved	absent	400, 1000, max 1200	wine-colored, light-yellow
<i>Cyanea ferruginea</i>	separated absolutely	straight, without anastomoses	absent	>400	palm-brown
<i>Cyanea purpurea</i>	separated absolutely	with numerous anastomoses, connected by net-shape	present	>80	purple

and a lot of long tentacles. *Cyanea nozakii* can be distinguished from *C. capillata*, *C. ferruginea* and *C. purpurea* (Table 5) by the characters of tentacular pouches being connected with gastric pouches on the fringe of the umbrella by transverse tubes, and that the peripheral canals have numerous anastomoses.

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