

Note

Effects of Temperature and Salinity on the Asexual Reproduction of *Nemopilema nomurai* (Scyphozoa: Rhizostomeae)

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Abstract – Asexual reproduction of polyps of *Nemopilema nomurai*, of which massive blooms have occurred in Korean waters every summer since 2003, were tested under 20 combinations of temperature (10, 15, 20, and 25°C) and salinity (12, 17, 22, 27, and 32 psu). Production of podocysts increased with increasing temperature (20 and 25°C), while strobilation and ephyra liberation occurred at low temperatures (10 and 15°C). Temperature also affected the initiation of ephyra liberation (approximately 25 days at 15°C, and 50 days at 10 and 20°C, respectively). The number of podocysts was only significantly different between 27 and 32 psu, and salinity had no significant effect on the excystment of podocysts, ephyra liberation, showing *N. nomurai* is euryhaline. These results demonstrated that temperature is an important factor on both the podocysts production and ephyra liberation, possibly explaining early spring liberation of ephyrae and continuous introduction of medusae into Korean coastal waters through summer to fall.

Keywords – asexual reproduction, *Nemopilema nomurai*, polyps, temperature, salinity

1. Introduction

Giant jellyfish *Nemopilema nomurai* medusae have massively occurred over last 10 years in Korean, Japanese and Chinese coastal waters, causing severe damages to the fishery industry and coastal power plant operations as well as stinging swimmers. The frequencies of bloom years have conspicuously increased compared to the past, while the scale and size of such blooms are showing year-to-year variations (Zhang et al. 2012; Kawahara et al. 2013; Wang et al. 2013; Sun et al. 2015). Anthropogenic environmental conditions along the Chinese coast and the

potential seeding and nursery grounds of this species have been put forward as possible reasons for causing the recent blooms (Kawahara et al. 2013; Uye 2008; Dong et al. 2010). However, the exact location of the habitats of polyps of the species is still unknown, while Toyokawa et al. (2012) firstly found only four and one individuals of wild ephyrae in the Yellow Sea and the East China Sea, respectively. Kawahara et al. (2013) showed that extreme conditions such as lower salinity, higher temperature or burial in the mud can induce dormant podocysts to excyst in the laboratory. Nevertheless, the various biological and environmental factors that determine the population size of *N. nomurai* medusa and the resulting blooms have not been clearly explained.

Most scyphozoan jellyfish alternates between a medusa (pelagic and sexual) and a polyp stage (benthic and asexual) during their life cycle. In general, asexual reproduction of benthic polyps has been considered to be the most decisive factor in determining the medusa population size in the following season (Arai 2009). Polyp budding and survival rates as well as the timing of asexual reproduction can differ according to environmental conditions and particular species (Willcox et al. 2007). Several factors such as temperature, light, food availability, predator density, concentration of chemical compounds, bacterial exudates, and the presence of zooxanthellae have been reported as triggers of asexual reproduction in scyphozoan jellyfish (Custance 1964; Spangenberg 1964a, 1964b, 1967, 1968; Loeb 1972; Coyne 1973; Silverstone et al. 1977; Hofmann et al. 1978; Hernroth and Gröndahl 1985; Keen and Gong 1989; Purcell et al. 1999a). Temperature, in general, is one of the most important factors influencing asexual reproduction in

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polyps (Coyne 1973; Kakinuma 1975; Brewer and Feingold 1991; Keen 1991; Purcell 1999a; Ishii and Watanabe 2003; Purcell 2007; Liu et al. 2009). Recently, several studies on the effect of temperature on the asexual reproduction of *N. nomurai* polyps have been conducted (Sun et al. 2014; Feng et al. 2015a, 2015b). In these studies, *N. nomurai* polyps survived at a wide range of temperatures but produced different effects on two types of asexual reproduction (podocyst production and strobilation). The effects of food supply and light intensity have also been reported. Under warm temperature conditions, abundant food supplies increased podocysts' production of polyps (Sun et al. 2014; Feng et al. 2015b), whereas light condition had no effect (Dong et al. 2015). Since the offshore area of the Changjiang River, which can be affected by freshwater, is considered to be a major breeding place (Sun et al. 2015), understanding the effects of salinity on the asexual reproduction of *N. nomurai* polyps is important for characterizing the massive occurrence of this species. Kawahara et al. (2013) and Dong et al. (2015) studied the effect of salinity on podocyst excystment and podocyst production, respectively. Dong et al. (2015) showed that *N. nomurai* polyps have an extensive salinity tolerance of 10–40 psu and podocyst production increased at low to middle levels of salinity rather than at high levels of salinity.

