DOCTORAL THESIS

A Physio-ecological Study of Ephyrae of the Common Jellyfish *Aurelia aurita* s.l. (Cnidaria: Scyphozoa), with Special Reference to their Survival Capability under Starvation

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Abstract

The moon jellyfish *Aurelia aurita* s.l. is the most common scyphozoan jellyfish in the coastal waters around the world, and the mass occurrences of this species have been reported from various regions. In recent decades, *A. aurita* blooms have become increasingly prominent in East Asian seas, causing serious problems to human sectors such as fisheries and coastal power plant operations. Therefore, it is important to identify causes for the enhancement of *A. aurita* populations to forecast likely outbreaks prior to the season of medusa blooms. In the population dynamics of scyphozoan jellyfish, the following two factors are important to determine the size of adult (medusa) population: (1) the abundance of benthic polyps, which reproduce asexually and undergo seasonal strobilation to release planktonic ephyrae, and (2) the mortality of ephyrae before recruitment to the medusa stage. Although much knowledge has been accumulated about physio-ecology of the polyp stage by previous studies, only few studies have been conducted for the ephyra stage.

The success for survival through larval stage is basically affected by two factors, viz. food availability and predation. For development to the medusa stage, ephyrae must start feeding before their nutritional reserves run out. However, they are functionally inefficient feeders compared to the medusa stage and the liberation of *A. aurita* ephyrae usually takes place during winter and early spring, when the biomass and production of prey zooplankton are the annual lowest. Therefore, starvation is considered to be a primary factor accounting for the mortality of ephyrae. The goal of this study is to understand physio-ecological characteristics of *A. aurita* ephyrae in order to enable forecast of medusa population outbreaks prior to regular medusa bloom season. For this, I conducted laboratory experiments mainly to examine the effect of starvation on various physio-ecological aspects of *A. aurita* ephyrae.

This thesis consists of 5 chapters. In Chapter 1, I extensively reviewed past and current scyphozoan jellyfish blooms in East Asian seas, in particular Chinese waters. Since I am a student from China, I also reviewed jellyfish studies in China, most of which were published in Chinese and hence are not easily accessible for non-Chinese researchers. These reviews can be useful to obtain specific jellyfish research and people's thoughts of jellyfish in China. Anyhow, the East Asian seas are a representative sea area in the world where massive jellyfish blooms recurrently take place. As *A. aurita* is the most prominent bloom forming species in this area, it is of importance not only to identify causes for the blooms but also forecast the blooms.

In Chapter 2, in order to evaluate starvation resistance and recovery capability in first-feeding *A. aurita* ephyrae, I determined the median longevity (ML_{50}), i.e. duration of starvation at which 50% of ephyrae die, and the point-of-no-return (PNR_{50}), i.e. duration of starvation after which 50% of ephyrae die even if they subsequently feed, at 15, 12 and 9°C. The ML_{50} were 50, 70 and 100 d, and the PNR_{50} were 33.8, 38.4 and 58.6 d at 15, 12 and 9°C, respectively. These PNR_{50} are nearly one order of magnitude longer than those of larval marine molluscs, crustaceans and fishes, demonstrating that *A. aurita* ephyrae have strong starvation resistance and recovery capability. By the time of the PNR_{50}, ephyrae showed significant body size reduction: ca. 30 and 50% decrease in disc diameter and carbon content, respectively.

In Chapter 3, I investigated the effect of starvation on respiration rate of *A. aurita* ephyrae, because their extremely long PNR_{50} was thought to be attributed to their low metabolic rates. The respiration rate of a newly released ephyra was actually very low, i.e. 0.24, 0.24 and 0.19 μl O_2 ephyra^{-1} d^{-1} at 15, 12 and 9°C, respectively. The respiration rate tended to decrease with the increase of starvation period, but statistical analysis did not detect the effect of starvation because of wide variation of respiration rate data. The carbon weight-specific respiration rates were constant for up to the period nearly PNR_{50}, indicating that the kinetics for basic metabolism is stable so far as metabolic substrate is available. The minimum food requirement based on the respiration rate was equivalent to 2.0, 2.0 and 1.6% of ephyra carbon weight at 15, 12 and 9°C, respectively. I also examined the effect of starvation on pulsation rate, since swimming ability is closely associated with feeding and escaping capabilities. The pulsation rate was accelerated by starvation for up to 20 d, indicating that moderately starved ephyrae actively swim so that they can capture more prey than newly released

ephyrae. The maximum swimming speed achieved by *A. aurita* ephyrae was 8.9 cm min^{-1}, suggesting that their main prey are confined to slow moving zooplankton such as barnacle nauplii, veliger larvae and hydromedusae. The pulsation rate decreased for ephyrae after 30 d of starvation, and hence the heavily starved ephyrae may be exposed to higher predation loss.

In Chapter 4, I examined whether a scyphozoan jellyfish *Chrysaora pacifica* acts as predators of *A. aurita* ephyrae, since extraordinarily long starvation resistance and strong recovery capability of *A. aurita* ephyrae implied that predation loss may probably be more important to determine their mortality in the field. I confirmed that *C. pacifica* young medusae could feed on *A. aurita* ephyrae. Based on the clearance rate determined for a *C. pacifica* young medusa (i.e. ca. 1.2 l $\mathrm{predator}^{-1}$ d^{-1}), the clearance of a medusa of 5 cm disc diameter was estimated to be ca. 150 l $\mathrm{predator}^{-1}$ d^{-1}, which may be significant to influence the mortality of *A. aurita* ephyrae.

In the last chapter (Chapter 5), I fully discussed the physio-ecological specificity of *A. aurita* ephyrae, in particular emphasis to adaptation mechanisms for starvation. In the Inland Sea of Japan, for example, the release of ephyrae is programmed to occur during winter and early spring (i.e. January-March), when the zooplankton biomass and production rates are at its annual lowest. Thus, it is very likely that newly released ephyrae are exposed to severe nutritional stress in this cold season of minimal food abundance. Extremely long PNR_{50} of *A. aurita* ephyrae may be a physiological as well as ecological adaptation allowing them to survive the first few months after release. In the Inland Sea of Japan, the mortality of ephyrae seems to be very high like in Tokyo Bay, where 99% of ephyrae die before young medusa stage, but actual causes for the mortality could not be identified in this study. Meanwhile, a sympatric scyphozoan *C. pacifica* can be one of prominent predators of *A. aurita* ephyrae. In order to make the forecast of *A. aurita* medusa population outbreaks in a reliable manner, detailed population dynamics studies particularly during the ephyra stage as well as more studies on predators are needed in the future.

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Chapter 1. General Introduction

1-1. Jellyfish blooms in East Asian seas, in particular Chinese waters

1-1-1. Mini-review of jellyfish studies in China, in particular edible jellyfish

Cnidarian jellyfish biodiversity and geographical distribution in Chinese waters

'Natural History' published during the Tsin Dynasty (265-420) may be the oldest record of jellyfish in China (Wu 1955). In this book, a philosopher Zhang Hua (232-300) described the use of jellyfish, perhaps *Rhopilema esculentum* Kishinouye, as food. Preliminary studies on jellyfish in China started nearly a thousand years ago, i.e. during the Song Dynasty (960-1279), a poet Shen Yuqiu (1086-1137) vividly described the morphology and some ecological characteristics of the edible jellyfish, perhaps *R. esculentum*, as well as symbiotic relationship with fish and shrimps in his poem, which reflected high level of ecological studies on jellyfish at that time (Gao et al. 2002).

In modern China, taxonomic and morphological studies of cnidarian jellyfish were extensively conducted mainly by Zheng et al. (1991), Gao et al. (2002), Hong & Lin (2010) and Dong et al. (2010). To my knowledge, at least 167 species of cnidarian jellyfish have so far been reported in various Chinese seas. I attempted to re-organize them according to the taxonomic system proposed by Daly et al. (2007), and made an inventory as shown in Table 1-1. There are 3 species in the class of Cubozoa, 122 species in Hydrozoa, 35 species in Scyphozoa and 7 species in Staruozoa. Although a rhizostome jellyfish *Stomolophus meleagris* L. Agassiz was mistakenly referred to in previous literatures published in China, and this species name was recently replaced with *Nemopilema nomurai* Kishinouye (Zhang et al. 2009, Dong et al. 2010, Liu et al. 2011). Table 1-1 also shows that the species diversity is lowest in the Bohai Sea, followed in order by the Yellow Sea, East China Sea and South China Sea, demonstrating that the jellyfish diversity becomes higher from temperate inshore area to subtropical offshore area.

These diversified jellyfish species may play their own ecological roles in the ecosystem of Chinese seas, primarily as carnivorous zooplankton, or tertiary producers, which feed on secondary producer such as herbivorous copepods, which further feed on primary producers such as diatoms and dinoflagellates. However, very few studies have been conducted in China on jellyfish ecological studies, in particular trophodynamic studies. However, as Chinese people have long appreciated jellyfish as traditional food, studies of the edible jellyfish, i.e. *R. esculentum*, have been extensively conducted. Research on the life cycle of this species was initiated in the 1970s and achieved in great success in 1980s. It is the paper by Ding & Chen (1981) that the morphological and ecological aspects of *R. esculentum* from fertilized eggs to ephyra stage were described for the first time. The elucidation of the life cycle of this species has greatly stimulated subsequent jellyfish industry such as artificial breeding and stock enhancement in China. In the last 10 years, the focus of jellyfish ecological research in China has shifted to inedible scyphozoan species, such as *Aurelia aurita* Linnaeus s.l., *Cyanea nozakii* Kishinouye and *N. nomurai* due to their frequent blooms (see below). Moreover, a 5-year (2010-2014) national research program is currently conducted in order to specify causes for jellyfish blooms and to develop countermeasures to alleviate the damage (Sun et al. 2011).

Historical aspects of jellyfish as commodity for Chinese people

China is the first country to process jellyfish for human consumption in the world, since Chinese people have been eating jellyfish since the third century at the latest (Morikawa 1984). According to Wu (1955), the literature ‘Natural History’ published during the Tsin Dynasty (265-420), in which a Chinese philosopher Zhang Hua (232-300) described the use of jellyfish as food, is the oldest record of eating jellyfish in China. Since then, jellyfish have become a popular menu of Chinese cuisine and it is rarely absent in celebratory Chinese banquet events (Hsieh et al. 2001, Omori & Nakano 2001). There are various methods for preparing jellyfish, cooked or uncooked, but the most common way is to eat them as a salad mixed with shredded vegetables, oil and venigar (Hsieh et al. 2001).

Medicinal values of jellyfish have also been recognized for a long time in China, (Omori 1981, Hsieh & Rudloe 1994). The famous medical expert Li Shenzhen (1518-1593) detailed the medicinal efficacy of jellyfish in his book 'Compendium of Materia Medica', the most comprehensive and top level research book in the history of traditional Chinese medicine (Gao et al. 2002). In this book, he described that jellyfish is alleged to remedy fatigue and exhaustion, stimulate blood flow during the menstrual cycle of women, ease any type of swelling, and cure children's urticarial and erysipelas, as well as burns (Hong 2002). In the book of 'Supplement to Compendium of Materia Medica' (Chen Zangqi 741), it was also recorded that jellyfish can detoxify the poisoning of puffer fish (Gao et al. 2002, Hong 2002). According to Hong (2002), there were also many researches about the medicinal values of jellyfish in modern China. For instance, jellyfish is believed to be effective in hypertension, chronic tracheitis, asthma, heat-phlegm cough, ulcers, goiter and cervical lymph node swelling. In addition, in Chinese folk remedies, it is told that the soup of bells of jellyfish with kelp and seaweed has an inhibiting effect from proliferation of cancer cells, and pickled bells of jellyfish with sugar cure sudden bleeding or continuation of lochia for women who have just given birth. Moreover, applying processed jellyfish bell on the infected skin are thought to be effective to cure carbuncles and erysipelas.

Even today, a considerable numbers of papers have been published in Chinese journals or magazines on the subject of medicinal functions of jellyfish. Being rich in collagen, jellyfish has potential applications in health protection, which may have potential to the usage of jellyfish in pharmaceutical, cosmetic and food industry. In addition, polypeptides and toxins extracted from jellyfish may also have potential of wide applications (Hsieh et al. 2001, You et al. 2007).

Studies of edible jellyfish

In China, there are at least 5 edible jellyfish species, e.g. *R. esculentum*, *Rhopilema hispidum* Vanhoffen, *N. nomurai* (formerly calls as *S. meleagris*, see above), *Lobonema smithi* Mayer and *Lobonemoides gracilis* Light, all belonging to the order of Rhizostomeae (Hong 2002, Hong & Zhang 1982). Among them, *R. esculentum* is the most abundant and popular species, and also has the highest commercial value (Dong et al. 2009). This species is widely distributed in coastal waters along entire China (Dong et al. 2010, Dong et al. 2014). The body size of adult medusae is normally 25-60 cm in bell diameter, the largest individuals being >100 cm. The body color is variable: red, white, pale blue or yellow in the Bohai Sea and Yellow Sea, and reddish brown in the East China Sea (Jiang et al. 2007, Dong et al. 2014). The population of *R. esculentum* in China is considered to be made up by several local subpopulations, which have different reproduction habits and migration patterns (Jiang et al. 2007, Dong et al. 2014).

Although *R. esculentum* is harvested commercially almost whole areas along Chinese coast, the major fishing grounds are Liaodong Bay in Liaoning Provence, Lvsi area in Jiangsu Provence, Zhoushan area in Zhejiang Provence and Mindong area in Fujian Provence, where the water depths are shallower than 30 m (Table 1-2). Medusae of *R. esculentum* are usually caught by multiple drift nets, each of which has a dimension of 30-50 m in length and 8-12 m in height, like gill nets for fish. The number of nets equipped by a boat, being different depends on the power of boat engine, is generally 10-30. When fishing, the nets are casted perpendicularly to the flow direction. Medusae are also harvested individually by scoop nets from boats.

The historical change in annual harvest of *R. esculentum* in China from 1955 to 2013 is shown in Fig. 1-1. The annual catch fluctuated between 36,440 and 581,930 tons wet weight from 1955 to 1984, prior to the initiation of stock enhancement. In the 1980s, due to rapid economic development and large profits of jellyfish fishery, the number of fishing boats remarkably increased in Chinese coastal waters (see the case in Liaodong Bay in Fig. 1-2). By increased fishing pressure on jellyfish stock, jellyfish fishery was gradually waning. Due to overexploitation, a sharp decline in the catch of natural *R. esculentum* populations emerged after 1975 (Fig. 1-1, Huang et al. 1985, Liu et al. 1992, Dong et al. 2014).

In order to meet the increasing demand for the edible jellyfish, intensive research on the reproduction, culture and stock enhancement of *R. esculentum* was undertaken during the 1980s and 1990s (Dong et al. 2009). In Liaodong Bay, preliminary as well as experimental stock enhancements were conducted 11 times between 1984 and 2004 (Dong et al. 2009), and artificially raised juvenile medusae ranging from 0.2 to 17.3 million individuals were released in each case (Dong et al. 2013). Since the 1990s, the stock enhancement has also been conducted in Shandong, Hebei and Zhejiang Provinces, resulting into a significant increase in the annual catch (Fig. 1-1).

In 2005, a much larger-scale stock enhancement was conducted in Liaodong Bay, and a similar scale project continued for 6 years until 2010. During this period, total of 1,648 million of juveniles (bell diameter: >1 cm) were released in Liaodong Bay, and total of 25.24 million medusae were recaptured, with the value of 334 million Yuan (Table 1-3) (Dong et al. 2013). The overall mean recapture rate was 1.77% and the ratio of the input (cost for culturing juvenile jellyfish) to the output (value of the sales) was about 1:18, demonstrating that the stock enhancement project of *R. esculentum* is economically profitable (Table 1-4). Actually, *R. esculentum* is the most important fishing resource in 5 coastal cities of Liaoning Provence, and the revenue earned from the jellyfish fishery accounts for about half of the annual income for fishermen (Dong et al. 2013).

Due to establishment of the artificial breeding technique in addition to high commercial price, aquaculture of *R. esculentum* has become thriving in recent years. Many earthen ponds, which were previously used for shrimp and/or fish aquaculture, have recently been converted to jellyfish aquaculture, and the pond-cultured medusae have acquired higher reputation than wild-caught ones (You et al. 2007). In Liaoning Province alone, there were at least 8000 hectares of earthen ponds being used for jellyfish aquaculture in 2003, yielding approximately several hundreds kg wet weight per hectare (Guan et al. 2004).

The harvested medusae are cut into two parts, i.e. umbrella and oral arms, because of different market prices, the latter being more expensive than the former, removed attached slime with water, and processed generally three times with solutions of mixture of soda, salt and alum in different ratios. However, the processing procedures are often confidential, and specific treatments vary from place to place (You et al. 2007). The products are sold in not only Chinese market but also international market, particularly Japanese market. The processed jellyfish can be preserved for up to one year at room temperatures, and for >2 years if they are kept at cool temperatures (Hsieh et al. 2001). In coastal areas, fresh jellyfish as a salad with seasonings and dressings without prior soda-salt-alum treatment have become a popular menu recently. As jellyfish markets are always undersupply to meet the demand in China, artificial jellyfish meat, which is made from sodium alginate, are sold on the markets (You et al. 2007).

1-1-2. Problematic jellyfish blooms in East Asian seas, in particular Chinese waters

The edible jellyfish *R. esculentum* is a representative jellyfish species, which provides benefits to human being. There are, however, jellyfish species, which bloom massively and cause negative impact to various human activities. In East Asian seas, *A. aurita* s.l., *C. nozakii*, *Chrysaora pacifica* (Goette) and *N. nomurai* are typical scyphozoan jellyfish species causing problematic blooms. Recently, Condon et al. (2013) have analyzed the long-term fluctuations in jellyfish biomass on a global scale, and found that the variations seem to be cyclic rather than a monotonous increase. They have also found the geographical variations in long-term trends of jellyfish increase/decrease, and the East Asian seas are one of representative regions where recent increase in jellyfish biomass is prominent, as was also reported by Brotz et al. (2012) based on historical analysis of jellyfish biomass at the scale of Large Marine Ecosystem. Below, I will summarize the recent and current problematic blooms in the East Asian seas by species.

Aurelia aurita s.l.

The moon jellyfish of the genus *Aurelia* Linnaeus are the most common scyphozoans with a worldwide distribution in coastal and neritic waters between 70° N and 40° S (Mills 2001, Dawson & Martin 2001, Lucas 2001), and in East Asian coastal waters, *A. aurita* s.l. (see below for taxonomic status) is the most common and abundant scyphozoan species. Blooms or population outbreaks of this species have always caused serious problems to human sectors, such as fisheries and coastal power plant operations (Sato 1967, Kuwabara et al. 1969, Uye & Ueta 2004). In Japanese waters, the first problematic bloom of *A. aurita* was reported in Tokyo Bay, where aggregated medusae clogged screens of power plant seawater intakes as to result into blackout of Tokyo metropolitan area in the 1960s, when the bay was heavily eutrophicated by increased industrial and sewage discharge (Sato 1967, Kuwabara et al. 1969, Matsueda 1969). Since then, *A. aurita* became one of the most dominant zooplankton components in Tokyo Bay (Omori et al. 1995, Toyokawa et al. 2000). In the Inland Sea of Japan, *A. aurita* population significantly increased since the 1980s, based on the results of an extensive poll of fishermen questioning the time of jellyfish increases and associated nuisance to fisheries (Uye & Ueta 2004). Concomitantly, it was in the summer of 2000, when a remarkable bloom, which had never been reported, occurred in waters along approximately 100 km of the coastline in Uwa Sea, western Shikoku, with estimated biomass of ca. 9×10^4 tons wet weight (Uye et al. 2003). The bloom of this species has become also prominent in Ise Bay, middle part of Japan (Aoki et al. 2012), and the population increase of this species may have occurred in major Japanese bays and inlets judging from recent increase in mass-media articles on this matter.

In Korean waters, the first shut down of a nuclear power plant caused by large aggregations of *A. aurita* medusae occurred in 1996 (Han & Uye 2010). Since then, coastal power plant shut downs due to aggregated *A. aurita* medusae have become more frequent and serious, and at the same time the nuisance to fisheries has also become increasingly significant (Lee et al. 2006, Han & Uye 2010). In addition, extensive seasonal blooms of *A. aurita* have now become common in eutrophicated bays and inlets, such as Masan Bay, Jinhae Bay, Saemangeum and Sihwa Lake (Han & Uye 2010, Han et al. 2012).

In Taiwan, surveys have only been conducted in Tapong Bay, southern Taiwan, where *A. aurita* population has markedly increased; the annual maximum abundance increased from <1 medusa m^{-3} in 1999 to 14.5 medusae m^{-3} in 2002 (Lo & Chen 2008). Before January 2003, the oysters and fish were extensively cultured in Tapong Bay, and *A. aurita* kept abundant during sampling between April 1999 and May 2002. However, after removal of oyster culture rafts, which might work as substrates for polyps, *A. aurita* disappeared (Purcell et al. 2007).

Few reports are available in regard to *A. aurita* blooms in China. The geographical distribution of this species is confined mainly to shallow coastal waters of the Bohai Sea and Yellow Seas, i.e. Liaoning, Shandong and Hebei Provinces (Dong et al. 2010, Dong et al. 2014). It seems that blooms of *A. aurita* have become more prominent in recent decades as to cause negative impacts on local fisheries and coastal power plant operations in these areas. In severe cases, aggregated medusae caused temporal shutdowns of the power plants (Dong et al. 2010, Dong et al. 2014). For example, during the period from June to September in 2007, large-scale bloom of *A. aurita* occurred in coastal waters along Yantai City and Weihai City, Shandong Province, where such large-scale blooms rarely occurred before (Su & Wang 2007, Zheng et al. 2010). In July 2008, over 4000 tons wet weight of clogged *A. aurita* medusae were removed from the intake screens of a coastal power plant in Qinhuangdao City, Shandong Province (Dong et al. 2010). In August 2008, 20-50 tons of *A. aurita* medusae were cleaned up from the clogged intake screens of a power plant in Weihai City (Dong et al. 2010). On July 7 and 8, 2009, over 10 tons of medusae clogged the intake screens of a power plant in Qingdao City, Shandong Province (Dong et al. 2010).

Little has been studied on the seasonal population dynamics of *A. aurita* in Chinese waters. In northern Chinese waters, ephyrae of this species usually occur in middle or late spring, and they become mature in summer and die in late autumn. For example, in Jiaozhou Bay, Shandong Province, ephyrae occurred at mean densities between 0.1 and 2.9 ephyrae m^{-3} from April to June, and adult medusae occurred at a mean density of 1.3 medusae m^{-3} in July (Wan & Zhang 2012, Dong et al. 2014). The highest density of *A. aurita* encountered was 123 medusae m^{-3} in August 2011 by visual observation (Wang et al. 2012, Dong et al. 2014).

Cyanea spp.

In Japan, *C. nozakii* is one of scyphozoan species to occur abundantly during summer in the Inland Sea of Japan (Kinoshita et al. 2000, Uye & Ueta 2004) and Ariake Sea, western Kyushu (my personal observation). They are nuisance to fisheries because they clog very badly fishing nets with sticky slime and spoil fish inside the nets with strong venomous nematocysts (Uye & Ueta 2004).

In Chinese waters, four species of the genus *Cyanea* Peron et Lesueur have been reported, i.e. *C. nozakii, C. capillata* Linnaeus*, C. ferruginea* Eschscholtz and *C. purpurea* Kishinouye (Gao et al. 2002, Dong et al. 2005). Among these, *C. nozakii* is the most common and widely distributed along Chinese coastal waters (Dong et al. 2005). The populations of *Cyanea* spp. have obviously increased since the end of the 20th century, as hitherto unobserved large-scale and prolonged blooms have become prominent in the Bohai, Yellow and East China Seas (Peng & Zhang 1999, Dong et al. 2006). Zhong et al. (2004) speculated that *C. nozakii* is a warm-temperature and high-salinity species, because it often occurred abundantly when water temperatures were high, i.e. between 23 and 26.8°C.

Blooms caused by *Cyanea* spp. are thought be deleterious to fishing activities, since they grow much larger body size than *A. aurita* and carry numerous and long tentacles with venomous nematocysts which can kill relatively large prey organisms such as juvenile fish, shrimps, crabs and mollusks (Peng & Zhang 1999, Zhong et al. 2004). Hong (2002) reported that a *Cyanea* medusa could consume more than a thousand fish larvae per day. It is interesting to note that *Cyanea* spp. also ate other jellyfish species such as *A. aurita* and *R. esculentum* (Hansson 1997a, Kinoshita et al.

2000, Ge & He 2004, see also below). Due to their voracious predation capability, their growth rate is also very rapid as they could grow from just a droplet size in May to ca. 1 m in bell diameter by the end of September (Peng & Zhang 1999, Zhong et al. 2004).

In 1997-1999, when *Cyanea* spp. bloomed in the southern Yellow Sea, catch of *R. esculentum* was greatly reduced in the major fishing grounds such as Lvsi, Dasha and Changjiang River estuary (Peng & Zhang 1999). In Changjiang River estuary, *R. esculentum* was gradually replaced with *Cyanea* spp. in summer and fall in these years, and they accounted for 85% of the total medusa numbers fished in November 2003 (Xian et al. 2005). Moreover, *Cyanea* spp. outbreaks occurred in Liaodong Bay in 2004, which were considered to be the main reason for 80% reduction of *R. esculentum* catch (Ge & He 2004). Causes for the prominent *Cyanea* spp. blooms in Chinese waters are still an open question, but overfishing, eutrophication and increase of temperature and salinities were suggested as potential factors (Zhong et al. 2004, Xian et al. 2005). Dong et al. (2010) argued that recent prominent blooms of *A. aurita* in addition to *R. esculentum* stock enhancement project may enhance the food supply, so that *Cyanea* could take advantage of these.

Chrysaora pacifica

Chysaora pacifica is a common scyphozoan species, appearing as medusae in spring and early summer in the Inland Sea of Japan (Uye & Ueta 2004, Ueda 2007). This species often co-occurs with *A. aurita* medusae and causes serious nuisance in fisheries. The outbreaks of this species often ruin fishing nets, spoil fish inside the nets and severely sting fishermen by its sticky and highly toxic tentacles. In addition, they are strong predators and food competitors of larval fish, shrimps and crabs (Uye & Ueta 2004, Ueda 2007).

In Chinese waters, another species of the genus *Chrysaora*, *C. helvola* Brandt has been recorded in East China Sea and South China Sea (Gao et al. 2002, Hong & Lin 2010, Dong et al. 2010). However, no bloom information has been reported. In

Korean waters, no information of this genus has been available.

Nemopilema nomorai

Nemopilema nomurai is one of the largest jellyfish in the world, attaining a bell diameter to ca. 2 m and a body weight to >200 kg wet weight (Kishinouye 1922, Omori & Kitamura 2004). In Japanese waters, the mass occurrence of *N. nomurai* used to occur very infrequently, once per ca. 40 years, i.e. in 1922 (Kishinouye 1922), 1958 (Shimomura 1959) and 1995 (Yasuda 2004, Kawahara et al. 2006, Uye 2008). However, from the turn of this century the population outbreaks occurred very frequently; out of 11 years between 2002 and 2013, 7 years were blooming years (i.e. 2002, 03, 04, 05, 06, 07 and 09) (Uye 2011, Kawahara et al. 2013). Massive aggregation of *N. nomuraii* caused severe damage in local fisheries by breaking fishing nets, decreasing fish catch and stinging fishermen (Uye 2008). For example, in 2005 there were more than 100,000 complaints from fishermen and monetary loss was estimated to be 30 billion Japanese Yen (Uye 2011). In 2009, *N. nomurai* capsized a trawl boat on which there were three fishermen, who were fortunately rescued.

In China, *N. nomurai* was referred to as *S meleagris* in all Chinese literatures before 2007 (see above), and this species has been regarded as an edible jellyfish species although the product is inferior to *R. esculentum* (Hong & Zhang 1982, Hong 2002, Gao et al. 2002). Medusae of *N. nomurai* are mainly distributed in the southern Yellow Sea and northern East China Sea (Hong et al. 1985, Gao et al. 2002, Ding & Cheng 2007) and the medusa population is transported north by prevailing current in summer and autumn (Li et al. 2007). The largest *N. nomurai* individual reported in Chinese waters is 135 cm in bell diameter (Zhang et al. 2012).

The population dynamics of *N. nomurai* has been studied in the East China Sea (Li et al. 2009) and Liaodong Bay (Dong et al. 2013). In the East China Sea, the average bell diameter was 27 cm in mid-June 2008, and grew rapidly in July and August to reach to the annual maximum size (104 cm). Thereafter, the body started to shrink; the average bell diameter was 76 cm in early September and 51 cm in late-September (Li et al. 2009). In Liaodong Bay, the medusa body size seems to be smaller in corresponding periods compared to that in the East China Sea. In 2008-2011, *N. nomurai* started to appear in the plankton in early-June, when average bell diameter was 3.5-6.5 cm. Their average diameter was 9.4-13.8 cm in late-June, 17-25 cm in early-July, 25-32 cm in late-July, and 35-40 cm in mid-August. Then, sexual reproduction started and simultaneously somatic growth ceased (Dong et al. 2013).

Massive blooms of *N. nomurai* were reported in the Yellow Sea and northern East China Sea in 2003 and 2006 (Cheng et al. 2004, Ding & Cheng 2007, Zhang et al. 2012) and in 2005 and 2007 in Liaodong Bay (Dong et al. 2010). Although the biomass of *N. nomraii* has rarely been reported in China, Ding & Cheng (2007) reported the average biomass was 7,144, 2,292 and 608 kg per haul of trawl net in September 2003, 2004 and 2005, respectively. Zhang et al. (2012) reported that the average biomass was 17,604 kg km^{-2} which represented 86.1%, on average, of the total jellyfish catch in the southern Yellow Sea in August and September 2006.

Although no detailed surveys to monitor long-term occurrence of *N. nomurai* have been conducted, recent studies suggested the increase of population size in the Yellow and East China Seas during the last two decades. Cheng et al. (2004) reported that the annual fish catch declined by 64% in the Yellow Sea and northern East China Sea, while the annual catch of large jellyfish, i.e. *N. nomurai* and *Cyanea* spp., increased 3.5 times during the period from 2000 to 2003. Yan et al. (2004) analyzed the relationships between jellyfish stock size and fish catch based on surveys conducted in the southern Yellow Sea and northern East China Sea during the period from 1990 to 2003, and found a significant increase of jellyfish biomass in the 2000s than in the early 1990s, but fish resources significantly decreased.

Causes for the recent recurrent *N. nomurai* blooms in Chinese water are still puzzling, although anthropogenic impacts to the coastal environment and ecosystem associated with boosting Chinese economy may be important. To identify causes for the blooms, it is important to investigate benthic polyps *in situ*. Locations of polyp habitat have not been detected yet, although 5 ephyrae of *N. nomurai* have been found in Chinese waters by recent studies, one specimen in the northwestern East China Sea and four specimens in the Yellow Sea (Toyokawa et al. 2012). Dong et al. (2012) described the life cycle and morphological characteristics of *N. nomurai* based on laboratory-reared specimens, and *in situ* survey on benthic life stage of this species remain to be conducted.

1-2. Taxonomic status of the genus *Aureli*a and formally called *Aurelia aurita*

In East Asian waters, under a common name of the moon jellyfish belonging to the genus *Aurelia* Linnaeus, two species have been recognized, viz. *A. aurita* Linnaeus and *A. labiata* Linnaeus, the former being distributed mainly in temperate to sub-tropical regions and the latter in temperate to sub-boreal regions (Schroth et al. 2002). It has been widely recognized that cnidarian medusae like *Aurelia* lack in stable morphological characteristics because of gelatinous body form, and even a single species shows wide morphological variations depending on geographical locations and rearing conditions (e.g. wild versus aquarium specimens). Hence, the taxonomy of the genus *Aurelia* has been conducted by Dawson (2003), Dawson & Jacobs (2001), Dawson & Martin (2001) and Ki et al. (2008), using molecular techniques, which distinguish genotypes. They collected specimens from many parts of the world, and found that there are at least 10 cryptic species (i.e. *Aurelia* sp. 1~10) in addition to hitherto established species, viz. *A. aurita* Linneus s.s., *A. labiata* and *A. limbata* Brandt. The species of *A. aurita* s.s. is distributed only in the Atlantic Ocean, mainly in European coastal waters. Hence, the species we have formerly referred to *A. aurita* is no longer *A. aurita* s.s. Dawson (2003) and Ki et al. (2008) examined the genotypes for specimens from Japan, Korea, California in the USA and Australia, and found that they all are highly identical (99.6 similarity) as to designate them temporarily as *Aurelia* sp. 1. Until this *Aurelia* sp.1 has been established officially as a new species, I remain referring to *A. aurita* s.l. and use it (often just *A. aurita*) in my thesis throughout.

1-3. Seasonal life cycle of *Aurelia aurita* in East Asian waters

Like most scyphozoans, the genus *Aurelia* has a bipartite life cycle consisting of a benthic asexually-reproducing polyp stage and a planktonic sexually-reproducing medusa stage, as schematically depicted in Fig. 1-3. Mature female and male medusae produce eggs and sperms, respectively, which get fertilized to form zygotes (i.e. fertilized eggs). The zygotes develop into planula larvae on the oral arms of female medusae, and leave the medusae to swim out into the water to find substrate in often overhanging position to attach. Then, settled planulae metamorphose into polyps. Mature polyps reproduce asexually by means of budding, fission and podocyst formation, among which the budding being the most common, to increase themselves to develop colonies. Polyps metamorphose into strobilae by specialized transverse fission to produce ephyrae, each of which swims off one by one to develop into mature medusa. Thereby, the life cycle is performed. The planktonic stage lasts usually for less than a year, but the benthic stage lasts for multi-years.

In East Asian waters, like in other temperate waters, the life cycle proceeds on a seasonal basis as summarized as follows (Omori et al. 1995, Watanabe & Ishii 2001, Lo & Chen 2008, Toyokawa et al. 2000, 2011，Han & Uye 2010). Strobilation takes place usually during the coldest seasons, i.e. in winter and early spring. Newly released ephyrae grow very slowly until the water temperature significantly warms up in mid-spring, when they start rapid growth in exponential manner until they sexual mature in summer. After spawning, they shrink themselves gradually and die off usually in autumn. The bell diameter of fully-grown adult medusae is normally 20-30 cm, and the largest individuals exceed 40 cm (M. Omori, personal comm.). The longevity of medusae usually ranges from 4 to 8 months. However, medusae can overwinter in some locations such as Urazoko Bay (Yasuda 1971), Tokyo Bay (Omori et al. 1995) and the Inland Sea of Japan (Uye & Ueta 2004), where the maximum longevity may apparently be longer than a year.

1-4. Brief overview of previous studies on physio-ecology of *Aurelia* ephyrae

Ephyra is the youngest planktonic life stage of scyphomedusae, showing basically a disc-like form characterized by 8 marginal lobes with disc diameter of 2-5 mm (Kakinuma 1975, Holst 2012a). The morphological characteristics of *Aurelia* ephyrae are described by Straehler-Pohl & Jarms (2010), Straehler-Pohl et al. (2011) and Holst (2012a). As shown in Fig. 1-4, newly released *A. aurita* ephyrae have 8 marginal lobes, each with a pair of lancet-like lappets and rhopalium. The body diameter represented by a distance from rhopalium to rhopalium is ca. 2 mm. Rhopalar clefts are U-shaped and about half of depth as the ocular clefts separating the marginal lobes. The manubrium is cruciform and four lips are often present at mouth. The gastric pouch is primitive, not being separated by wall, and 1-2 gastric filaments are present in each quadrant. Newly released ephyrae do not have typical nematocyst cluster patterns and marginal tentacle buds.

The feeding ecology of *Aurelta* ephyrae has been conducted by Sullivan et al. (1997) and Båmstedt et al. (2001). Sullivan et al. (1997) investigated prey capture behavior in detail, and demonstrated that relatively large prey with slow escape velocities such as hydromedusae are the favorable prey for ephyrae. Båmstedt et al. (2001) studied growth of newly released *A. aurita* ephyrae fed five different food types, and found that the difference of food type was highly significant in their growth. Low growth rates (4-9% d^{-1}) were attained when they were fed with large-sized copepod *Calanus finmarchicus* Gunnerus copepodites. When fed with the cryptophyte *Rhodomonas baltica* Karsten, the ephyrae showed the growth rates of 7-11% d^{-1}. Suspended POM sustained the growth rates of 7-9% d^{-1}, whereas fresh bivalve meat, manually placed at the mouth of ephyrae, resulted to the highest growth rates of 12-14% d^{-1}.

Dietary information for *A. aurita* ephyrae is not extensive, but the analysis of gastric contents from various previous studies revealed that variety of prey types such as phytoplankton, tintinnids, rotifers, nauplii of copepods and barnacles, copepodites and adult copepods, and hydromedusae were ingested (Olesen 1995, Sullivan et al. 1997, Båmstedt et al. 2001, Ishii et al. 2004). Moreover, Skikne et al. (2009) reported that *A. labiata* ephyrae were capable of utilizing dissolved organic matter to support their survival, when they were kept under no or insufficient food supply conditions.

Information on digestion time of *A. aurita* ephyrae is also very few, but the previous study by Martinussen & Båmstedt (1999) is the most comprehensive one. The digestion time was found to decrease with increasing food concentration and size of ephyrae and to increase with increasing size and number of prey, although there was large variability depending on prey type; mean digestion time being 0.85, 2.38 and 3.26 h for *Artemia* nauplii, copepods and herring larvae, respectively (Martinussen & Båmstedt 1999, 2001).

The growth, pulsation and respiration rates of *Aurelia* ephyrae have been reported to be affected primarily by temperature. Båmstedt et al. (1999) examined the growth rates at different temperatures; the rate at 18^{o}C was 5.4 times higher than that at 6^{o}C. Widmer (2005) studied the growth rates of newly released *A. labiata* ephyrae at 10 different temperatures from 8 to 28^{o}C; the rate significantly increased with increasing temperature up to 21^{o}C, and then gradually reduced as the temperature further increased to 28^{o}C. Dillon (1977) showed that the pulsation rates of *A. aurita* ephyrae; the rate was significantly higher at 20^{o}C than at 10^{o}C, but reduced gradually at 25 and 35^{o}C. A similar result was also reported for *A. aurita* ephyrae; the pulsation rate increased significantly with increasing temperature from 11 to 25^{o}C but reduced at temperatures above 25^{o}C (Mangum et al. 1972). The respiration rates of *A. aurita* ephyrae were studied in only two previous studies (Kinoshita et al. 1997, Møller & Riisgård 2007a). The respiration rate was reported to be 0.62 and 0.74 µl O_2 ephyra^{-1} d^{-1} at 10 and 15^{o}C, respectively by Kinoshita et al. (1997). It was 0.42 µl O_2 ephyra^{-1} d^{-1} at 15^{o}C by Møller & Riisgård (2007a). These results indicate that environmental conditions, particularly temperature, can influence the physiological activities of ephyrae of the genus *Aurelia*.

1-5. Importance to examine the survival of ephyrae in *Aurelia aurita* population dynamics and objectives of this study

The survivorship of larvae is one of the most important factors determining recruitment into adult populations and subsequent adult population size of marine organisms, since larvae are generally most vulnerable and hence regarded to be critical life stage. The success for survival through early larval stages is basically affected by two factors, viz. food availability and predation (Blaxter & Hempel 1963, Bailey & Houde 1989, Paschke et al. 2004, Giménez & Anger 2005). Newly hatched larvae must start feeding to gain exogeneous energy to grow until endogeneous energy, which is often stored in yolk substance, runs out to avoid complete starvation. However, in natural conditions, food supply is usually insufficient and predators are always dwelling. Under such conditions, only a very small portion of larvae can survive and recruit into adult stage. Hence, studies to investigate the survival/mortality of larvae have been one of the central studied in fish resource dynamics (Blaxter & Hempel 1963, Houde 1974, Yúfera et al. 1993, Dou et al. 2002, 2005, Shan et al. 2008, 2009).

Unlike fish larvae, which hatch out usually from eggs, scyphomedusa ephyrae do not hatch out from eggs, but are released from strobilae. However, like fish larvae, they are the youngest planktonic stage to recruit into adult (i.e. medusa) population. They are small in size, having limited swimming ability, and their feeding organ, i.e. manubrium, is primitive, implying very vulnerable stage. Hence, the mortality during this stage can greatly affect the abundance of adult medusae (Lucas 2001). Compared to polyp stage and medusa stage, ephyra stage has been much understudied (see Arai 1997). Like other marine animal larvae, ephyrae must start feeding before their nutritional reserves derived from parent polyps run out. In addition, the liberation of *A. aurita* ephyrae usually takes place during winter and early spring, when the biomass and production of prey zooplankton are the annual lowest. These facts make the first-feeding ephyrae to be the life stage most susceptible to food scarcity.

So far, no studies have been conducted to investigate the survival of natural *A. aurita* ephyra population, except for a study by Ishii et al. (2004) in Tokyo Bay. Ishii et al. (2004) reported that the survivorship from newly released ephyrae to young medusae was only about 1%, which means that about 99% of the newly released ephyrae died during the ephyra stage. This result implied that the high mortality pattern of ephyrae followed general patterns observed in fish population recruitment. However, nothing has been known about mechanisms to cause such a high mortality. It is of great importance to reveal the mechanisms controlling the survival of ephyrae, which is a basic parameter to enable forecast of medusa bloom intensity prior to medusa season.

In the light of current jellyfish population increase particularly in East Asian waters, my ultimate research goal is to develop methodologies to forecast *A. aurita* medusa bloom intensity. To achieve this, it is foundamentally necessary to clarify the physio-ecological properties of *A. aurita* ephyrae. Hence, in my thesis study, I conducted laboratory experiments to examine the effect of starvation on their survival, respiration and pulsation rates, and to investigate their capability to recover from starvation damage and their mortality by a possible predator, *Chrysaora pacifica*, another scyphozoan jellyfish, which co-occurs in many Japanese coastal waters.