We tested temperature and salinity effects on the survival rate, podocyst formation, podocyst excystment, strobilation frequency and ephyrae liberation during asexual reproduction of *N. nomurai* in the laboratory.

2. Materials and Methods

Nemopilema nomurai eggs were obtained from mature individuals collected at Yeosu (34°33.634'N, 127°53.062'E) in November 2008 and artificially fertilized in the laboratory. Polyps developed from planula larvae were cultured at 18°C and 30 psu in filtered seawater. For the temperature-salinity experiment, five polyps were placed in each polystyrene petri dish (ø 80 mm × 50 mm; 250 ml) in GF/F filtered seawater. The petri dishes were left alone for one week so that polyps could attach themselves safely on the surface inside the petri dishes. Damaged or poorly attached polyps were replaced with fresh polyps before starting the experiment. The calyx diameter of the polyps used in the experiments was approximately 1 mm. Each polyp was fed daily three individuals of newly hatched nauplii of *Artemia* sp. (< 24 hours old, body length approximately 650 µm, weigh: 0.83 µg C). Polyps that were

newly excysted from podocysts were fed a single *Artemia* nauplius whereas those undergoing strobilation were not fed. Feeding for each polyp resumed after the liberation of all ephyrae was finished. The experiment was carried out on the basis of two orthogonal treatments; one involved four temperature levels (10, 15, 20, and 25°C) and the other five salinity levels (12, 17, 22, 27, and 32 psu). Water temperature and salinity were slowly (approximately 1°C d⁻¹, 2 psu d⁻¹) changed by placing the experimental petri dishes in different incubator rooms and adding distilled water. Temperature was controlled using an MTI-201 Multi Thermo Incubator (EYELA, JAPAN) and salinity was checked daily using an YSI30 (YSI Inc., USA). The experiment was conducted under conditions of darkness, while polyps were briefly exposed to light from the microscope and room during feeding, cleaning, and observation for data collection. Living polyps, newly produced podocysts, excysted polyps from podocysts, duration of strobilation, and newly liberated ephyrae were counted daily under a dissecting microscope (ZEISS, Stemi-2000C). The experimental project began on July 17, 2009 and all experiments were run for 70 days.

To analyze the combined effects of temperature and salinity on the asexual reproduction of polyps, a two-way analysis of variance (ANOVA) was used after testing the data for normality and equality of variance. If the overall ANOVA results were significant, a Turkey HSD test was performed to confirm it. All tests were performed with SPSS 12.0 and a $P < 0.05$ level was considered significant.

3. Results

Survival rate

The survival rate attained in all temperature-salinity regimes, except for the 25°C-32 psu regime, was 100% in the first 40 days of the experiment (Fig. 1). At the end of the experiment, no salinity regime at 15°C maintained a survival rate of 100%. The number of liberated ephyrae was the greatest at 15°C, and many polyps died after finishing strobilation and ephyrae liberation.

Podocysts production

During the whole period of the experiment, 25% of all polyps of *Nemopilema nomurai* reproduced podocysts (Fig. 2). Polyps produced podocysts at 12, 17, 22, and 27 psu under 20 or 25°C, and at 32 psu under 15°C, respectively (Fig. 3). No podocysts were produced at 10°C under any salinity