1-6. Concept of point-of-no-return

The hypothesis that starvation during the larval stage of fishes is an important regulator of recruitment to the adult population has a long and illustrious history. Hjort (1914) appears to have been the first to formally propose a causal link between feeding, larval survival and recruitment. He considered that the time when fish larvae transition from endogenous (yolk sac) to exogenous feeding is the most vulnerable period in the life cycle of fish and suggested that food supply might be a major source of recruitment variation either directly (through starvation) or indirectly (through prolonged development resulting in increased exposure to other sources of mortality such as predation). He proposed that when food is limiting during this transition, a high proportion of the larval population would die from starvation. In contrast, when food is abundant at this time, survival would be high. Hjort (1914) also proposed that variation in the intensity of starvation druing this transition to exogenous feeding could explain the enourmous fluctuations in year-class strength obsevered in Norweigian herring and cod. As knowledge of larval fish biology increased rapidly in the 1960s and 1970s, Hjort's idea gained widespread recognition and acceptance.

The concept of 'point-of-no-return or PNR' was for the first time defined for herring larvae by Blaxter & Hempel (1963). According to Blaxter & Hempel (1963), this is a threshold point during progressive starvation when 50% of starved larvae are still alive but unable to feed even if food become available, and the survivors cannot successfully complete the ontogenetic development afterwards. Fish ecologists also termed it 'irreversible starvation' or 'ecological death'. Being a critical point of larval survival, the PNR has been regarded as an important parameter in the larval stage and has been studied in many fishes, crustaceans and molluscans. However, no research on the PNR has been reported in jellyfish.

In this study, I applied the concept of PNR to *A. aurita* ephyrae to examine their starvation resistance and recovery capability. Determination of their PNR and its relationships to physical, chemical and biological environmental conditions during ephyra release season may help estimate the survivability (or mortality) of ephyrae, which would contribute to a better understanding of factors controlling their recruitment to the medusa population.

Chapter 2. Survival capability of *Aurelia aurita* s.l. ephyrae under starvation

2-1. Effect of temperature on the strobilation: a preliminary study to point-of-no-return experiment

Introduction

As described in Chapter 1, the life cycle of *A. aurita* is consisted of alternation between sexual medusoid and asexual polypoid stages. The production of new planktonic stage called "ephyrae" is achieved by means of metamorphosis called "strobilation" of benthic polyps. During this process, the stalk of polyps is segmented transversely by constrictions, which become deeper to form disks, each of which develops into an ephyra. This process contributes to the propagation of medusa population, because a single *A. aurita* polyp is capable of producing up to 20-30 ephyrae (Berrill 1949).

Previous studied have demonstrated that the induction of strobilation in *A. aurita* polyps is frequently attributed to or correlated with changes in several environmental factors, including temperature, light and food (Custance 1964, Spangenberg 1964a, b, 1968, Coyne 1973, Keen & Gong 1989, Purcell 2007, Liu et al. 2009), in addition to biochemical compositions, particularly iodine containing thyroxin (Silverstone et al. 1977). Among these, temperature has decisive effects on strobilation, since the main strobilation season is coincided with the period of annual lowest temperature (Omori et al. 1995, Toyokawa et al. 2000, Ishii et al. 2004). However, the response to temperature differs depending on geographical locations; for example for *A. aurita* in subtropical Taiwan, seasonally warm temperatures (i.e. 19-32°C) accelerate the strobilation (Liu et al. 2009), which is different from the response of *A. aurita* in temperate regions. For instance, Han & Uye (2010) examined the effects of temperature and food supply on asexual reproduction rate of *A. aurita* polyps originally from Honjo Area, a part of brackish-water Lake Nakaumi located between Shimane and Tottori prefectures, and found that temperatures below 14°C induced strobilation. Therefore, as a preliminary study prior to the experiment to investigate the survival capability of *A. aurita* ephyrae under starved conditions, I conducted a laboratory experiment to examine the effect of temperature on the strobilation of *A. aurita*.

Objective of this study has two-folds. The first objective is to examine temperature effect on the induction of strobilation in order to compare with results of previous studies. The second objective is to establish technical know-how in induction of strobilation of these polyps in order to provide sufficient numbers of ephyrae as experimental specimens for various experiments.

Materials and Methods

Planulae of *A. aurita* were obtained from the oral arms of matured medusae in Hakata Bay, northern Kyushu, in summer of 2010. They were placed in plastic containers (diameter: 15 cm, depth: 6.5 cm) containing ca. 1 l of filtered (0.2 μm) seawater of salinity 32 at 25^{o}C in darkness to allow them to settle on the wall of containers. After transformation to polyps, they were fed *ad libitum* with newly hatched *Artemia* sp. nauplli once or twice weekly, followed by replacement of the seawater. These polyps were maintained as stock cultures.

Total of some 100 fully developed, 16-tentacled polyps of a similar body size on the wall of the stock-culture containers were gently removed by a dissecting needle and they were individually transferred into small plastic dishes (diameter: 3.5 cm, depth: 1 cm), which were then placed in larger plastic containers (diameter: 15 cm, depth: 6.5 cm) containing ca. 1 l of filtered (0.2 μm) seawater of salinity ca. 32. One week later, when most of the polyps had attached to the bottom of the dishes, three lots each consisting of 6 or 7 polyps were transferred directly from 25^{o}C to each of 5 different temperatures (i.e. 9, 12, 14, 16 and 18^{o}C). Hence, each temperature treatment consisted of three large plastic containers, each containing 6 or 7 polyps and 0.5-l filtered seawater. The polyps were monitored daily for 90 days. During the experiment, the polyps were kept starved to eliminate the effect of food supply, and the seawater was replaced with freshly prepared one at 20-d intervals.

Statistical test to analyze among means at respective temperatures was carried out with one-way ANOVA (SPSS 13.0 software), and when the ANOVA results were significant, Tukey's pair-wise comparison was used to ascertain significant differences between the treatment means.

Results

Morphological changes during the strobilation

A general feature of morphological changes during the strobilation is like follows. A transversal constriction appeared first on the stalk of polyps, and then the number of constrictions increased during a few days. The polyps started to resorb their tentacles and almost at the same time the whole polyp body turned gradually to reddish. After the tentacles were completely resorbed, the formation of lappet muscle started. The constrictions of polyp stalk became deeper as to form multi-layered discs, which extended gradually 8 marginal lappets. When each disc was transformed to near-ephyra form, it began pulsation. Then, a developed ephyra detached one by one from the posterior part of strobilae. The basal part of strobilae regenerated into a small but well-proportioned polyp.

Strobilation timing, duration and rario

No polyps died during the experiment. As shown in Fig. 2-1, the onset of strobilation, which was defined by starting of transversal segmentation of the polyp stalk, occurred first for a polyp 17 days (Day 17) after transferred to 14^{o}C, where the strobilated polyps gradually increased to 8 individuals on Day 40. No further strobilation took place by the end of experiment. At 12^{o}C, the first strobilation occurred on Day 31, followed a rapid and prominent increase of strobilation up to Day 42. A total of 13 polyps completed strobilation at this temperature. At 9^{o}C, the strobilation occurred for the first time on Day 41, and increased to 13 individuals on Day 70. At 16^{o}C, the first strobilation took place on Day 39, and total of 5 polyps completed strobilation. At 18°C, only a single polyp strobilated on Day 83. All polyps strobilated only once during 90 days of experiment.

The mean durations (± SD) needed for the start of strobilation (or pre-strobilation periods) were 51.0±1.7, 38.6±6.5, 31.1±7.9, 49.7±6.1 and 83 d at 9, 12, 14, 16 and 18°C, respectively (Fig. 2-2). Because of insufficient data at 16 and 18°C, statistical analysis was possible only for the data at remaining temperatures, where there were significant differences with temperature (one-way ANOVA, $P < 0.05$), and the pre-strobilation period was significantly shorter at 14°C than at 9°C (Tukey's pair-wise comparison, $P < 0.05$).

The durations from the onset of transverse constriction to the completion of liberation of the last ephyra were defined as strobilation period. The mean strobilation periods (± SD) were 22.7±2.9, 10.9±1.2, 9.2±1.0, 5.3±1.8 and 5 d at 9, 12, 14, 16 and 18°C, respectively (Fig. 2-2), demonstrating significant differences with temperature (one-way ANOVA, $P < 0.01$). The strobilation periods were significantly shorter at 12 and 14°C than at 9°C (Tukey's pair-wise comparison, $P < 0.01$).

Of total of 20 polyps used at each experimental temperature, 13, 13, 8, 5 and 1 polyps performed strobilation at 9, 12, 14, 16 and 18°C, respectively (Fig. 2-1), which corresponded to 64.3, 65.1, 39.7, 26.2 and 4.8% at respective temperatures (Fig. 2-3). The mean strobilation ratios were significantly different with temperature (one-way ANOVA, $P < 0.05$), and the ratio at 18°C was significantly lower than that at 9 and 12°C (Tukey's pair-wise comparison, $P < 0.05$).

Ephyrae production

The time series pattern of cumulative numbers of ephyrae produced (Fig. 2-4) was similar to the pattern of strobilation incidence (Fig. 2-1). The maximum ephyrae produced was 36 at 9°C, and a similar production was also achieved at14°C. The numbers were followed in order at 12, 16 and 18°C (Fig. 2-4). The mean numbers of ephyrae produced per strobila were 2.8±0.4, 2.3±0.3, 4.1±0.1, 2.1±0.6 and 4 at 9, 12, 14, 16 and 18°C, respectively (Fig. 2-5), showing significant differences with temperature (one-way ANOVA, $P < 0.01$). The mean ephyrae production at 14°C was significantly higher than that at other temperatures (Tukey's pair-wise comparison, $P < 0.01$).

Discussion

The effect of lowering temperature on the induction of strobilation of *A. aurita* demonstrated in this experiment was essentially the same as previous results. Kroiher et al. (2000) reported that the reduction of temperature could cause strobilation in *A. aurita* polyps from North Sea Luc, France, and a recent study by Holst (2012b) also showed that in *A. aurita* from Helgoland, Germany, significantly higher percentages of polyps strobilated after they were exposed to temperatures below10°C than those kept constantly at 15°C. In Japanese *A. aurita*, the main period of strobilation occurs also following a seasonal temperature decrease. Kakinuma (1975) reported that in *A. aurita* polyps from Mutsu Bay, northern Japan, the strobilation occurred when temperature fell below 18°C. Han & Uye (2010) reported that *A. aurita* polyps from Honjo area, southwestern Japan, ceased feeding and subsequently strobilated when transferred to temperature below 14°C. In the strain used in this study (from Hakata Bay), strobilation occurred in the temperature range between 9 and 18°C. Although the strobilation at 18°C was much tardy compare to lower temperatures, this is the upper critical temperature to induce strobilation in *A. aurita* polyps from Hakata Bay.

This study confirmed that temperature did affect the timing of strobilation. The strobilation occurred earliest at 14°C, and at either 12 or 16°C the onset of strobilation delayed by about 1-3 weeks. Result of this study is different from previous studies. In southern Taiwan, the strobilation of *A. aurita* took place faster at higher temperatures in a temperature range between 20 and 30°C (Liu et al. 2009). A similar finding was also reported for the sibling species, i.e. *A. labiata* in Washington, northeast Pacific, where the strobilation occurred faster at warmer temperatures in the temperature range between 7 and 20°C (Purcell 2007). In contrast, Kroiher et al. (2000) reported that greater the reduction in temperature, the earlier the onset of strobilation of *A.*

aurita polyps. Han & Uye (2010) also reported that *A. aurita* polyps strobilated more quickly at 10°C than those at 14°C. I assume that the different response to temperature reduction between this study and the study by Han & Uye (2010) is attributed to different physiological conditions of polyps, which have adapted to environmental conditions of respective habitats.

To eliminate the effect of food supply, the polyps were kept starved after they were transferred to lowered temperatures. Hence, the strobilation occurred only once for all polyps during the 90-day experiment, and fewer numbers of ephyrae were produced per polyp (i.e. 2-4). If they were fed, they might have strobilated multiple times and produced more numbers of ephyrae, as had been observed for well-fed *A. aurita* polyps (Thiel 1962, Spangenberg 1968) as well as *A. labiata* polyps (Purcell 2007).

Taking the effects of temperature on 3 biological parameters influencing ephyra production rate (i.e. pre-strobilation period, strobilation ratio and numbers of ephyrae produced per polyp), an exposure to temperatures between 12 and 14°C is the most efficient method to obtain sufficient numbers of ephyrae in a shortest time interval. Therefore, strobilation in all following experiments was induced by exposure stock-cultured polyps to temperatures of 12-14°C. Moreover, in order to prepare sufficient number of ephyrae, excess *Artemia* sp. nauplii were offered at least twice per week before the initiation of segmentation of polyps.

Summary

In order to investigate the effect of temperature on the induction of strobilation of *A. aurita* polyps, 20 polyps, which had been kept at 25°C, were transferred to 5 lowered temperatures (i.e. 9, 12, 14, 16 and 18°C) under darkness without food supply, and monitored for 90 days. The time for the onset of strobilation (or pre-strobilation period) was significantly affected by temperature, and the mean pre-strobilation period was shortest at 12 and 14°C. The strobilation ratio was also affected by temperature, being highest (ca. 65%) at 9 and 12°C. The duration for strobilation (or strobilation period) tended to be shorter at warmer temperatures. The mean number of ephyrae produced per polyp tended to be similar at all temperatures, but it was highest at 14°C. These results showed that for the induction of strobilation of *A. aurita* polyps the exposure to temperatures below 18°C was required. In order to obtain numerous *A. aurita* ephyrae as experimental specimens, ca. 14°C was judged to be the most suitable temperature for artificial induction of strobilation.

2-2. Body size reduction, longevity and point-of-no-return in ephyrae

Introduction

In the light of recurrent jellyfish blooms and associated negative impact to human sectors as well as to marine ecosystem health, it is important to identify causes for the blooms, forecast outbreaks prior to blooms, and develop countermeasures. Size of medusa populations are affected essentially by two biological factors: (1) the abundance of benthic polyps, which reproduce asexually and undergo seasonal strobilation to release planktonic ephyrae, and (2) the mortality of ephyrae before recruitment to the medusa stage. Much knowledge has been accumulated about physio-ecology of polyps in previous studies: among various environmental factors, increase in temperature (i.e. global warming), food supply (i.e. eutrophication) and/or artificial structures with overhanging surfaces accelerates the polyp asexual reproduction rate, thus boosting the polyp populations (Coyne 1973, Keen & Gong 1989, Watanabe & Ishii 2001, Wilcox et al. 2007, Han & Uye 2010, Lucas et al. 2012, Duarte et al. 2013). In contrast, no studies have been conducted in regard to the mortality of ephyrae, except for a preliminary study by Ishii et al. (2004) of *A. aurita* in Tokyo Bay, where approximately 99% of the newly released ephyrae die before they become young medusae. However, the causes for such high mortality remained largely unidentified.

In marine invertebrates and fishes, the chance for survival through the early larval stages is mainly affected by food availability and predation (Bailey & Houde 1989, Paschke et al. 2004), at least when physico-chemical conditions in the environment are favorable. Newly hatched larvae, in general, contain energy reserves derived from egg yolk, and they must start feeding within a limited time to avoid starvation. The length of this critical period for larval development can be defined by the 'point-of-no-return' (PNR), the duration of starvation to a stage at which larvae die, even if they then obtain food. The first estimation of time to PNR was conducted in herring (*Clupea harengus*) larvae by Blaxter & Hempel (1963). Since then, this index has been studied in many marine animals, in order to evaluate their starvation resistance and to understand the factors affecting recruitment to their post-larval stages.

Unlike the majority of marine animals, ephyrae of scyphozoan jellyfish are not derived from eggs, but from the strobilation of their parental polyps. However, like other marine animal larvae, in order to develop to an advanced stage they must start feeding before their nutritional reserves derived from the parent polyps run out. In general, ephyrae are inefficient feeders compared to medusae, because they lack similar bell structure and generate only a small vortex of feeding current (Costello & Colin 1994, Sullivan et al. 1997), and their narrow tube-like manubrium is less effective than a medusa's four-branched oral arms. In addition, the release of ephyrae from strobilating *A. aurita* polyps usually takes place during winter and early spring (Toyokawa et al. 2000, Lucas et al. 2012, see also Chapter 2-1), when the biomass and production of their food (i.e. micro- and mesozooplankton) are the lowest. Therefore, I hypothesized that starvation is a primary factor accounting for the mortality of ephyrae. To assess this working hypothesis, I conducted laboratory experiments to examine the effect of starvation on their survival and capability to recover from starvation and then develop to advanced stages.

Materials and Methods

Starvation experiment

The stock-cultured *A. aurita* polyps maintained at ca. 25^{o}C were transferred to 14^{o}C to induce strobilation and release of ephyrae (see Chapter 2-1). Newly released ephyrae (<24 h old) were placed individually in wells of 6-well polystyrene culture plates containing 10 ml of the filtered seawater, salinity 32. Totals of 250, 220 and 260 ephyrae were kept in darkness at 9, 12 and 15^{o}C, respectively, in thermostatically controlled incubators. Seawater in the wells was replaced every second day. The selection of 3 different temperatures (i.e. 9, 12 and 15^{o}C) was attributed to *in situ* seasonal temperature range, at which *A. aurita* ephyrae might experience.

Ten randomly selected ephyrae from each temperature were taken every 2 d, placed individually, manubrium side up in a small glass container and photographed with a digital camera attached to a stereomicroscope. After being photographed, they were returned to their original wells or transferred to new plates for feeding (see below). The morphometry of the ephyrae was examined by measuring 5 dimensions to the nearest 0.01-0.02 mm following Straehler-Pohl & Jarms (2010): total body diameter (TBD), disc diameter (DD), central disc diameter (CDD), marginal lappet length (MLL), and rhopalial lappet length (RLL) (Fig. 2-6), using image-analysis software (Image J, National Institute of Health, USA).

Feeding was initiated for groups of 10 starved ephyrae, at 2 to 4 d intervals for up to 84 d, by introducing 20 newly hatched *Artemia* nauplii to their wells daily. After the ephyrae fed for ca. 6 h, the remaining nauplii were removed and the seawater was replaced. Fed ephyrae were monitored daily until they died off or grew to the advanced ephyrae stage, at which the adradial canal between the perradial canal and the interradial canal extends to the central disc margin (Fig. 2-7). Ephyrae showing no pulsation after several stirrings of the seawater with a pipette were judged to be dead.

The median longevity (ML_{50}) was determined as the duration of starvation at which 50% of ephyrae had died. The point-of-no-return (PNR_{50}) was determined as the duration of starvation at which only 50% of ephyrae could recover from starvation and grow to the advanced ephyra stage.

Measurements of carbon and nitrogen contents

Nine lots, each consisting of approximately 600 ephyrae newly released from the stock-culture polyps, were transferred to a glass container containing 5 l of filtered seawater, salinity 32. Three containers were held at each of 9, 12 and 15°C, respectively, in darkness. The seawater was gently circulated by aeration (15 ml min^{-1}) from a glass pipette to keep the ephyrae suspended. The seawater was replaced weekly.

At 10-d intervals, triplicate samples, each consisting of 20 to 110 ephyrae, were randomly picked up from each container, and at least 5 ephyrae from each sample were photographed under a stereomicroscope to measure DD. These specimens were placed onto a pre-combusted and pre-weighed GF/F glass-fiber filter (diameter: 25 mm), and rinsed with 3% isotonic ammonium formate to remove external salts. The filter was then placed in a plastic case and dried in an electric oven (Tabai, LG-112) at 60°C for 24 h, followed by placement in a desiccator for 3-5 mon until analysis. Dry weight was determined on a microbalance (Mettler Toledo, Type MT 5) to the nearest 0.1 µg, and carbon and nitrogen contents were analyzed with an Elemental Analyzer (PerkinElmer, 02400II CHNS).

To compare the mean values among different experiments, one-way or two-way ANOVA were used (SPSS 10.0 software). When the ANOVA results were significant ($P<0.05$), Tukey's pair-wise comparisons were performed to ascertain the significance of differences between treatment means.

Results

Morphological changes during starvation

A series of morphological changes in ephyrae kept starved at each of 9, 12 and 15°C are depicted in Fig. 2-7. Newly released ephyrae from strobilating polyps were reddish in body color. As starvation advanced this reddish color gradually faded, and at the same time the body diameter decreased accompanied by thinning and reduction of the marginal lappets. As starvation was further prolonged, the marginal lappets almost disappeared and pulsations became less frequent. Finally, starved ephyrae became reduced to a rod-like oral core.

The morphological changes were slower at lower temperatures as demonstrated by the decrease in DD (Fig. 2-8). Mean DD was 2.3±0.04 (SD) mm on Day 0 (D0), with no significant differences among the temperature groups (one-way ANOVA, $P > 0.05$). Mean DD on D50 were 1.18±0.06, 1.58±0.19 and 1.66±0.20 mm at 15, 12 and 9°C, respectively, and were significantly different among the groups (one-way ANOVA, $P<0.01$). By fitting a linear regression, the overall decrease rate was greatest (0.021

mm day^{-1}) at 15°C, intermediate (0.019 mm day^{-1}) at 12°C, and lowest (0.012 mm day^{-1}) at 9°C. However, there were only small changes in body proportions, such as RLL/MLL and CDD/TBD (Fig. 2-7), at least during the initial halves of all starvation experiments (Fig. 2-9). At 12°C, for example, both RLL/MLL and CDD/TBD were constant until D50-60, after which RLL/MLL decreased and CDD/TBD increased, both significantly (Tukey's test, $P<0.05$). At 9°C, both RLL/TMLL and CDD/TBD were constant until D76, thereafter CDD/TBD increased significantly (Tukey's test, $P<0.05$). RLL/TMLL tended to decrease after D76, however, Tukey's test did only show significant difference between D12-16 and Day 84 ($P<0.05$). On the days of PNR_{50} (33.8, 38.4 and 58.6 d at 15, 12 and 9°C, respectively, see below), the mean DD were 1.36±0.06, 1.69±0.10 and 1.65±0.27 mm, respectively, ca. 30% reduction compared to mean DD at release newly.