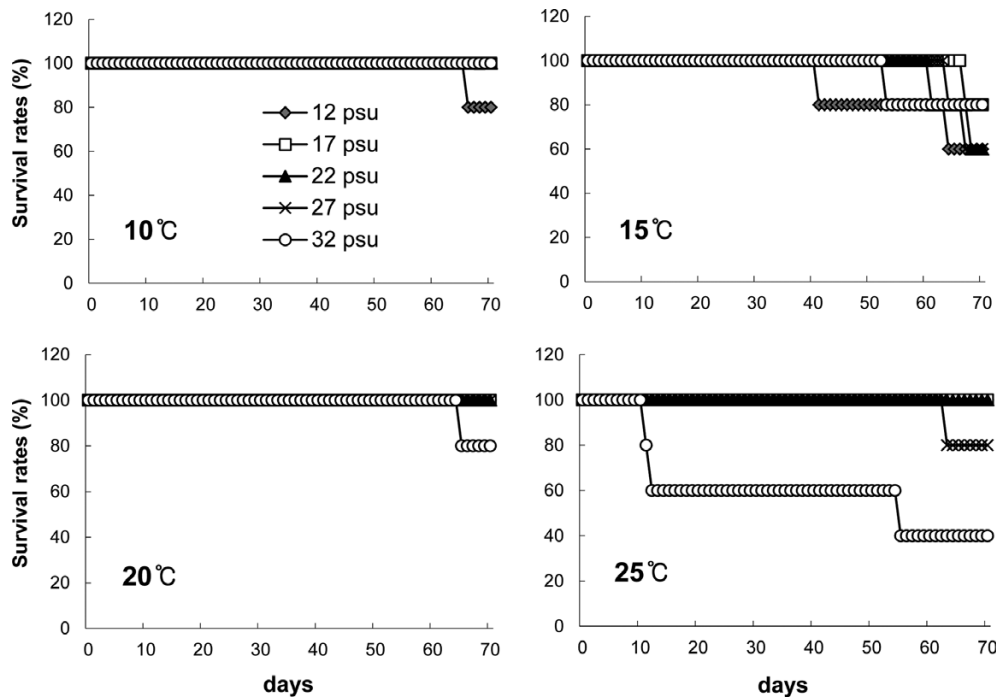


Fig. 1. Survival rates of polyps of *N. nomurai* in combined conditions of 4 temperature and 5 salinity levels during the 70-days experiment



Fig. 2. A colony of podocysts of *N. nomurai*. Scale bars = 1 mm

conditions. Temperature had a significant effect on podocyst production ($F = 11.835$, $df = 3$, $P < 0.001$); more podocysts were produced at higher temperature (20 and 25°C) than at lower temperature (10 and 15°C). Salinity seemed to have less effect on podocyst production compared to temperature; the number of podocysts was only significantly different between 27 and 32 psu regimes ($F = 2.567$, $df = 4$, $P = 0.044$).

Podocysts excystment

Podocysts were excysted in all regimes, except under conditions of 15°C-32 psu and 25°C-17 psu (Fig. 3). Neither

temperature ($F = 0.818$, $df = 1$, $P = 0.371$) nor salinity ($F = 1.995$, $df = 4$, $P = 0.12$) had a significantly different effect on the excystment of podocysts except for those two regimes. Newly produced polyps had an initial calyx diameter of 400 μm approximately and showed four tentacles.

Strobilation

Strobilation rate was higher at lower temperature (10 and 15°C, the highest) than at higher temperature (20 and 25°C) (Table 1). No strobilae were produced at 25°C in any of the salinity regimes. The time necessary for strobilae formation shortened with increasing temperature: 11.2 days, 4.7 days and 3.3 days at 10, 15 and 20°C, respectively. In addition, re-strobilated individuals were observed in the 15°C-17 psu, 15°C-22 psu, 20°C-17 psu regimes.

Ephyrae liberation

More ephyrae were liberated at lower temperature (10 and 15°C) than at higher temperature (20 and 25°C, Fig. 4). Temperature had a significant influence on the number of ephyrae liberated ($F = 49.075$, $df = 3$, $P = 0.001$), whereas the effect of salinity was not significant ($F = 0.538$, $df = 4$, $P = 0.708$). At 15°C, strobilae started to liberate ephyrae 25 days after the experiment began, while production of ephyrae took twice as long (> 50 days) at 10 and 20°C. A maximum

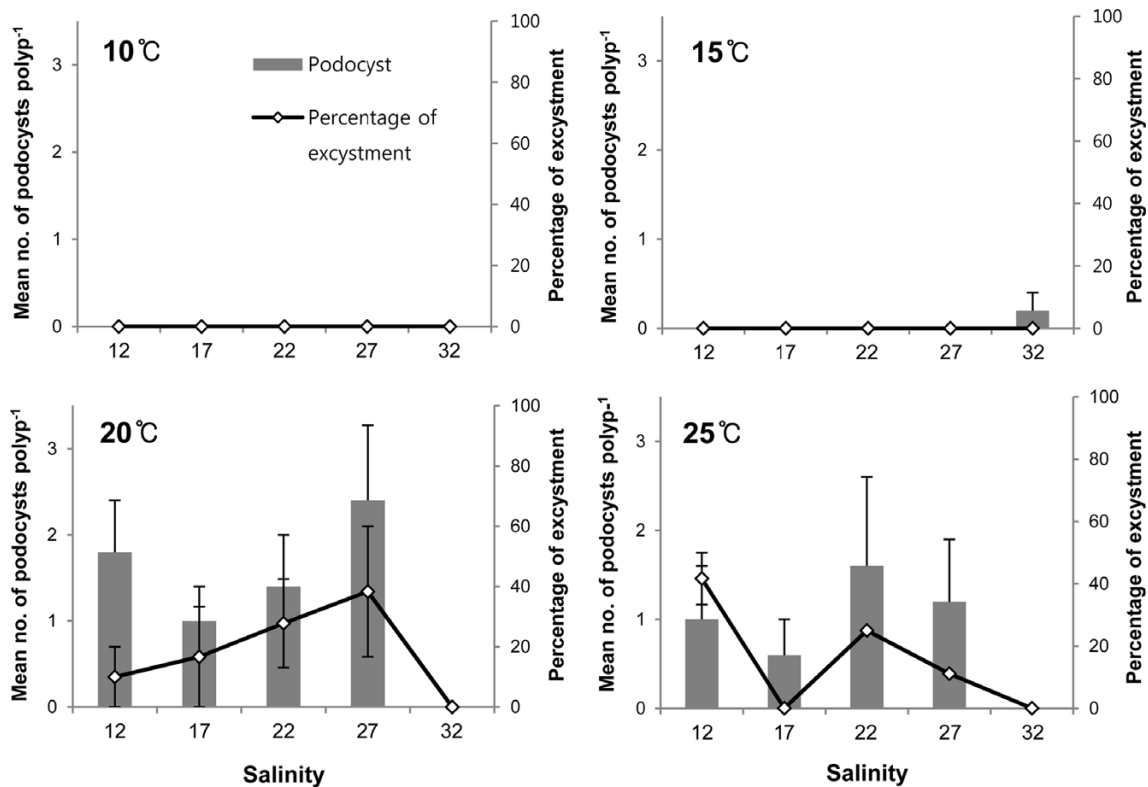


Fig. 3. Mean number of podocysts of *N. nomurai* produced per polyp and percentage of excystment of the species at 20 combined conditions of temperatures and salinities

Table 1. Effects of combined variations of temperature and salinity on strobilation rate of *N. nomurai*

Temperature (°C)	Strobilation rate (%)					Duration of formation of strobilae (days)
	Salinity (psu)					
	12	17	22	27	32	
10	100	100	100	60	-	11.2 (± 3.7)
15	100	100	100	100	60	4.7 (± 2.2)
20	-	40	20	-	20	3.3 (± 0.5)
25	-	-	-	-	-	-

of four ephyrae per strobila was liberated into the water within a few days after the completion of strobilation. Newly liberated ephyrae soon began to swim using lappets and started to consume *Artemia* nauplii.