Survivorship and median longevity

Ephyrae did not die at all until D44, D62 and D92 at 15, 12 and 9°C, respectively, and thereafter they died off rapidly (Fig. 2-10). At 15°C, the ML_{50} was recorded on D50, the final day of the starvation experiment due to death of all the experimental ephyrae. The ML_{50} estimates were 70 and 100 d and the maximum longevities were 80 and 118 d at 12 and 9°C, respectively. The relationship between ML_{50} (d) and temperature (T, °C) was expressed by: $ML_{50} = 282e^{-0.116T}$ (Fig. 2-12).

Point-of-no-return

Ephyrae fed without prior starvation could swim actively to capture and ingest 5-8 *Artemia* nauplii per day, and they grew to the advanced ephyra stage (mean DD: 4.0±0.11 mm) in averages of 5.0, 4.2 and 6.0 d at 15, 12 and 9°C, respectively (Fig. 2-13), with significant differences among the groups (one-way ANOVA, $P<0.05$). On the other hand, with increasing duration of starvation, ephyrae gradually lost their swimming capability, and they could capture fewer *Artemia* nauplii.

At 15°C, all ephyrae, which had been starved for ≤28 d, could successfully develop to the advanced ephyra stage. When the starvation ran ≥30 d, the success declined sharply until D40, when no recovery was possible. By fitting a linear regression, the PNR_{50} was determined to be 33.8 d (Fig. 2-11). At 12°C, nearly 100% of ephyrae that had been starved for up to D36 successfully developed to the advanced ephyra stage. No recovery was possible when starvation was ≥48 d. The PNR_{50} was estimated to be 38.4 d (Fig. 2-11). At 9°C, recovery success was nearly 100% for the ephyrae up to D48, and the PNR_{50} was 58.6 d (Fig. 2-11). The relationship between the PNR_{50} (d) and temperature (T, °C) was expressed by $PNR_{50} = 127e^{-0.092T}$ (Fig. 2-12).

The duration needed to reach the advanced ephyra stage after feeding began (DR, d) increased exponentially with increasing initial starvation duration (D, d) as expressed by $DR=4.80e^{0.040D}$, $DR=6.85e^{0.021D}$ and $DR=7.69e^{0.017D}$ at 15, 12 and 9°C, respectively (Fig. 2-13).

Decrease in carbon and nitrogen weight during starvation

The mode of shrinkage in DD of starved ephyrae kept collectively in filtered seawater was essentially the same as for those kept individually in well plates (Figs. 2-7, 2-8). Mean carbon and nitrogen weights of newly released ephyrae were 6.6±0.23 and 1.5±0.05 μg, respectively, without significant differences among the groups (one-way ANOVA, $P>0.05$), and their carbon contents (C, μg) decreased exponentially with starvation duration (D, d), as expressed by $C = 6.7e^{-0.026D}$, $C = 6.4e^{-0.019D}$ and $C = 6.8e^{-0.017D}$ at 15, 12 and 9°C, respectively (Fig. 2-14A). As for nitrogen (N, μg) decreased esimilarlly with starvation duration (D, d), as $N = 1.4e^{-0.021D}$, $N = 1.6e^{-0.018D}$ and $N = 1.6e^{-0.016D}$ at 15, 12 and 9°C, respectively (Fig. 2-14B). Relative carbon and nitrogen contents in ephyrae at the PNR_{50} were estimated to be 51, 58 and 42%, and 48, 52 and 42% of the initial contents at 15, 12 and 9°C, respectively. The two-way ANOVA showed that neither temperature, starvation duration nor their interaction significantly affected the C:N ratios ($P>0.05$ in each case). The overall mean C:N was 4.2±0.14 (Fig. 2-14C).

Discussion

Because of absence of either inner or outer skeletons, a significant de-growth is one of the specific features in cnidarian jellyfish under starvation, and this experiment confirmed that de-growth of *A. aurita* ephyrae was remarkable. The characteristic disc-form body with 8 extended marginal lappets gradually shrank, and by the time of the PNR_{50}, DD decreased to about two third of their original DD. Then, they finally deformed into a rod-like lump, which looked hardly identifiable to be an ephyra. It might be noteworthy that even in such heavily deformed ephyrae, a part of their body could constrict, showing a sign of life.

As the starvation prolonged, the vitality of ephyrae gradually diminished as manifested by their ability to recovery from starvation damage (i.e. PNR_{50}). In marine invertebrates and fishes, newly hatched larvae can be regarded as a critical life stage, since they must start feeding within a limited time, i.e. PNR_{50}, to avoid death by starvation (Blaxter & Hempel 1963, Bailey & Houde 1989, Paschke et al. 2004). Hence, the PNR_{50} has been studied in many marine animals in order to evaluate their starvation resistance and to understand the factors affecting recruitment to their post-larval stages. Although scyphozoan ephyrae are not derived from eggs, but from strobilating polyps, they likewise have to feed before their PNR_{50}, to recruit to the medusa population. Previous studies have determined the PNR_{50} for planktonic larvae of molluscs, crustaceans, and fishes (see Chapter 5). At 15°C, the average PNR_{50} estimated for molluscs, crustaceans and fishes are 7.3, 4.8 and 5.8 d, respectively. In marked contrast, the PNR_{50} for *A. aurita* ephyrae was 33.8 d, demonstrating that they are capable of enduring extraordinarily long starvation compared to the larvae of other taxa.

This strong starvation resistance of *A. aurita* ephyrae can be attributed to their low metabolic demands, equivalent to 2-3% of body carbon weight d^{-1} (Fig. 2-14), relative to copious endogenous carbon reserves (mean: 6.6 μg C $ephyra^{-1}$). Assuming that proteins are the major organic constituents and metabolic substrate, as was confirmed by the overall mean C:N ratio of 4.2 (Fig. 2-14), and that the respiratory quotient is 0.8 (Ikeda et al. 2000), the respiration rates indirectly estimated from their carbon weight reductions are 0.40, 0.28 and 0.27 μl O_2 ephyra^{-1} d^{-1} at 15, 12 and 9°C, respectively. This rate at 15°C is comparable to the rate (0.42 μl O_2 ephyra^{-1} d^{-1}) reported by Møller & Riisgård (2007a), and lower than the rate (0.74 μl O_2 ephyra^{-1} d^{-1}) determined by Kinoshita et al. (1997).

The results of this experiment showed that *A. aurita* ephyrae lost ca. 50% of initial carbon by PNR_{50}. The loss of body carbon biomass during starvation up to PNR_{50} is, in general, much smaller in other taxa: 16% loss for *Maja brachydactyla* Herbst (Guerao et al. 2012), 25-34% loss for *Carcinus maenas* Linnaeus (Dawirs 1987), 21% loss for *Hyas araneus* Linnaeus (Anger & Dawirs 1982). However, the loss is exceptionally high (44-51%) for *Euphausia superba* Dana (Ross & Quetin 1989). These facts demonstrate that *A. aurita* ephyrae are capable of recovering from extremely low food conditions that larvae of other taxa may not tolerate.

In this study, newly released *A. aurita* ephyrae showed high starvation resistance and recover capability, which indicate that starvation may not the major factor to account for the mortality of ephyrae. However, the survivorship of ephyrae in natural waters is very low, for instance, only 1% in Tokyo Bay (Ishii et al., 2004). I suspect that this high mortality might be due to predation loss rather than starvation. The survival capability of ephyrae in the field in relation to ambient environmental conditions will be discussed in General Discussion (Chapter 5).

Summary

Newly released ephyrae of *A. aurita* must start feeding before stored energy runs out, and hence they are subjected to high mortality before development to medusa stage and are regarded as one of the most critical life stages of scyphozoan medusae. In order to demonstrate their ability of starvation tolerance, newly released ephyrae were exposed to prolonged starvation at three different temperatures, i.e. 9, 12 and

15^{o}C, and their morphological changes, longevity (ML_{50}) and point-of-no-return (PNR_{50}) were investigated.

Ephyrae of *A. aurita* showed extremely strong starvation resistance as manifested by their PNR_{50} of 33.8, 38.4 and 58.6 d and by their ML_{50} of 50, 70 and 100 d at 15, 12 and 9^{o}C, respectively, being nearly one order of magnitude longer than those of larvae of other marine taxa such as molluscs, crustaceans and fish. Such extremely strong resistance to starvation was attributed to lower metabolic rate, which accounted for 2-3% of body carbon per day, relative to copious carbon content of newly released ephyra (i.e. 6.6 μg C ephyra^{-1}). Ephyra's body size, e.g. DD, decreased to ca. 30%, and carbon and nitrogen contents decreased to ca. 50% of the original contents by the time of PNR_{50}. The strong starvation resistance of *A. aurita* ephyrae might indicate that the starvation due to food scarcity may not be a major factor to determine the mortality of ephyrae. More detailed studies particularly in the field are needed.

Chapter 3. Effects of starvation and temperature on the metabolism and locomotion of *Aurelia aurita* s.l. ephyrae

3-1. Effects of starvation and temperature on respiration rates

Introduction

Metabolism is the chemical processes that occur within a living organism in order to maintain life, and can be defined in general as the sum of all processes through which protoplasm is formed from food (i.e. anabolism) and broken down into waste matter (i.e. catabolism), with release of energy. Energy gained through the process is stored exclusively in the form of adenosine triphosphate (ATP), and used for various activities (locomotion, production of new tissue, ion pumps, etc.) of living organisms. ATP is generated from the tricarboxylic-acid (TCA) cycle, for which oxygen is required to drive. Therefore, metabolic rates can often be determined as oxygen consumption rates or respiration rates (Ikeda et al. 2000).

From a physio-ecology point of view, studies on the metabolic rates of jellyfish are important not only to gain knowledge of the activity levels of organisms, but also to assess the loss of assimilated energy. The latter also gives the information fundamental to estimates of the minimum food requirement and feeding rate (Schneider 1989, Uye & Shimauchi 2005, Ishii & Tanaka 2006, Purcell et al. 2010). During recent decades, respiration rates of jellyfish, particularly *A. aurita*, have been extensively studied (Larson 1987, Kinoshita et al. 1997, Uye & Shimauchi 2005, Ishii & Tanaka 2006, Møller & Riisgård 2007a). However, the measurements were confined to the medusa stage, and respiration rates of ephyrae have seldom been measured (Purcell et al. 2010).

As demonstrated in Chapter 2, the PNR_{50} of *A. aurita* ephyrae were extraordinarily long, i.e. 33.8, 38.4 and 58.6 d at 15, 12 and 9°C, respectively. Thus, I considered that such long PNR_{50} was attributed to extremely low metabolic rates of starved ephyrae, which was already indicated by the very slow reduction rates of body carbon contents with prolonged starvation (see Fig. 2-14A). To make sure the lower metabolic rates of *A. aurita* ephyrae under starvation, actual measurements of their respiration rates were conducted under similar experimental setup used in Chapter 2.

Materials and Methods

The stock-cultured *A. aurita* polyps maintained at ca. 25°C were transferred to 13°C to induce strobilation and release of ephyrae. Newly released ephyrae were kept starved in plastic containers containing ca. 1 l of filtered seawater (salinity: 32) maintained at three different temperatures (i.e. 9, 12 and 15°C) in darkness for various periods, ranging from 0 to 60 d, prior to respiration measurement experiments. The aerated filtered seawater used in the respiration experiments was produced by air stone aeration for ca. 1 h. In each experiment, 20 to 50 ephyrae were pipetted into a small vial (ca. 10 ml volume), seawater in which was completely replaced with the aerated seawater, and then transferred into a DO bottle (60.0 ml volume) containing the same aerated seawater. Three bottles were prepared for either respiration measurement or control, and they were placed in dark incubators for 72 h with periodical (4-8 h intervals) upside-down turnings of the bottles by hands. The selection of numbers of ephyrae (20-50) and incubation duration (72 h) was gained based on preliminary determination of the respiration rate of an ephyra, so that the consumption of DO would be larger than the precision level (0.02 mg O_2 l^{-1}) of a fluorescence DO meter (WTW, Multi 3410 with FDO 925 probe). DO before and after the experiment was measured, and ephyrae used in the experiment were observed under a stereomicroscope to check their survival. At least 10 of them were photographed by a digital camera to measure their size. The respiration rates in different treatments were analyzed by one-way or two-way ANOVA (SPSS 13.0 software). If the overall ANOVA results were significant ($P<0.05$), the means were compared using Tukey's pair-wise comparisons.

Results

As described in Chapter 2, the size and morphology of ephyrae changed with prolonged duration of starvation, and these changes were more rapid in higher temperature treatments.

The mean (± SD) respiration rate of a newly released ephyra was 0.24±0.07, 0.24±0.03 and 0.19±0.06 μl O_2 ephyra^{-1} d^{-1} at 15, 12 and 9°C, respectively (Fig. 3-1), although there was no significant difference among them (One-way ANOVA, $P>0.05$). The respiration rates showed a general trend of decreasing with increasing starvation period; in the beginning the decrease was relatively smooth and small, but after 30 to 40 d of starvation, it appeared to be rapid. The rate decreased nearly to or below half of the rate shown by a non-starved ephyra, when the starvation was longer than PNR_{50} (Fig. 3-1). However, the statistical tests failed to show any significant difference of the respiration rates with temperature (two-way ANOVA, $P>0.05$), duration of starvation (two-way ANOVA, $P>0.05$) or their interactions (two-way ANOVA, $P>0.05$) during the first 30 days of starvation. Meanwhile, the respiration rate on Day 0 was significantly higher than the respiration rate on Day 30 (Tukey's pair-wise comparison, $P<0.05$). At 9 and 12°C, there was no significant difference in the respiration rate with the duration of starvation (one-way ANOVA, $P>0.05$). However, at 15°C the duration of starvation did show significant difference in respiration rate between Day 0 and Day 40 (one-way ANOVA, $P<0.05$).

The carbon weight-specific respiration rates were calculated by dividing individual respiration rates by individual carbon weight (see Fig. 2-14A). The mean (± SD) carbon weight-specific respiration rate of a newly released ephyra was 35.6±10.3, 37.9±4.2 and 29.4±9.4 μl O_2 mg C^{-1} d^{-1} at 15, 12 and 9°C, respectively (Fig. 3-2), without significant difference with temperature (one-way ANOVA, $P>0.05$). The specific respiration rates were almost constant over the starvation period up to 40 d (Fig. 3-2), as the statistical test did not show any significant difference in the rates with temperature (two-way ANOVA, $P>0.05$), duration of starvation (two-way ANOVA, $P>0.05$) or their interactions (two-way ANOVA, $P>0.05$). Moreover, at each temperature, one-way ANOVA failed to detect any significant difference in the rates with duration of starvation (*P*>0.05).

Discussion

This is the first study to measure the respirations for newly released *A. aurita* ephyrae (mean DD: 2.02±0.19 mm), since previous workers measured the respirations for slightly advanced ephyra stage, whose DD was 4.2 mm (Kinoshita et al. 1997) and 5.1 mm (Møller & Riisgård 2007a). The respiration rate at 15°C can be calculated to be 0.42 μl O_2 ephyra^{-1} d^{-1} (Møller & Riisgård 2007a) and 0.74 μl O_2 ephyra^{-1} d^{-1} (Kinoshita et al. 1997). Compared to these rates, the respiration rate measured at 15°C in this experiment (i.e. 0.24 μl O_2 ephyra^{-1} d^{-1}) was significantly lower.

In jellyfish respiration measurements, Purcell et al. (2010) pointed out several factors influencing actual measurements, which includes (1) acclimated temperatures, (2) feeding conditions of specimens before experiment, (3) volume of respiration chamber, (4) acclimation and incubation time, and (5) activity of animals during experiment, although no standardized protocols have not been established. In this study, *A. aurita* ephyrae were treated with great care before and during the respiration experiments to reduce errors as small as possible, the obtained data had substantially wide variations so that each mean value had relatively wide SD. These might preclude the statistical analysis from detecting the effects of temperature and starvation duration on the respiration rates in a significant level. However, the general trend was clear that the respiration rates reduced with the increase of starvation duration, although temperature effect was not significant.

It is worth mentioning the difference in the respiration rates of newly released ephyrae (i.e. 0.24, 0.24 and 0.19 μl O_2 ephyra^{-1} d^{-1} at 15, 12 and 9°C, respectively) from those determined indirectly from the decrease of carbon contents (i.e. 0.40, 0.28 and 0.27 at 15, 12 and 9°C, respectively, Fig. 2-14). I suspect that the placement of ephyrae into a small volume of DO bottle might reduce their swimming activity, which caused lower respiration rates compared to indirect estimation, where ephyrae were allowed to swim freely (see Chapter 2).

Since the carbon weight-specific respiration rates were stable irrespective of starvation duration, the decrease of body carbon weight was responsible for reduced individual-level respiration rates for starved ephyrae. This fact also suggests that the basal metabolism maintains at a certain fixed level for *A. aurita* ephyrae so far as their metabolic substrate is available. It is noteworthy that even starved ephyrae near PNR_{50} could maintain this metabolic kinetics.

The mean carbon weight-specific respiration rates of newly released *A. aurita* ephyrae were converted to dry weight-specific respiration rates by using a dry weight and carbon convertion factor of 0.33 (measured value in this study), i.e. 11.7, 14.5, and 14.6 $\mu l\ O_2\ mg\ DW^{-1}\ d^{-1}$ at 9, 12 and 15°C, respectively, for comparison to the rates of planktonic larvae of other marine animals (i.e. mollusca, crustacean and fish, see Table 3-1). The tabled data show that the dry weight-specific respiration rates range from 139.2 to 333.8 $\mu l\ O_2\ mg\ DW^{-1}\ d^{-1}$ for molluscans, from 9.6 to 504 $\mu l\ O_2\ mg\ DW^{-1}\ d^{-1}$ for crustaceans, and from 39 to 154.1 $\mu l\ O_2\ mg\ DW^{-1}\ d^{-1}$ for fish. Compared to these values, the rates of *A. aurita* ephyrae are, in general, much lower.

Based on the respiration rate, the minimum food requirement can be estimated as

$$MFR = k \times R \times RQ / A,$$

where MFR is minimum food requirement ($\mu g\ C\ g^{-1}\ ephyra^{-1}\ d^{-1}$), k is constant (0.375 $\mu g\ C\ \mu g^{-1}\ O_2$), R = respiration rate ($\mu g\ O_2\ ephyra^{-1}\ d^{-1}$), RQ is respiratory quotient (assuming 0.8 due to protein dominated metabolism, Ikeda et al, 2000), A is assimilation efficiency (assuming 0.8, Schneider 1989). MFR for a newly released ephyra was calculated to be 0.13, 0.13 and 0.10 $\mu g\ C\ ephyra^{-1}\ d^{-1}$ at 15, 12 and 9°C, respectively, each corresponding to 2.0, 2.0 and 1.6% of ephyra carbon weight.

Summary

As *A. aurita* ephyrae showed extremely long PNR_{50} probably due to their lower metabolic rates, actual measurements of respiration rates were conducted at 15, 12 and 9°C, for the specimens kept starved for various periods. The mean respiration rate of a newly released ephyra was 0.24, 0.24 and 0.19 $\mu l\ O_2\ ind.^{-1}\ d^{-1}$ at 15, 12 and 9°C, respectively, and the rate tended to decrease with the increase of starvation duration. However, the effect of starvation was not statistically detected because of wide variations of data within a given experiment, which consisted of 3 bottles for control as well as with animals. The carbon weight-specific respiration rates did not change significantly with starvation duration, indicating that the kinetics of the basic metabolism may be stable so far as the metabolic substrate is available. The dry weight-specific respiration rates of newly released *A. aurita* ephyrae (i.e. 11.7-14.6 µl O_2 mg DW^{-1} d^{-1}) were nearly one order of magnitude lower compared to the rates of planktonic larvae of other taxa (e.g. molluscs, crustaceans and fish).

3-2. Effects of starvation and temperature on swimming ability

Introduction

Locomotion or swimming is important for *A. aurita* ephyrae to capture food, avoid predators and maintain their orientation in the water column. Costello et al. (1998) demonstrated that ephyrae spend the bulk of natural existence actively swimming, and Sullivan et al. (1997) documented the importance of swimming motions for capture of prey by ephyrae. Thus, an understanding of swimming activity of ephyrae is a prerequisite for understanding of survival and growth of *A. aurita* populations. Several studies have researched on the pulsation rate of *A. aurita*. However, among these studies, only Mangum et al. (1972) and Dillon (1977) have studied the pulsation rate for ephyrae. Both studies showed that the pulsation rate was strongly influenced by temperature.

As demonstrated in Chapter 2, *A. aurita* ephyrae have strong starvation resistance and recovery capability. However, I speculate that ephyrae in the field may not survive as long as observed in the laboratory, since morphological damages caused by starvation may reduce their swimming ability, which would reduce prey encounter rate, prey capture success and ability of avoidance from predators. To test this speculation, I conducted the laboratory experiments to investigate the effect of starvation duration and temperature on the swimming activity of *A. aurita* ephyrae.