4. Discussion

We tested the effects of temperature and salinity on the survival rate, podocysts production and excystment, as well as strobilation and ephyrae liberation in *Nemopilema nomurai* polyps. Temperature seems to be an important factor in exerting a strong influence on podocyst production rate in scyphozoans. And optimal temperature for podocyst formation may be

dependent on the species. The podocyst formation of *N. nomurai* occurred significantly at higher temperatures (20 and 25°C) in this study. This result is similar to those results produced by Sun et al. (2014) and Feng et al. (2015a, 2015b). Feng et al. (2015a) that showed that maximum production of podocysts of *N. nomurai* occurred in polyps warmed to 27°C, and Feng et al. (2015b) reported that numbers of podocysts were significantly increased by prolonged exposure in an environment of 18–25°C. These results demonstrate that warm temperatures are beneficial for the production of prodocysts. A similar pattern of maximum production of podocysts at warm temperatures was also observed in *Rhopilema esculentum*: within the range from 15 to 30°C, podocyst production was enhanced as the

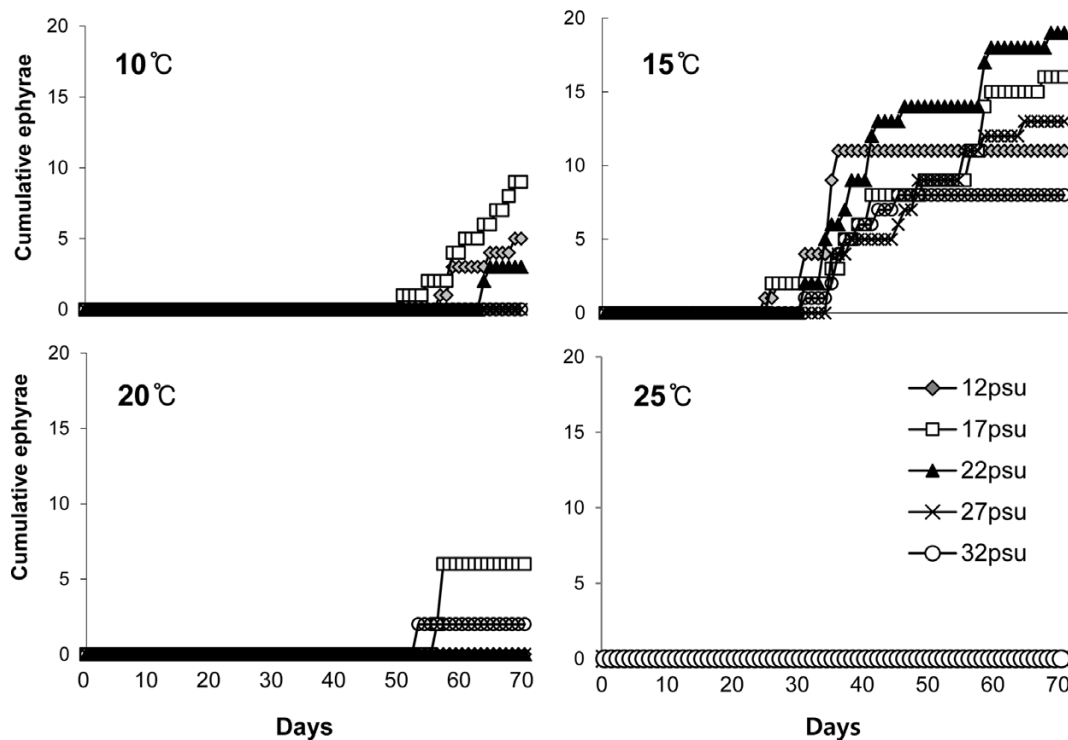


Fig. 4. Cumulative numbers of ephyrae under 20 combined conditions of temperatures and salinities

temperature increased (Lu et al. 1997). Polyps in *Cyanea capillata* and other *Cyanea* sp. also produced podocysts at high temperatures, while their excystment occurred at low temperatures in Chesapeake Bay (Cargo 1974; Brewer and Feingold 1991). According to Feng et al. (2015b), *C. nozakii* polyps also produced many podocysts at warm water temperatures above 18°C. In contrast, podocyst formation increased when the temperature fell below 2 to 4°C in *Chrysaora quinquecirrha* (Cargo and Schultz 1967).