Materials and Methods

Total of 60 newly released *A. aurita* ephyrae originating from stock-cultured polyps were prepared, and they were individually placed in wells of 6-well polystyrene culture plates containing 10 ml of filtered seawater of salinity 32. Each lot consisting of 20 ephyrae was transferred to three temperatures (i.e. 9, 12 and 15^{o}C), and kept starved for up to 60 d. The seawater in the wells was replaced twice weekly. Newly released ephyrae at each temperature were photographed under a stereomicroscope to measure their size, and used for the experiment to measure their pulsation rates. Pulsation rate of each ephyra was measured at every 10-day interval.

For the pulsation determination, an ephyra was transferred to a 1-liter plastic bottle filled with seawater of respective temperature, and then its pulsations were counted with a hand-held counter for one min for three successive min. The experiment was conducted under dim light. The mean pulsation rate was determined from 3 counts for each of specimens. Statistical analysis of treatment means was carried out with two-way ANOVA (SPSS 13.0 software) and Tukey's pair-wise comparisons to ascertain the significant differences between treatment means.

Results

The mean (± SD) disc diameter of newly released ephyrae used in this experiment was 2.16±0.17 mm. Twenty ephyrae died during the experiment due perhaps to the mechanical damage with pipetting. At the end of the experiment, there were 14, 13 and 13 ephyrae remaining at 9, 12 and 15°C, respectively, and they all looked active.

The mean (± SD) pulsation rate of newly released ephyrae was 18.9±6.4, 20.4±11.3 and 28.1±13.7 beats indiv.$^{-1}$ min^{-1} at 9, 12 and 15°C, respectively (Fig. 3-3), with significant difference with temperature (one-way ANOVA, $P<0.05$). Over the starvation period up to 50 days, two-way ANOVA showed a significant effect of starvation on pulsation rate ($P<0.01$), but did not show any significant effect of temperature ($P>0.05$) and their interactions ($P>0.05$). Tukey's test showed that the pulsation rate on Day 0 was significantly lower than that on Day 10, Day 20 and Day 30 ($P<0.01$), the same test also showed that the rate on Day 20 was significantly higher than that on Day 0, Day 40 and Day 50 ($P<0.01$).

Discussion

As *A. aurita* ephyrae are tactile predators without any ability to detect prey remotely, swimming and feeding are closely related each other. In this study, the maximum pulsation rate recorded was 49.3 beats min^{-1}, indicating that *A. aurita* ephyrae are cruising predators, which swim almost continuously. If one pulsation can generate a movement of 1.8 mm, as was observed by Sullivan et al. (1997), the maximum average swimming speed of *A. aurita* ephyrae would be 8.9 cm min^{-1}. The ephyrae cannot chase prey with swimming speed higher than them, but can encounter with swimming prey. However, even in the latter case, the prey with higher swimming speeds can escape from the feeding current generated by ephyra's disc pulsation (Sullivan et al. 1997) and even shake off the manubrium. Therefore, *A. aurita* ephyrae are expected to capture primarily slow moving prey, such as fish eggs, barnacle nauplii, veliger larvae and hydromedusae. Copepod nauplii (escape speed: 120 cm min^{-1}) and copepodites and adults (escape speed: > 300 cm min^{-1}) may not be the primary prey for *A. aurita* ephyrae.

In this study, ephyrae could actively swim at all three temperatures, and their pulsation rates did not differ significantly among the temperatures tested (an exception was for newly released ephyrae), which is contrary to the previous results. Both Mangum et al. (1972) and Dillon (1977) found that the pulsation rate increased with increasing temperature up to 25°C, and then decreased with further temperature increase. A similar temperature effect was also found for *A. aurita* medusae (Olesen 1995, Hansson 1997b, Martinussen & Båmstedt 2001). The difference between this study and the previous ones might be attributed to longer time adaption of ephyrae to experimental temperatures in this study compared to the previous ones, where ephyrae were exposed to experimental temperatures rather suddenly. Over the temperature range at least between 9 and 15°C, where *A. aurita* ephyrae usually experience in the field, they can swim always actively to seek food and escape from predators.

It was an interesting finding that the pulsation rates of *A. aurita* ephyrae after 10 and 20 days of starvation were significantly higher than those of ephyrae of newly released. This result indicates that starvation may accelerate pulsation in order to search for more prey. The pulsation rate culminated on 20 d after starvation, and thereafter the rate decreased. The decrease of pulsation rates together with body size shrinkage may significantly reduce the feeding capability of *A. aurita* ephyrae. In addition, decrease of pulsation can also cause the reduction of escaping ability from predators, leading to higher mortality of *A. aurita* ephyrae in the field.

Summary

As swimming capability is closely associated with feeding and escaping abilities of *A. aurita* ephyrae, the effects of temperature and starvation on their pulsation rates were examined. The maximum pulsation rate taken by *A. aurita* ephyrae was 49.3 beats min^{-1}, which represents the maximum swimming velocity to be 8.9 cm min^{-1}. This swimming speed is much lower compare to common zooplankton such as copepods, so that ephyrae can capture primarily slow moving prey. The pulsation rates were not affected by temperature at least over the range between 9 and 15^{o}C. However, they were influenced by starvation duration; the pulsation increased for those starved for 10 to 20 d, and thereafter the pulsation decreased with further increase of starvation period. Starvation-derived decrease in pulsation together with associated body shrinkage may lead to lower encounter rate of prey and lower escaping ability from predators.

Chapter 4. *Chrysaora pacifica*: a potential predator of *Aurelia aurita* s.l. ephyrae

Introduction

As demonstrated in Chapter 2, newly released *A. aurita* ephyrae have extraordinarily long starvation resistance and strong recovery capability, implying that starvation may not be the major factor to cause mortality in the ephyra stage, and instead predation loss may probably be more important to determine the mortality of ephyrae in the field. Therefore, it is required to investigate the effect of predation on the survivability of *A. aurita* ephyrae.

Little information is available in regard to predators and their predation rates on *A. aurita* ephyrae. In the Inland Sea, for example, during *A. aurita* ephyrae releasing season, i.e. winter and early spring, fish, particularly larval fish, are very scarce in the plankton, although they occur much more numerously in late spring and early summer. On the other hand, some cnidarian jellyfish, mainly hydrozoan medusae in addition to a scyphozoan medusa, *C. pacifica*, occurs often abundantly. These facts imply that jellyfish may be more important than fish as possible predators of *A. aurita* ephyrae. Predation on jellyfish by different species of jellyfish is widely known, and some scyphozoan medusa species such as *Cyanea* spp. were reported to consume *A. aurita* medusae (e.g. Purcell 1991, Båmstedt et al. 1997, Hansson 1997a, Titelman et al. 2007, Bayha et al. 2012). However, the predation on ephyrae has seldom been studied. It is a common practice in many Japanese commercial aquaria for ephyrae and medusae of *A. aurita* not needed for Moon Jelly exhibits to be given as food to *C. pacifica* (K. Okuizumi of Kamo Aquarium, Tsuruoka, personal comm.). Further, Sato et al. (1996) observed in the laboratory that a *C. pacifica* of BD = 9.0 cm was capable of consuming daily two *A. aurita* medusae (BDs = 8.5 and 9.0 cm), whose body weight was nearly double the predator's own. These facts imply that *C. pacifica* can be a prominent predator of *A. aurita*. In Tokyo Bay, Ishii et al. (2004) also speculated that *C. pacifica* medusae may the potential predator of *A. aurita* ephyrae without any confirmed evidence.

Therefore, I hypothesized that *C. pacifica* may be the potential predator of *A. aurita* ephyrae in the field. To test this hypothesis, I conducted laboratory experiment to examine the predation on *A. aurita* ephyrae by *C. pacifica* young medusae.

Materials and Methods

Preparation of predators

Young medusae of *C. pacifica* were grown from stock cultured polyps maintained at 24°C in the Laboratory of Marine Ecosystem Dynamics of Hiroshima University, Higashi-Hiroshima, Japan. These polyps were originated from planulae produced by matured medusae collected in Ondo Strait, Inland Sea of Japan, in June 2012. To obtain ephyrae, strobilation was artificially induced by exposure of the polyps to 15°C. Newly released ephyrae were then maintained at 15°C in 0.2-µm filtered seawater and fed with newly hatched *Artemia* sp. nauplii until they developed to young medusa stage (disc diameter range: 9-15 mm).

Predation experiment

Twenty or fifty *A. aurita* ephyrae of ≤3 d old after release from the stock-cultured polyps were pipetted into a 450 ml glass bottle containing 0.2-µm filtered seawater of salinity 32. The ephyrae were allowed to acclimatize the experimental condition for >2 h, prior to an introduction of a *C. pacifica*. Then, filtered seawater was filled up to the brim and a plastic film was placed on the month of the bottle to prevent from trapping air bubbles before screw the cap. The bottles were wrapped with aluminum foil to darken the inside and secured in oblique position (45 degree) on a shaker (EYEL4, Tokyo Rikakikai Co. LTD) at 3.0 rpm to keep the organisms in suspension. Experiments were run for 2 h at ambient temperatures, which changed within a range between 11 and 14°C, close to natural water temperatures in spring when both *A. aurita* ephyrae and *C. pacifica* medusae co-counter. After the experiment, *C. pacifica* was pipetted from the bottle to the observation stage under a stereomicroscope, and was immediately photographed to measure the disc diameter as well to enumerate *A. aurita* ephyrae in the gastric pouch.

Predation capability of *C. pacifica* young medusae was assessed in terms of two parameters: clearance rate and predation rate. The clearance rate was determined by the following equation (Purcell & Cowan 1995),

$$CR = \frac{V}{n\,t}\ \ln\left(\frac{C_0}{C_t}\right),$$

where CR is clearance rate (l predator^{-1} h^{-1}), V is container volume (0.45 l), n is number of predators (1 predator), t is duration of experiment (2 h), and C_0 and C_t are numbers of prey at the beginning and end of experiment, respectively.

The ingestion rate was calculated by (Møller & Riisgård 2007b),

$$IR = CR \times C_m,$$

where IR is ingestion rate (number of prey predator^{-1} h^{-1}) and C_m is the geometric mean of prey concentration during the experimental duration, which was calculated from,

$$C_m = \exp\left[\frac{\ln(C_0 \times C_t)}{2}\right]$$

The mean rates at two different prey concentrations were analyzed using one-way ANOVA (SPSS 13.0 software).

Results

When a predator, *C. pacifica*, and a prey, *A. aurita* ephyra, were in close proximity each other, the latter was caught by the tentacles and/or oral arms of the former. Then, adhered prey was transported through the mouth to the gastric pouch (Fig. 4-1), where the digestion was applied. The decomposition of ephyrae started first in thinner posterior part of the marginal lappet, and then gradually spread to the central, oral part of the body.

Total of 48 predation experiments were conducted: 30 experiments at a density of 50 ephyrae bottle^{-1} and 18 experiments at 20 ephyrae bottle^{-1}. The numbers of ephyrae contained in the gut of *C. pacifica* are plotted against predators' disc diameter, which varied from 9 to 15 mm with overall mean of 11.9±1.5 mm (Fig. 4-2). The maximum prey number ingested in the bottles containing 50 ephyrae was 15 and that in the bottles containing 20 ephyrae was 9, and in total of 7 experiments no ingestion occurred. Such wide variations in the ingestion rate resulted into no significant regression between the ingestion rate and predators' body size, at least within this size range (Fig.4-2).

The mean (± SD) ingestion rates at two different prey densities were calculated; they were 0.8±0.6 predator^{-1} h^{-1} at 20 ephyrae bottle^{-1} to 1.3±1.0 predator^{-1} h^{-1} at 50 ephyrae bottle^{-1} (Fig. 4-3). However, statistical analysis did not show any significant difference between the two densities (one-way ANOVA, $P>0.05$).

The mean (± SD) clearance rates of *C. pacifica* in the feeding on *A. aurita* ephyrae were 0.029±0.024 and 0.051±0.041 l predator^{-1} h^{-1} at 50 ephyrae bottle^{-1} and 20 ephyrae bottle^{-1}, respectively (Fig. 4-4). The clearance rate increased significantly with decreasing ephyrae densities from 50 ephyrae bottle^{-1} to 20 ephyrae bottle^{-1} (one-way ANOVA, $P<0.05$).

Discussion

First of all, this study demonstrated that a scyphozoan medusa *C. pacifica* is capable of feeding on *A. aurita* ephyrae, confirming that this species is a potential predator. In this study, however, experiments were conducted only at two different densities of *A. aurita* ephyrae, which were apparently much higher than the densities encountered in the field. In addition, *C. pacifica* used were confined to only very young medusa, whose disc diameter was ca. 12 mm. The predation rates observed in this study appeared to be highly overestimated the rate in the natural conditions, because of extremely high densities of *A. aurita* ephyrae. The clearance rate tended to be higher at a lower prey concentration, a similar pattern observed in the functional response of marine zooplankton, which indicate that the clearance rate would become much high at much lower prey densities which are commonly encountered in the field.

Assuming that the clearance rate determined in the experiment at 20 ephyrae bottle^{-1} (or 44 ephyrae l^{-1}), i.e. ca. 0.05 l predator^{-1} h^{-1} or 1.2 l predator^{-1} d^{-1} is applicable to the field. Of course, this value is not significantly high to affect the mortality of *A. aurita* ephyrae. When the medusa grows to ca. 5 cm in disc diameter (i.e. roughly 5 times larger than the specimen used in the experiment, and the body volume would increase to 75 times), the clearance rate would accordingly increase to ca. 150 l predator^{-1} d^{-1}, which may become more realistic to influence the mortality of *A. aurita* ephyrae, which often occurs at >1 ephyra m^{-3} in the Inland Sea of Japan (Makabe et al. unpublished data).

So far, no information is available on the abundance and biomass of *C. pacifica* in the Japanese coastal waters, and hence no actual estimation of its predation pressure on *A. aurita* ephyrae in the field is possible at present. However, the seasonal occurrence of *C. pacifica* in the plankton (in January and February) slightly precedes the occurrence of *A. aurita* ephyrae (in February and March) (Thein et al. 2013), indicating that the latter is exposed to predation pressure by the former. Future studies, in particular, in the field, are needed to clarify the prey-predator relationship between *C. pacifica* medusae and *A. aurita* ephyrae.

Summary

As a scyphozoan medusa *C. pacifica* was suspected as one of potential predators of *A. aurita* ephyrae in the field, predation experiments were conducted using laboratory-reared *C. pacifica* young medusae as predators and *A. aurita* ephyrae as prey. Young medusae of *C. pacifica* actively captured *A. aurita* ephyrae with the tentacles and oral arms, and one medusa ate as many as 15 *A. aurita* ephyrae during 2 h experiment. The clearance rate of *C. pacifica* feeding on *A. aurita* ephyrae increased significantly with decreasing ephyrae densities. At 20 ephyrae bottle^{-1} (or 44 ephyrae l^{-1}), the clearance rate was ca. 1.2 l predator^{-1} d^{-1}. When *C. pacifica* grows to medusa of 5 cm disc diameter, the clearance rate would increase to ca. 150 l predator^{-1} d^{-1}, which may become more realistic to influence the mortality of *A. aurita* ephyrae.

Chapter 5. General discussion

5-1.Extraordinary duration to *PNR_{50}* in *A. aurita* ephyrae

The result of this study demonstrates that *A. aurita* ephyrae possess strong starvation resistance as manifested by the estimates of their ML_{50} and PNR_{50}. It is interesting to compare the PNR_{50} for *A. aurita* ephyrae to those previously determined for planktonic larvae of marine animals such as molluscs, crustaceans and fishes. In determination of PNR_{50} in the latter groups, the methodology was basically similar to that used in this study, i.e. the larvae that had been kept starved for various periods of starvation were examined whether they were capable of recovering from the starvation damage and developing into post-larval stage by feeding. The available data on PNR_{50} and temperatures at which the PNR_{50} were determined were collated for 4 molluscan, 20 crustacean and 35 fish species (Table 5-1), and these two parameters (i.e. PNR_{50} and temperatures) are plotted in Fig. 5-1. The compiled data show a general trend that PNR_{50} (d) of each taxonomic group are negatively related to temperature (T, ^{o}C), as expressed by $PNR_{50}=16.9e^{-0.056T}$ for molluscs, $PNR_{50}=11.1e^{-0.060T}$ for crustaceans and $PNR_{50}=12.7e^{-0.052T}$ for fishes. At 15°C, the average PNR_{50} values estimated for molluscs, crustaceans and fishes are 7.3, 4.8 and 5.8 d, respectively. In marked contrast, the PNR_{50} for *A. aurita* ephyrae was 33.8 d, demonstrating that they are capable of enduring extraordinarily long starvation compared to the larvae of other taxa.

5-2. Physiological characteristics of *A. aurita* ephyrae to enable long PNR

The strong starvation resistance of *A. aurita* ephyrae can be attributed to their low metabolic rate relative to copious endogenous carbon reserves (mean carbon content: 6.6 μg C ephyra^{-1}). In Chapter 3, I determined the respiration rate of a newly released ephyra at 15°C to be 0.24 μl O_2 ind^{-1} d^{-1}, which is significantly lower than the 15°C rate of 0.42 μl O_2 ind^{-1} d^{-1} reported by Moller & Riisgård (2007a) and 15°C rate of 0.74 μl O_2 ind.$^{-1}$ d^{-1} determined by Kinoshita et al. (1997). Moreover, all of these estimates are much lower than the respiration rates of other zooplankton taxa having similar carbon contents. Assuming a carbon:dry weight ratio of 0.45 (Uye 1982), the respiration rate of crustacean zooplankton, primarily copepods, from the Inland Sea of Japan (Uye & Yashiro 1988) can be estimated as 2.55 µl O_2 ind^{-1} d^{-1} at 15°C. A similar calculation can be made by interpolation of the equation derived from various zooplankton taxa from the world oceans (Ikeda 1974): 1.68 µl O_2 ind^{-1} d^{-1}. The extremely lower respiration rates of *A. aurita* ephyrae compared to other taxa are also demonstrated when the rates are expressed in terms of dry weight-specific respiration rates (see Table 3-1, Fig. 3-4). Hence, I conclude that the low metabolism per unit body (either dry or carbon) mass is specific to *A. aurita* ephyrae. This conclusion, however, is contradictory to recent publications by Acuña et al. (2011) and Pitt et al. (2013). They have reported that the respiration rates of jellyfish are similar to other metazoans (e.g. crustaceans and fish) when scaled to carbon content. Interpolation of 6.6 µg C (carbon weight of an *A. aurita* ephyra) to the equations presented by Acuña et al. (2011) and Pitt et al. (2013) gives the respiration rates: 2.9 and 2.6 µl O_2 $animal^{-1}$ d^{-1}, respectively, values being much greater than any mentioned above for *A. aurita* ephyrae.

This study showed that carbon and nitrogen contents of *A. aurita* ephyrae lost by ca. 50% by PNR_{50}. The loss of body carbon biomass during starvation up to PNR_{50} is, in general, much smaller than other marine taxa as already described in Chapter 2. These facts demonstrate that *A. aurita* ephyrae are capable of recovering from extremely low-food conditions that larvae of other taxa may not tolerate. The somatic C:N ratio did not change significantly over the starvation period (overall mean: 4.2), indicating that proteins are the major organic constituents and metabolic substrates of *A. aurita* ephyrae. The constancy in carbon weight-specific respiration rates up to PNR_{50} suggest that the kinetics of basal metabolism in *A. aurita* ephyrae is uniform so far as the metabolic substrates decrease to about a half of initial level. Hence, the decrease of individual respiration rates with the increase of starvation period is attributed simply to the decrease of amount of metabolic substrates available.

5-3. Ecological significance of long PNR_{50} in *A. aurita* ephyrae

As the strobilation was induced most at temperatures below ca. 14°C, the release of ephyrae of *A. aurita* is programmed to occur during winter and early spring, in accordance with the annual temperature fluctuation (range: 10-28°C) of the Inland Sea of Japan (Uye & Shimauchi 2005, Thein et at. 2012). A similar seasonal strobilation schedule is observed in many temperate regions (Lucas 2001, Miyake et al. 2002). However, it is difficult to assess the success of feeding and subsequent development of wild ephyrae, since information on their feeding and *in situ* food supply is inadequate. Although dissolved organic matter was reported to be effective as a nutritional source for ephyrae under starvation conditions, it is a meager one and allows only slight increase of their survival (Skikne et al. 2009). Phytoplankton are likely less important food for the net growth of ephyrae compared to zooplankton (Båmstedt et al. 2001). Examination of stomach contents of wild caught ephyrae and laboratory experiments to test various diets have revealed that the main foods for *A. aurita* ephyrae are small and slow-swimming zooplankton, such as tintinnids, rotifers, nauplii of copepods and barnacles, copepodites and adult copepods, and hydromedusae (Olesen 1995, Sullivan et al. 1997, Ishii et al. 2004). Sullivan et al. (1997) investigated prey capture behavior of *A. aurita* ephyrae in detail, and demonstrated that larger prey swimming continuously at low velocity are most vulnerable, suggesting slow-swimming hydromedusae may be more important than fast-swimming copepodite and adult copepods, and continuously swimming rotifers may be more valuable than intermittently swimming copepod nauplii. The limited ability of feeding of *A. aurita* ephyrae is also confirmed in this study (Chapter 3) by their pulsation rates; the maximum pulsation rate equates the swimming velocity of 8.9 cm min^{-1}, much slower than copepod nauplii whose escape speed is 120 cm min^{-1}. Therefore, slow swimming zooplankton may be the primary prey for *A. aurita* ephyrae, as was argued in the previous studies.

During the main season of ephyra release (i.e. January-March), mean zooplankton biomass over the entire Inland Sea of Japan is at its annual minimum (i.e. ca. 2 and 13 mg C m^{-3} for micro- and mesozooplankton, respectively) and zooplankton production rates are also the lowest (ca. 0.5 and 2 mg C m^{-3} d^{-1}, respectively, Uye et al. 1996, Uye & Shimazu 1997). Rotifers and hydromedusae, which may be suitable food for ephyrae, are never dominant in micro- and mesozooplankton communities. Thus, it is very likely that newly released ephyrae are exposed to severe nutritional stress in this cold season of minimal food abundance. In April, the Inland Sea of Japan significantly warms from the winter temperature minimum (to ca. 15°C), and zooplankton biomass increases to about 3 to 15 mg C m^{-3} for micro- and mesozooplankton, respectively. The production rates of those groups in April are on the order of 1 to 4 mg C m^{-3} d^{-1}, respectively (Uye et al. 1996, Uye & Shimazu 1997). Thus, ephyrae released early in the season (e.g. December-February) would be subjected to more starvation mortality than those released late in the season (e.g. March-April). Juding from the above-mentioned seasonal fluctuations in micro- and mesozooplaknton biomass and production rate as observed in the Inland Sea of Japan, I conclude that extremely long PNR_{50} may be a physiological as well as ecological adaptation allowing *A. aurita* ephyrae to survive the first few months after release, when food supply is generally lowest in many temperate coastal waters.

5-4. Mortality of *A. aurita* ephyrae in the field

Since food items are, in general, scarce and patchy in pelagic habitats, and predators are usually present, it is typical that planktonic larvae of many marine animals in nature are subjected to high mortality due to both food deprivation and predation loss (Bailey & Houde 1989, Paschke et al. 2004). The fate of *A. aurita* ephyrae is not likely an exception. In the innermost part of Tokyo Bay, Ishii et al. (2004) estimated the mortality from newly released ephyrae to young medusae of the natural *A. aurita* population. Based on the relative abundances of ephyrae in different developmental stages (ages), the cumulative mortality reached ca. 95% by age 4.6 d, and increased further to ca. 99% by the young medusa stage (20-28 d old). Ishii et al.

(2004) suspected that this high mortality was due to predation loss rather than starvation, since the eutrophic Tokyo Bay sustained extremely high zooplankton biomass (mean: 382 mg C m^{-3}) during the study period. Nevertheless, Ishii et al. (2004) failed to determine the actual predators of ephyrae in Tokyo Bay.

Makabe et al. (submitted) sampled *A. aurita* ephyrae at two locations in port areas of the Inland Sea of Japan: (1) Kuba and Ogata ports in Hiroshima Bay weekly from January to May 2010 and (2) at 6 ports (Harima, Mega, Himeji, Murotsu, Sakoshi and Hinase) in Harima Nada, eastern Inland Sea of Japan, where there are many artificial structures such as floating piers, buoys and old barges, the undersides of which often harbor polyp colonies that produce ephyrae (Miyake et al. 2002, Ishii & Katuskoshi 2010, Toyokawa et al. 2011, Duarte et al. 2013). Totals of 2,500 and 1,160 *A. aurita* ephyrae collected in Hiroshima Bay and Harima Nada, respectively, were photographed under the stereomicroscope to examine their morphometry as described in Chapter 2. As sampled ephyrae were preserved in 5% formalin-seawater solution, 15% shrinkage of their body was assumed after formalin fixation (Möller 1980) to reconstruct the frequency distribution of disc diameter (DD) for live ephyrae (Fig. 5-2 A, B, data provided from Makabe et al. unpulished).

Judging from a steep decline of larger ephyrae in the DD frequency distribution (Fig. 5-2), the mortality losses of field ephyrae appeared to be very great, although the actual rates could not be determine because no DD composition was available for newly released ephyrae and there were considerable exported ephyrae from port enclosures by tidal exchange. By detailed analysis of morphometry, only very small proportions of ephyrae (i.e. 0.9 and 1.5% in Hiroshima Bay and Harima Nada, respectively) were found to be significantly deformed by starvation (CDD/TBD >0.5 and RLL/MLL <0.3; see Fig. 2-6). As such deformation occurs only after starvation longer than PNR_{50} (Fig. 2-9), these individuals were destined to die of starvation. As it is impossible to detect starved ephyrae before PNR_{50} by means of biometric examination, the fraction of starved ephyrae may be much higher than the values mentioned above. Nevertheless, the examination of natural ephyra populations in the

Inland Sea of Japan confirms that starvation is among the factors to causing death of *A. aurita* ephyrae.

By the nature of physical characteristics of ephyrae, namely soft-bodies and slow swimming, they must be prone to predation, and consequently their mortality may be attributed to predation. Makabe et al. (unpublished information) examined gut contents of possible predators (e.g. hydromedusae and fish larvae) of ephyrae in some 200 plankton samples taken in winter and spring of 2010 and 2011 in Hiroshima Bay and Harima-Nada, the Inland Sea of Japan, but they could not find any explicit evidence of predation. Meanwhile, this study has revealed that a scyphozoan jellyfish *C. pacifica*, can capture and consume *A. aurita* ephyrae rather volatiously. So, I conclude that *C. pacifica* medusae, which often co-occur with *A. aurita* ephyrae in spring in the Inland Sea of Japan (Ueda 2007, Thein et al. 2013), may act as potential predators.

5-5. Future prospects for forecast of jellyfish blooms

For the forecast of *A. aurita* medusa population outbreaks, it is essential to determine the survival (or mortality) rates of newly released ephyrae, which are initially thought to be most critical in the life cycle stage. However, contrary to my working hypothesis, which speculates high vulnerability to starvation, *A. aurita* ephyrae show extraordinarily strong starvation resistance and recovery capability, implying that starvation may not be the major factor to influence the mortality of ephyrae. Therefore, detailed population dynamics studies, which traice the numerical abundance of the population from newly released ephyra stage to young medusa stage, as Ishii et al. (2004) preliminary conducted in Tokyo Bay, are essentially needed. Although this study revealed that a scyphozoan jellyfish *C. pacifica* is one of prominent predators of *A. aurita* ephyrae, more studies to search for potential predators and to estimate their predation impact are also required. The moon jellyfish *A. aurita* is undoubtedly the most extensively studied scyphozoan species, yet its ephyra stage is still greatly understudied, and many further studies are needed.

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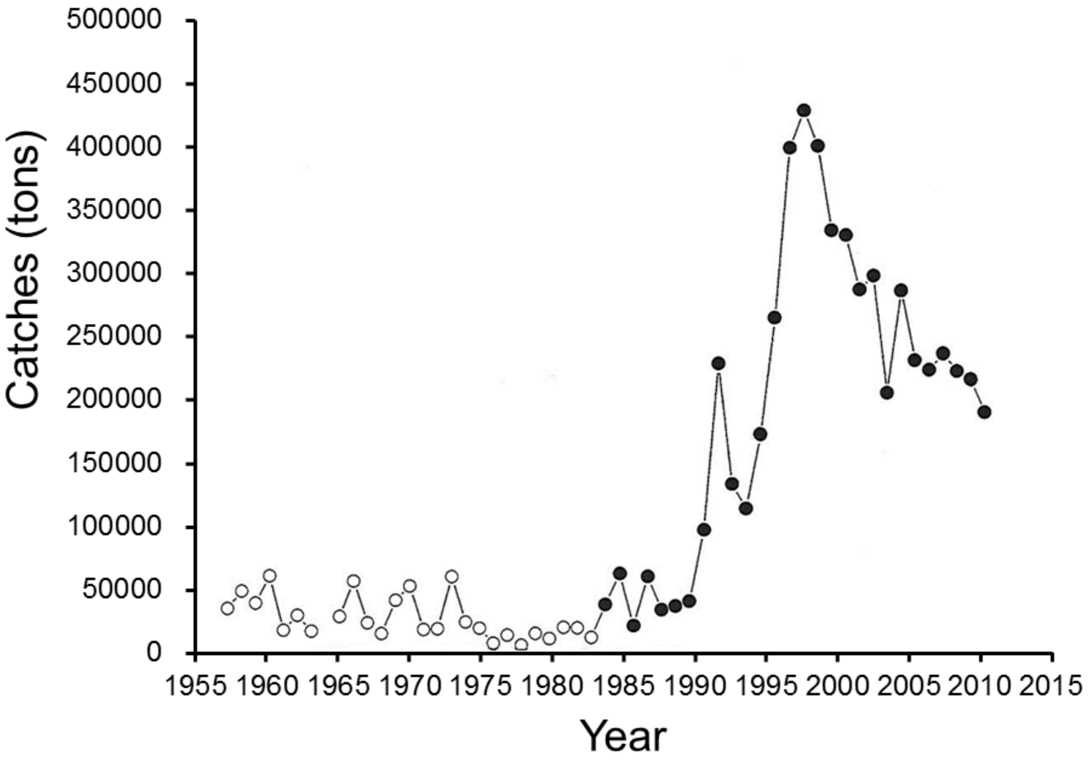

Fig. 1-1. Historical change in annual catch of *Rhopilema esculentum* in Chinese waters in tons wet weight. Open circles: harvest before stock enhancement; solid circles: harvest after stock enhancement (From Dong et al. 2014).

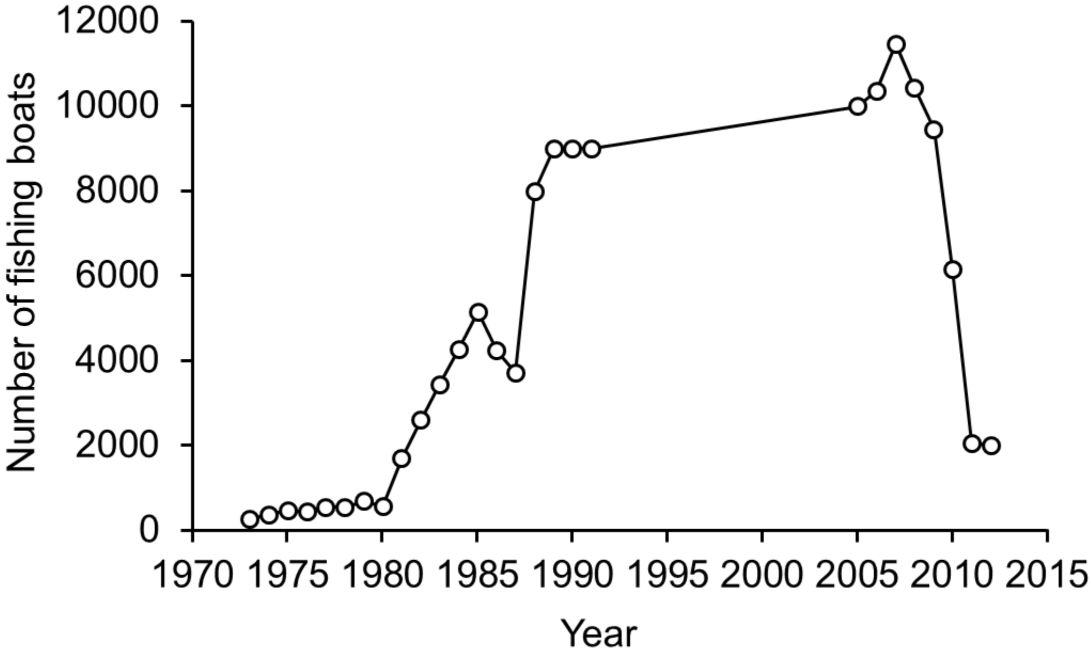

Fig. 1-2. Historical change in numbers of fishing boats in Liaodong Bay. Note that data between 1992 and 2004 are omitted because of considerable numbers of boats operating fishery prior to the official opening of fishing season (From Dong et al. 2013).

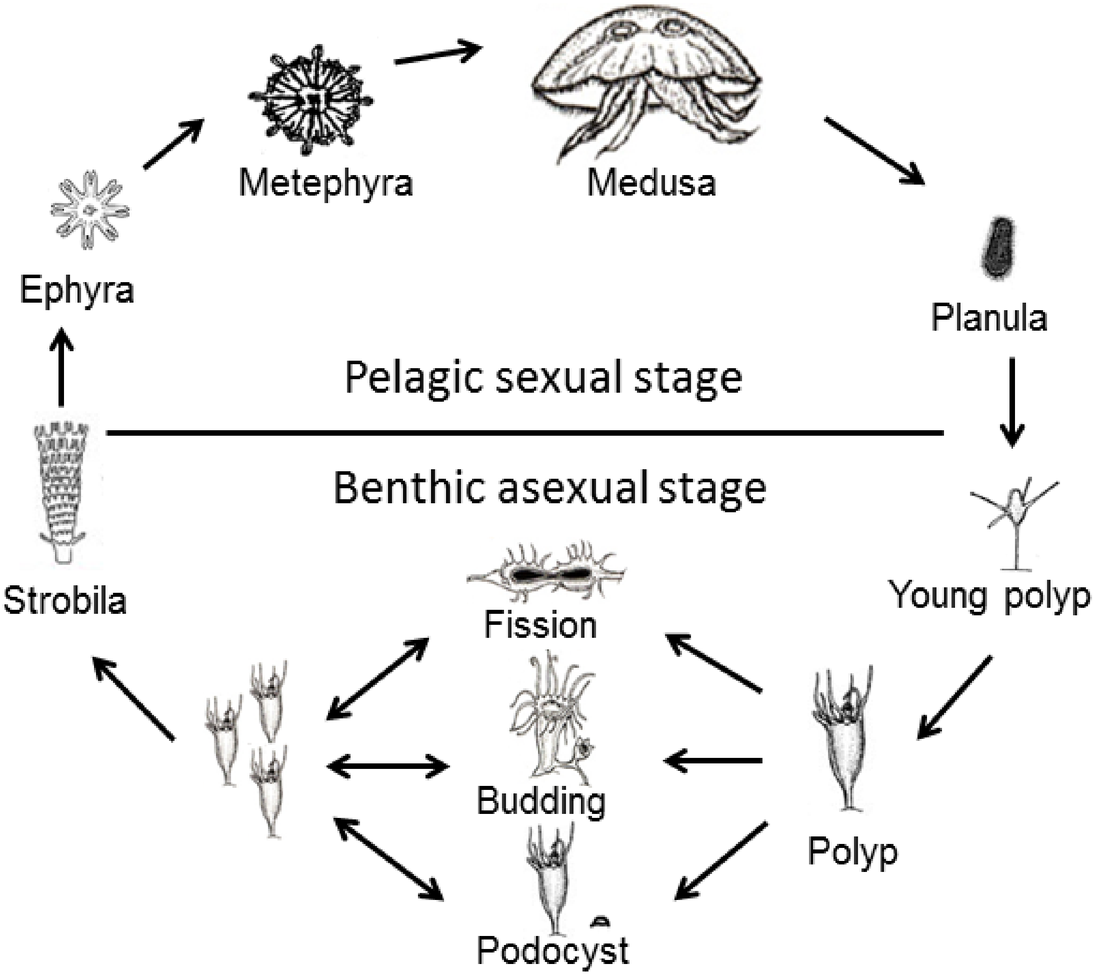

Fig. 1-3. Schematic diagram of the life cycle of the genus *Aurelia* (mainly from Yasuda 2007).

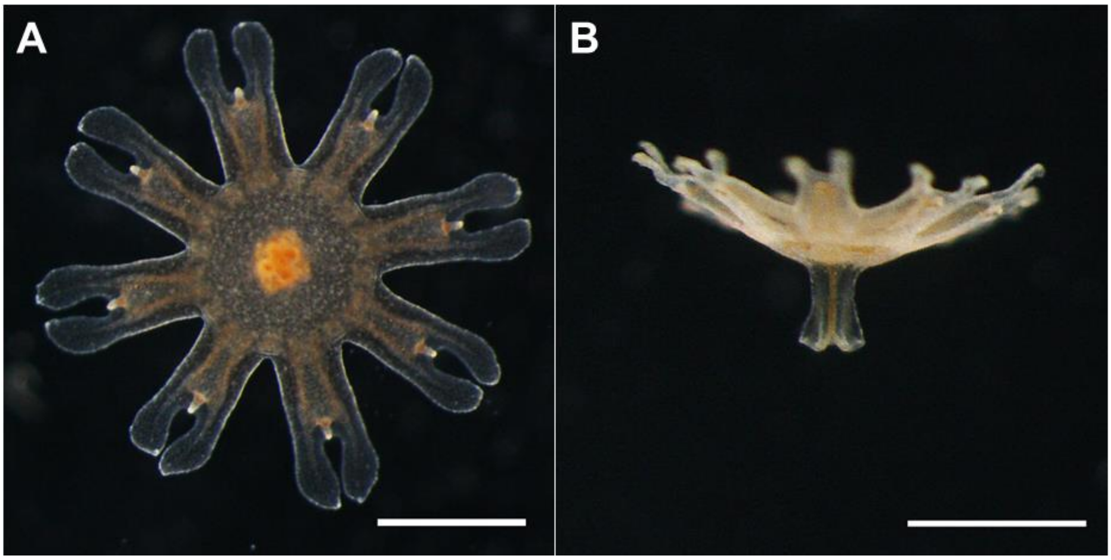

Fig. 1-4. Photography of a newly released *Aurelia aurita* ephyra. (A) Ventral view showing 8 fully extended marginal lappets. (B) Lateral view showing a protruded manubrium. Scale bars: 1 mm.

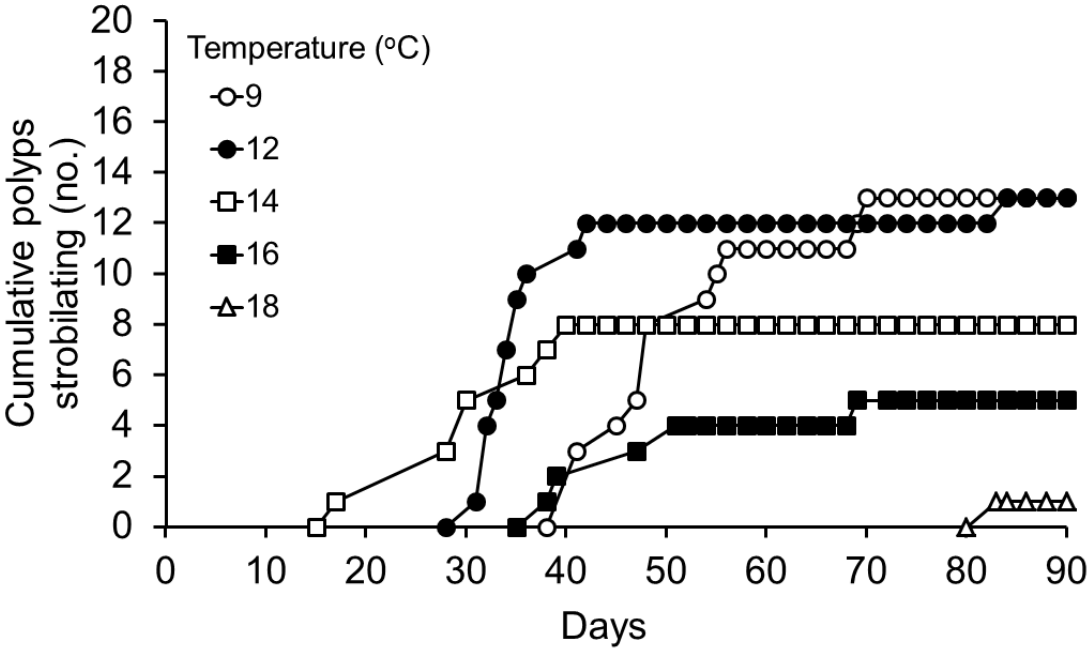

Fig. 2-1. Cumulative numbers of strobilating polyps of *Aurelia aurita* at 5 different temperatures (i.e. 9, 12, 14, 16 and 18°C) during 90 days of experiment under darkness.