The influence of environmental factors on podocyst excystment may be more difficult to determine. Kawahara et al. (2013) showed that extremely high temperatures (27 and 31°C), or extremely low salinity (8 and 16 psu) induced higher rates of excystment of 1–4 month-old podocyst of *N. nomurai*, suggesting that exposure of podocysts to low salinity, hypoxia or burial in organic-rich mud leads to higher numbers of polyps continuing on to become medusa blooms. Kawahara et al. (2013) also showed that there was no excystment at low temperatures (5–15°C) and little, if any at 19 and 23°C. Even though our experiment produced no data on excystment at lower temperatures (10 and 15°C) and higher salinity (32 psu), since podocysts were almost never produced, 10–38% of the podocysts were excysted in various ranges of salinity (12–27 psu) at 20°C, which was not much different from the

percentage of excystment (7–20%) at 19°C and 8–24 psu in the study by Kawahara et al. (2013). However, our experiment also showed a high percentage (38%) and high rate of excystment at 20°C of 27 psu. Furthermore, 11–42% of excystment at 12, 22 and 27 psu of 25°C was observed, which only partially coincided with the results of Kawahara et al. (2013).

Strobilation occurred more frequently at lower temperatures (10 and 15°C) with the highest rate at 15°C in this experiment. The onset of strobilation occurred in a wide range of temperatures from 10 to 20°C; however, strobilation and the initiation of ephyrae liberation occurred in a shorter period under 15°C under all salinity regimes, starting approximately 30–40 days after the experiment began. The cumulative number of ephyrae was also the greatest at 15°C. These results match well with those of Kawahara et al. (2013). In the East China Sea, the first massive annual occurrence of young medusae was observed in mid-May in 2005–2008 and in 2012–2013 (Yoon et al. 2014). It is assumed that the liberation of ephyrae starts to occur approximately in April. Considering the duration of the strobilation-ephyrae liberation, and the optimal temperature (15°C in this study), ephyrae can be supplied during quite a long period in spring and this might explain the continuous introduction of medusae into Korean coastal waters through summer and autumn (see also Kawahara

et al. 2006).

Several laboratory experiments have also shown that the optimal range of salinity for asexual reproduction in scyphozoans is species-specific. The numbers of polyps increased at high, intermediate and low salinity in *R. esculentum* (Lu et al. 1989), *C. quinquecirrha* (Purcell et al. 1999b), and *Moerisia lyonsi* (Ma and Purcell 2005), respectively. Polyps of *Aurelia* sp. were not affected by salinity (Willcox et al. 2007). The effect of the salinity gradient on the podocyst formation of *N. nomurai* in this experiment is less significant, podocyst production being conducted throughout a somewhat broad range of salinity except for 32 psu under both temperature conditions of 20 and 25°C. Dong et al. (2015) reported that the salinity range of 20–27.5 psu was best for the podocyst reproduction of *N. nomurai*. Considering both results, it seems that *N. nomurai* polyps are not very sensitive to salinity, but, on the other hand, high salinity does appear to promote the asexual reproduction of polyps.

From the results, polyps of *N. nomurai* are euryhaline organisms, mainly reproduced in warm seasons under a wide range of low salinity (12–27 psu), which matches with the environmental conditions of the Changjiang estuary (northwestern East China Sea), an area regarded as one of the potential breeding places (Toyokawa et al. 2012). However, the conditions under which the excystment of podocysts take place are still unclear, since the optimal temperatures for podocyst formation and excystment are both high temperatures; Kawahara et al. (2013) recorded higher rates of excystment at higher temperature at high salinity (33 psu) but our results showed high rates of excystment across a broad range of salinity at both 20 and 25°C, while both the experiments showed maximum frequency of strobilation at temperatures (11°C, 15°C and 15°C, respectively) lower than the optimal temperature for both podocyst formation and excystment. To gain a better understanding of in situ environmental factors in relation to polyp asexual reproduction and its contribution to medusa blooms in the next season, long term and long range experimental conditions are required to be set up to overcome the present shortage of data as well as to locate the habitats of actual polyp populations of this species.

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