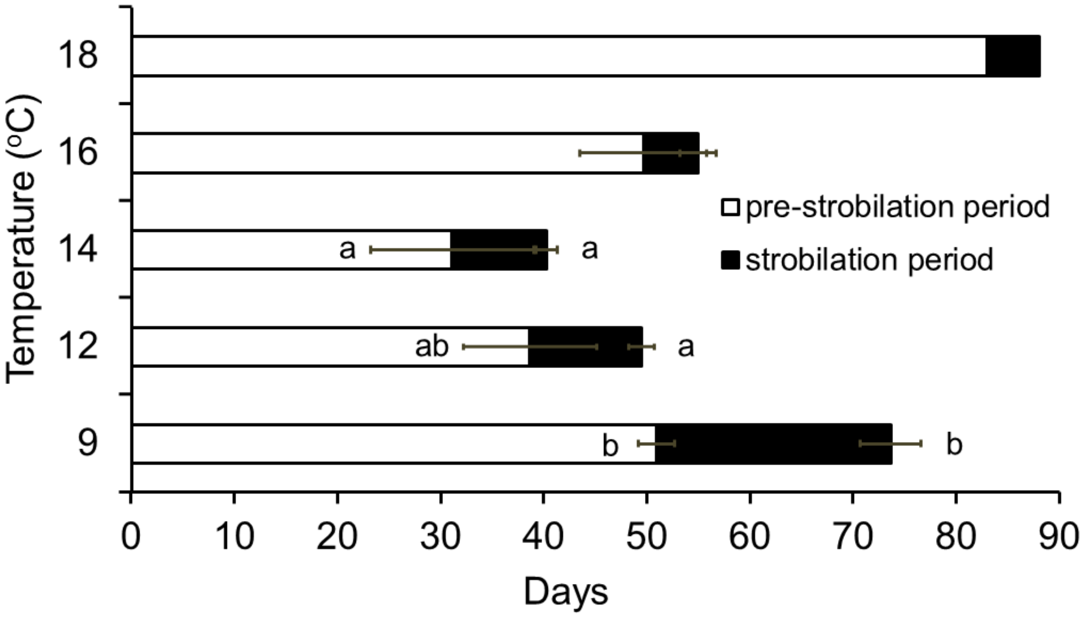

Fig. 2-2. Mean pre-strobilation periods (white bars) and strobilation periods (black bars) of *Aurelia aurita* at 5 different temperatures (i.e. 9, 12, 14, 16 and 18^{o}C) during 90 days of experiment under darkness. Means with different letters are significantly different. Horizontal bars: SD.

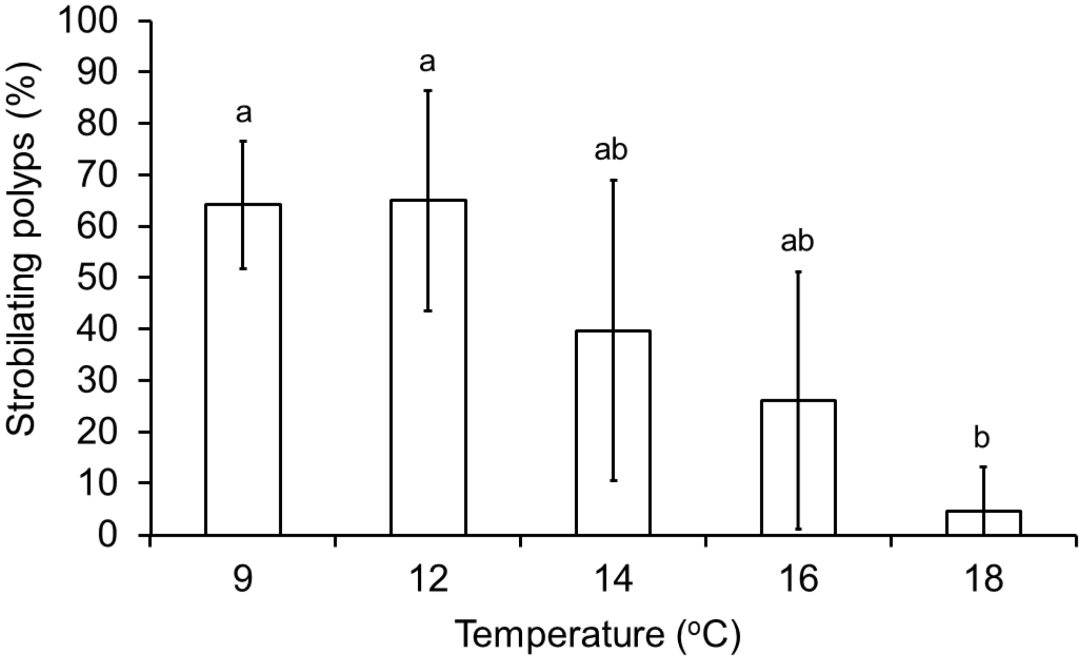

Fig. 2-3. The mean strobilation ratio of *Aurelia aurita* kept at 5 different temperatures (i.e. 9, 12, 14, 16 and 18°C) during 90 days of experiment under darkness. Vertical bars: SD. Means with different letters are significantly different.

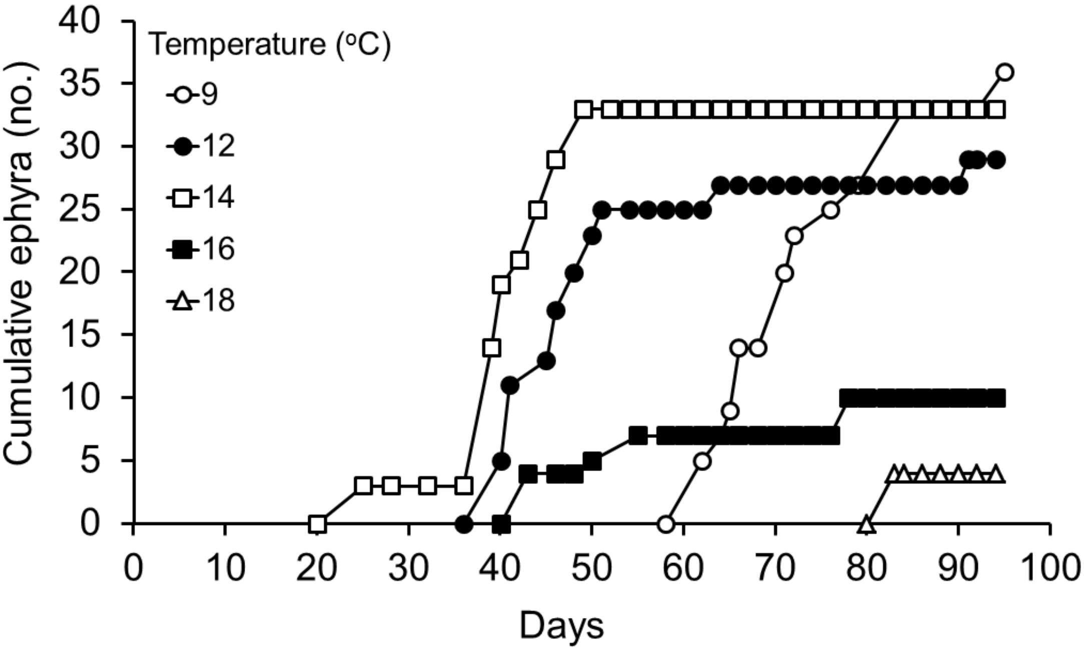

Fig. 2-4. Cumulative numbers of ephyrae of *Aurelia aurita* produced at 5 different temperatures (i.e. 9, 12, 14, 16 and 18^{o}C) during 90 days of experiment under darkness.

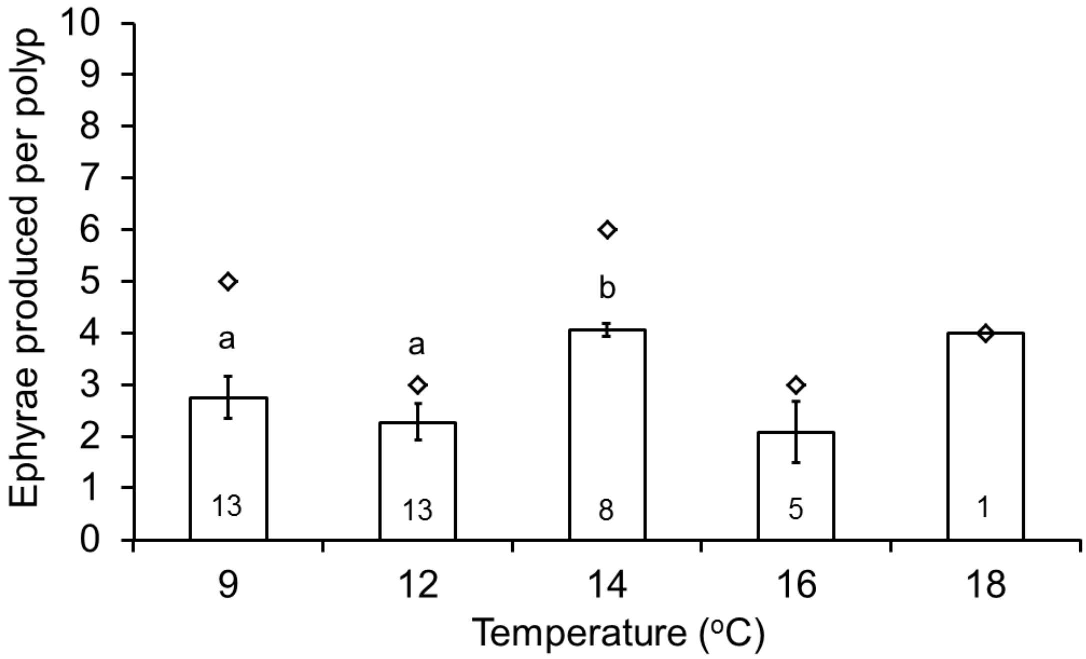

Fig. 2-5. Mean numbers of ephyrae of *Aurelia aurita* produced per polyp at 5 different temperatures (i.e. 9, 12, 14, 16 and 18°C) during 90 days of experiment under darkness. Numerals inside columns indicate the numbers of polyps used for the calculation. Diamonds denote the maximal number of ephyrae produced. Vertical bars: SD. Means with different letters are significantly different.

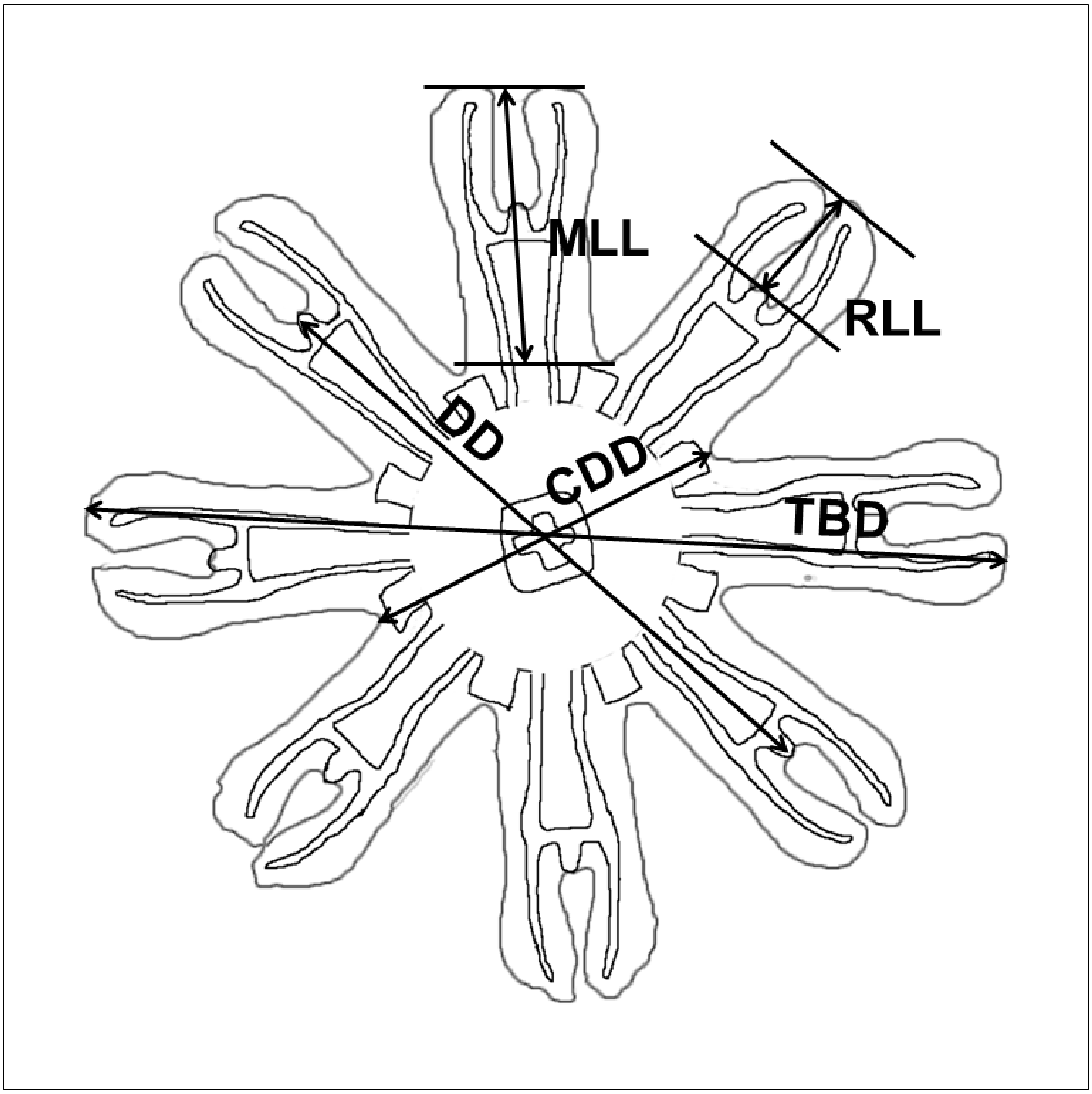

Fig. 2-6. Drawing of an *Aurelia aurita* ephyra showing measured dimensions. CDD: central disc diameter, DD: disc diameter, TBD: total body diameter, RLL: rhopalial lappet length, MLL: marginal lappet length.

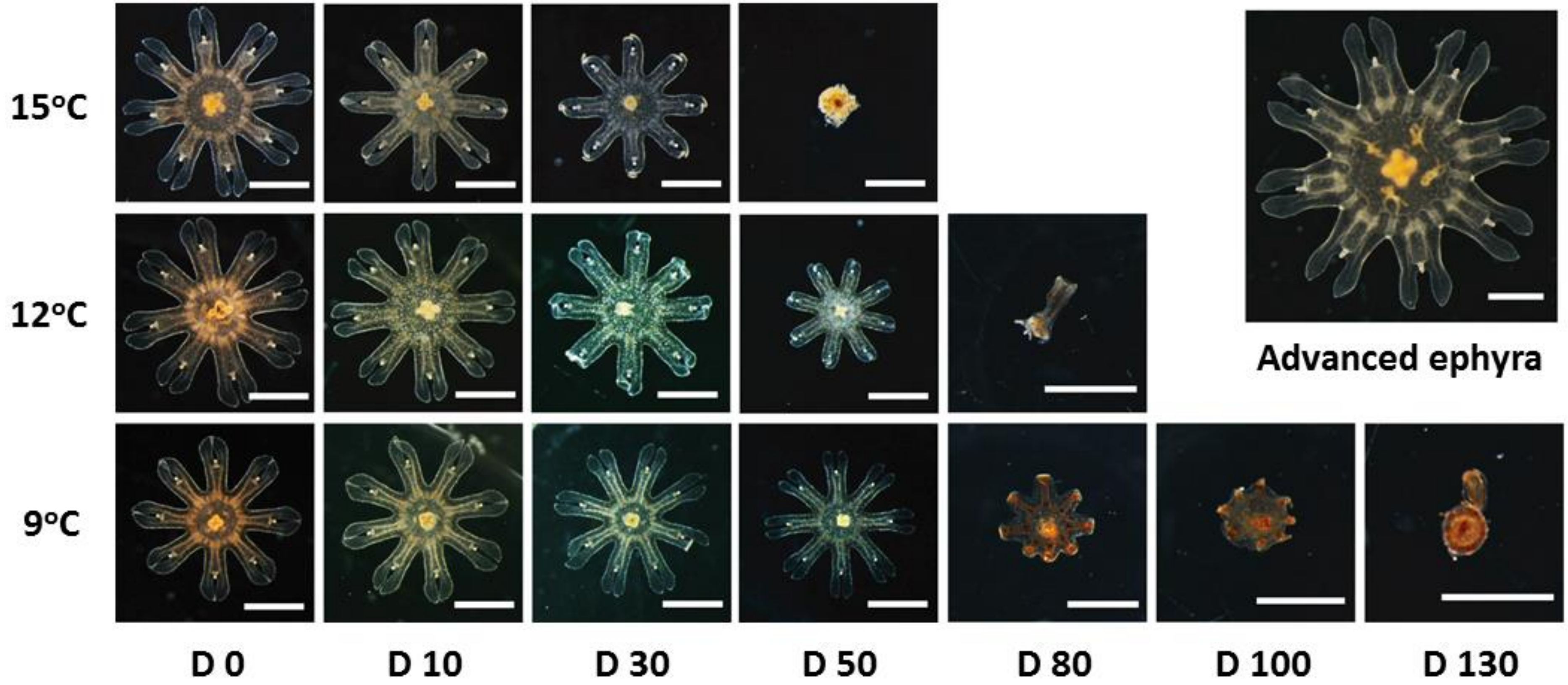

Fig. 2-7. Morphological changes in *Aurelia aurita* ephyrae kept starved for various periods at 9, 12 and 15^{o}C. The D numbers are the days of continuous starvation. An advanced ephyra is also shown. Scale bars: 1 mm.

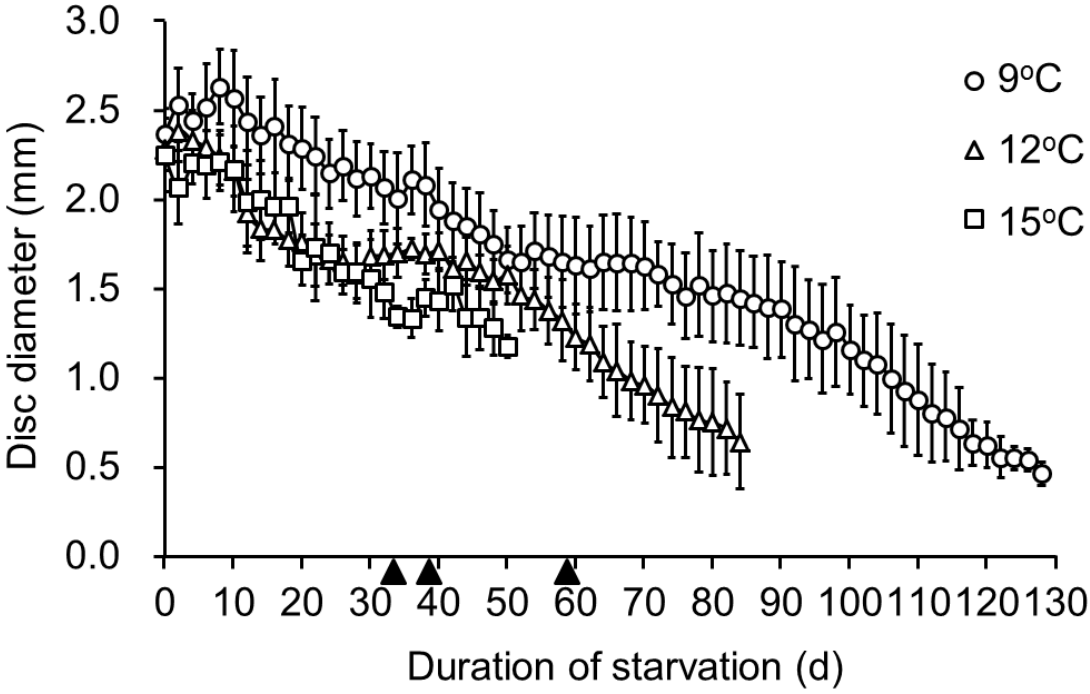

Fig. 2-8. Change in disc diameter (DD) of *Aurelia aurita* ephyrae kept starved for various periods at 9, 12 and 15°C. Error bars: SD. Filled triangles: PNR_{50} at 15, 12 and 9°C from left to right.

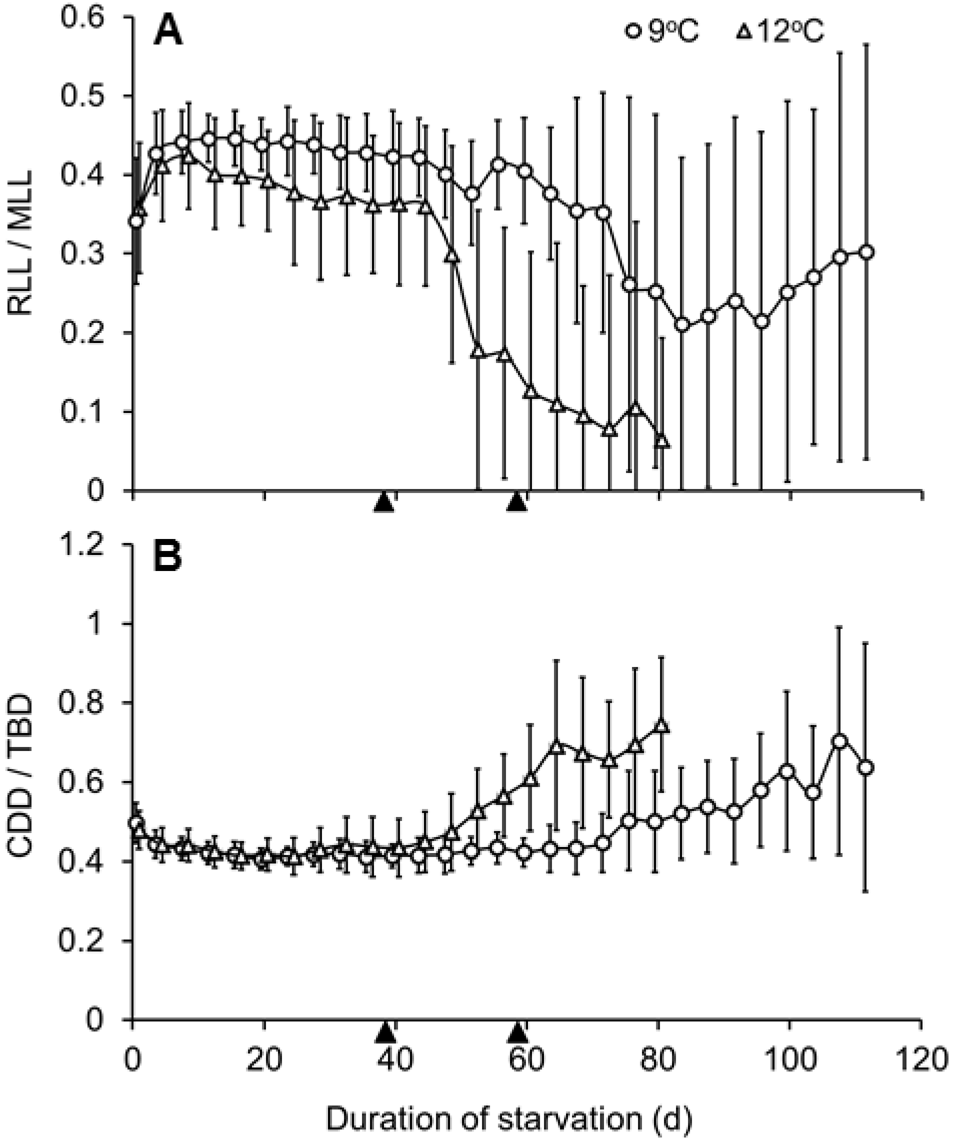

Fig. 2-9. Changes in body proportions of (A) RLL/MLL and (B) CDD/TBD of *Aurelia aurita* ephyrae kept starved for various periods at 9 and 12°C. Error bars: SD. Filled triangles: *PNR*$_{50}$ at 12 and 9°C from left to right.

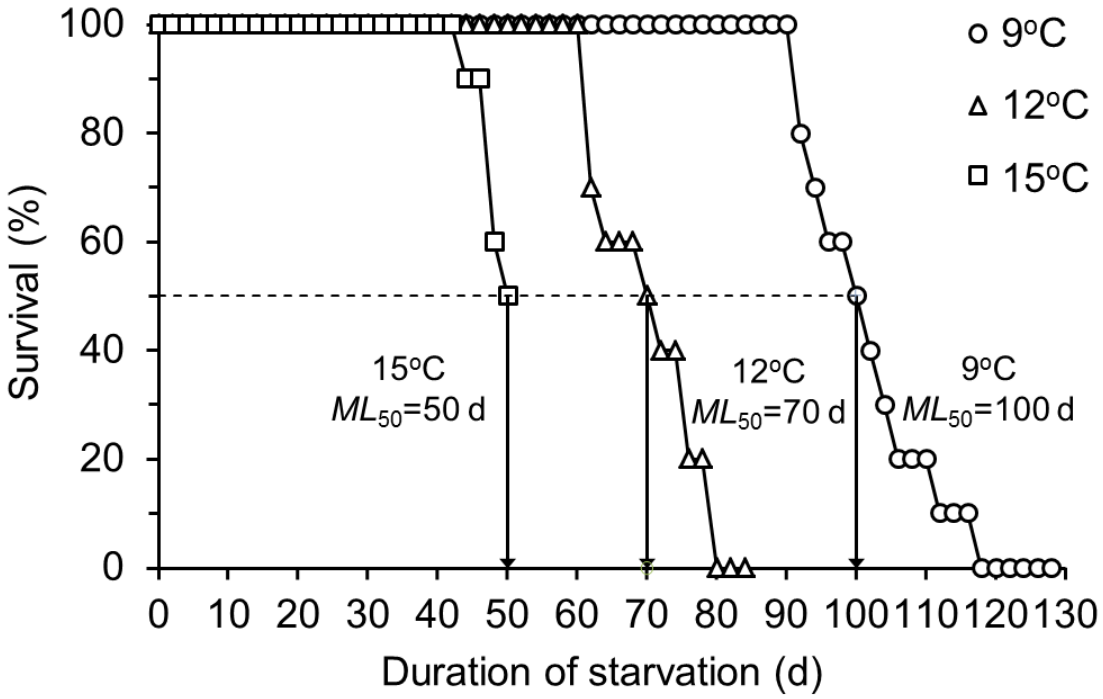

Fig. 2-10. Survival of *Aurelia aurita* ephyrae kept starved for various periods at 9, 12 and 15°C. Median longevity (ML_{50}) is the starvation period at which 50% of ephyrae had died.

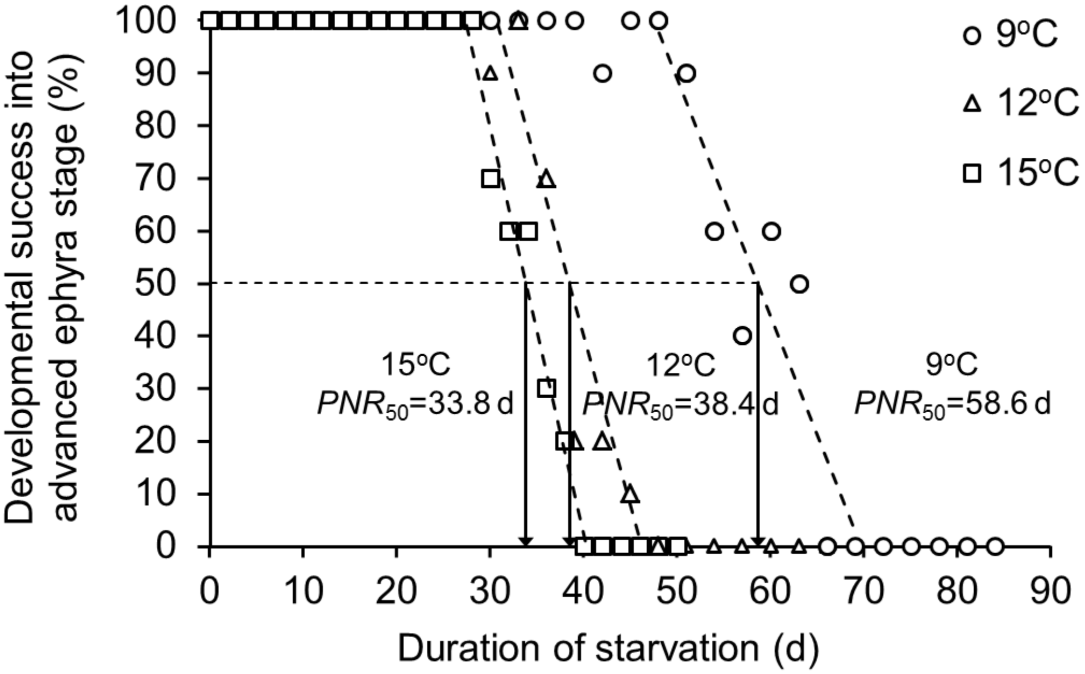

Fig. 2-11. Success of starved *Aurelia aurita* ephyrae in developing to become advanced ephyrae when given food after different intervals of starvation. Results shown for ephyrae held at 9, 12 and 15°C. Point-of-no-return (*PNR*$_{50}$) is the starvation period at which 50% of ephyrae remain capable of recovering from starvation damage and growing to become advanced ephyrae.

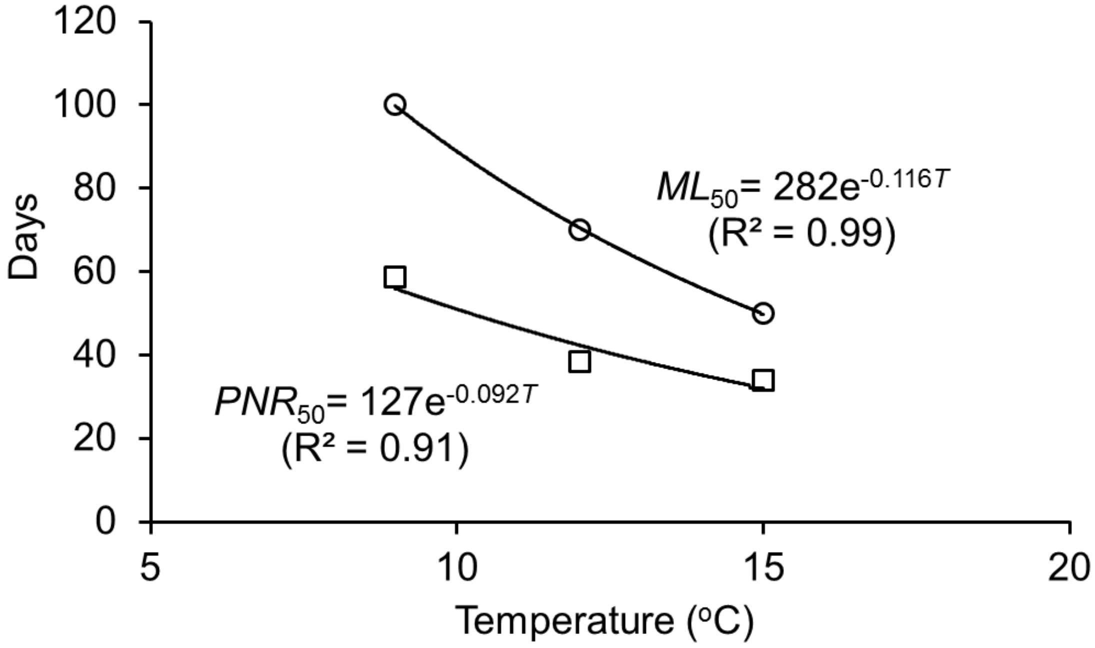

Fig. 2-12. Relationships of the median longevity (ML_{50}) and point-of-no-return (PNR_{50}) of *Aurelia aurita* ephyrae with temperature.

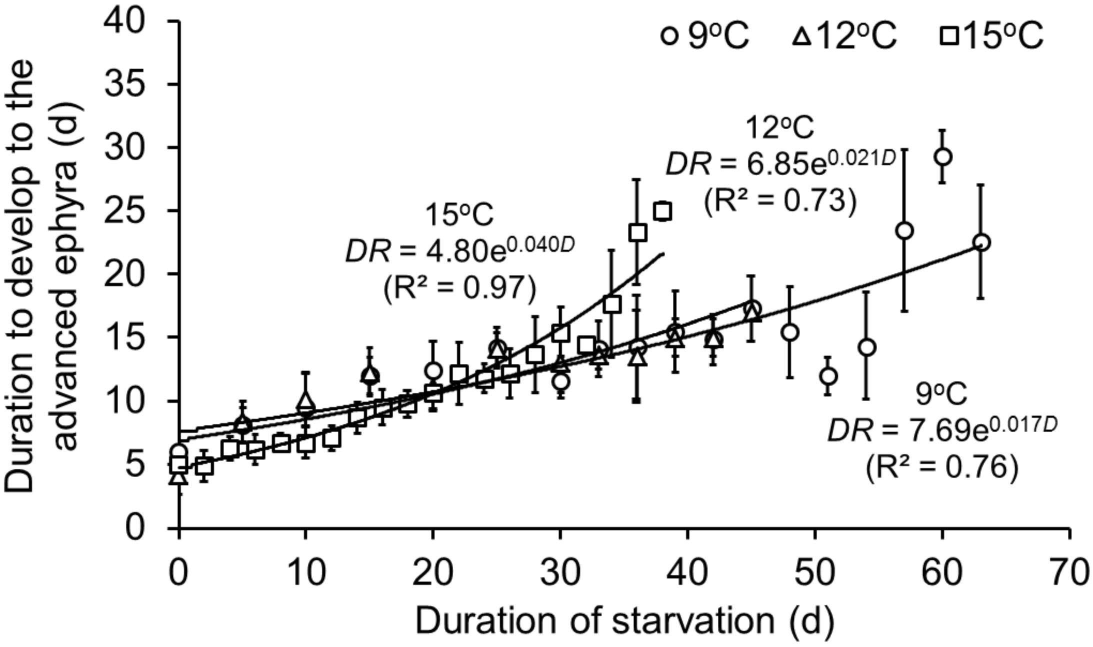

Fig. 2-13. Relationships between the duration required by initially starved *Aurelia aurita* ephyrae to develop into advanced ephyrae after feeding began and the durations of starvation at 9, 12 and 15°C. Error bars: SD.

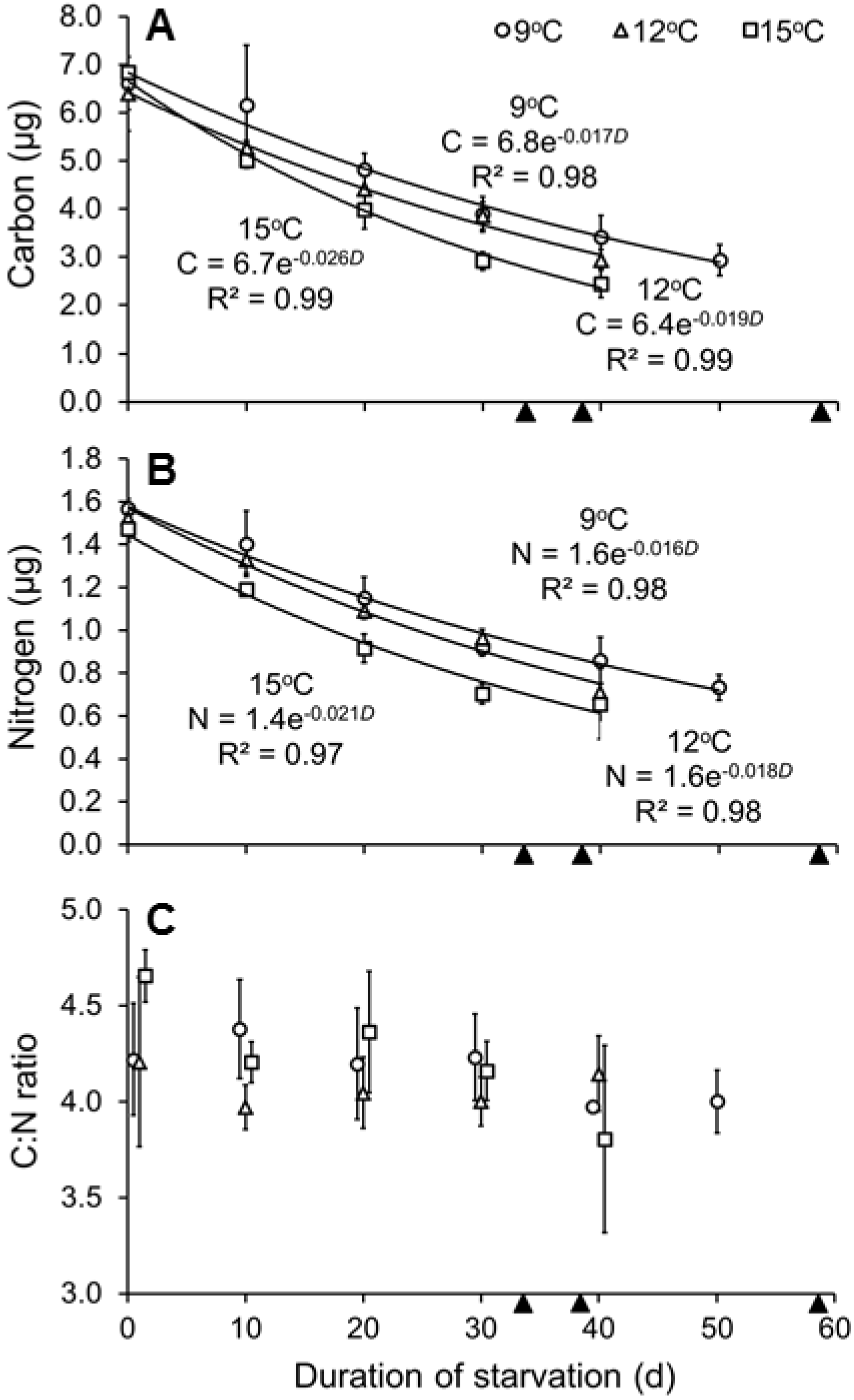

Fig. 2-14. Change in (A) carbon, (B) nitrogen and (C) carbon:nitrogen ratio (C:N) of *Aurelia aurita* ephyrae kept starved for various periods at 9, 12 and 15°C. Error bars: SD. Filled triangles: PNR_{50} at 15, 12 and 9°C from left to right.

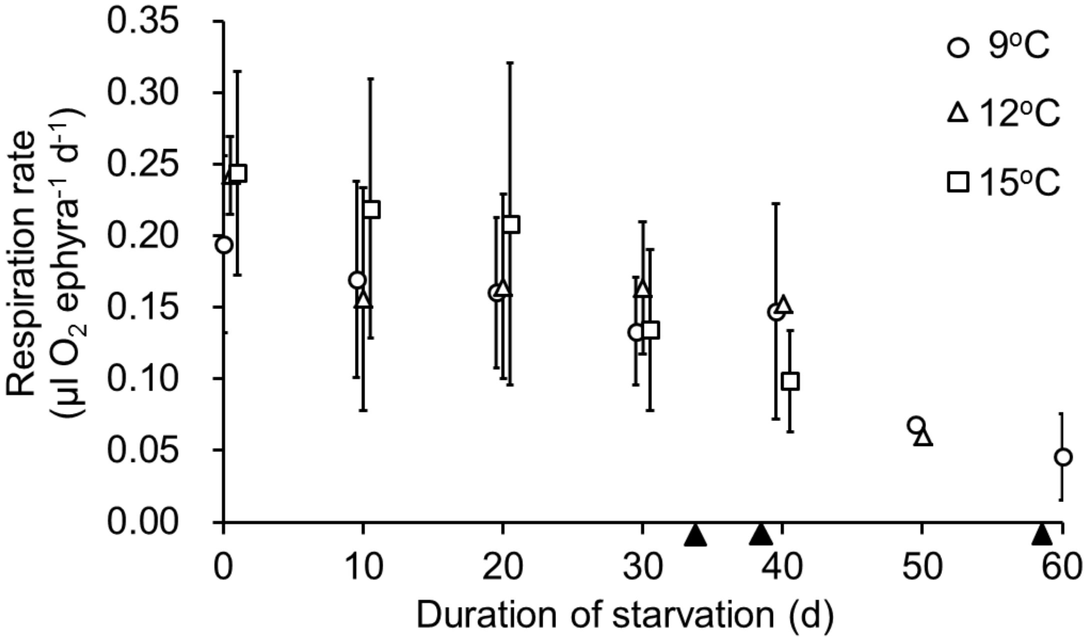

Fig. 3-1. The mean respiration rate of an *Aurelia aurita* ephyra kept starved for various periods at 9, 12 and 15°C. Error bars: SD. Filled triangles: PNR_{50} at 15, 12 and 9°C from left to right.

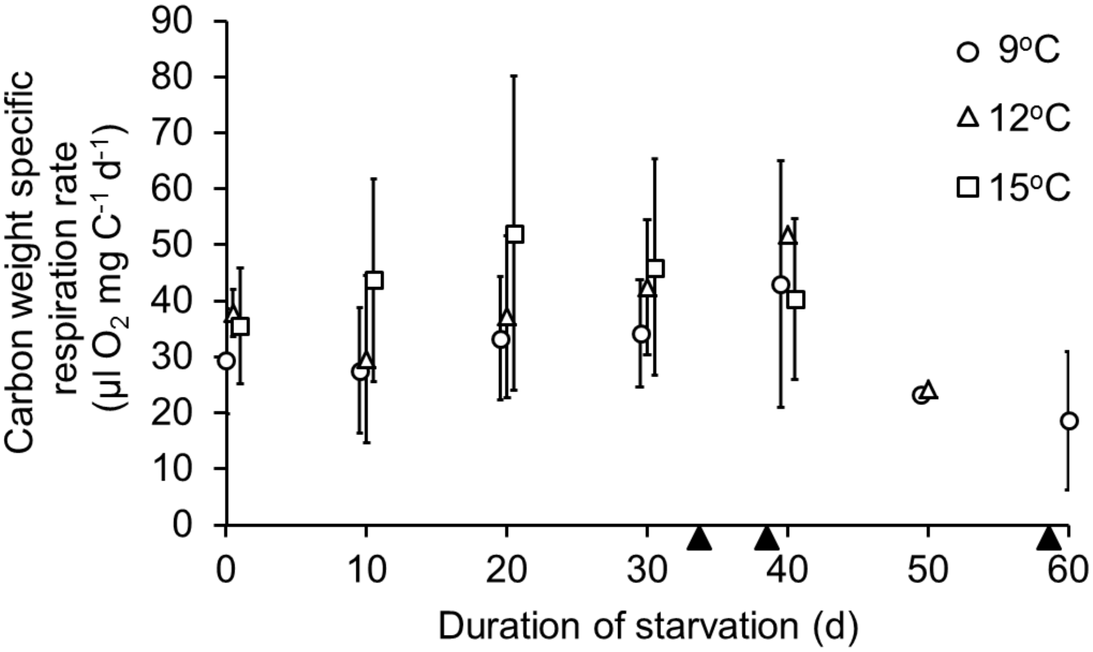

Fig. 3-2. The mean carbon weight-specific respiration rate of an *Aurelia aurita* ephyra kept starved for various periods at 9, 12 and 15°C. Error bars: SD. Filled triangles: PNR_{50} at 15, 12 and 9°C from left to right.

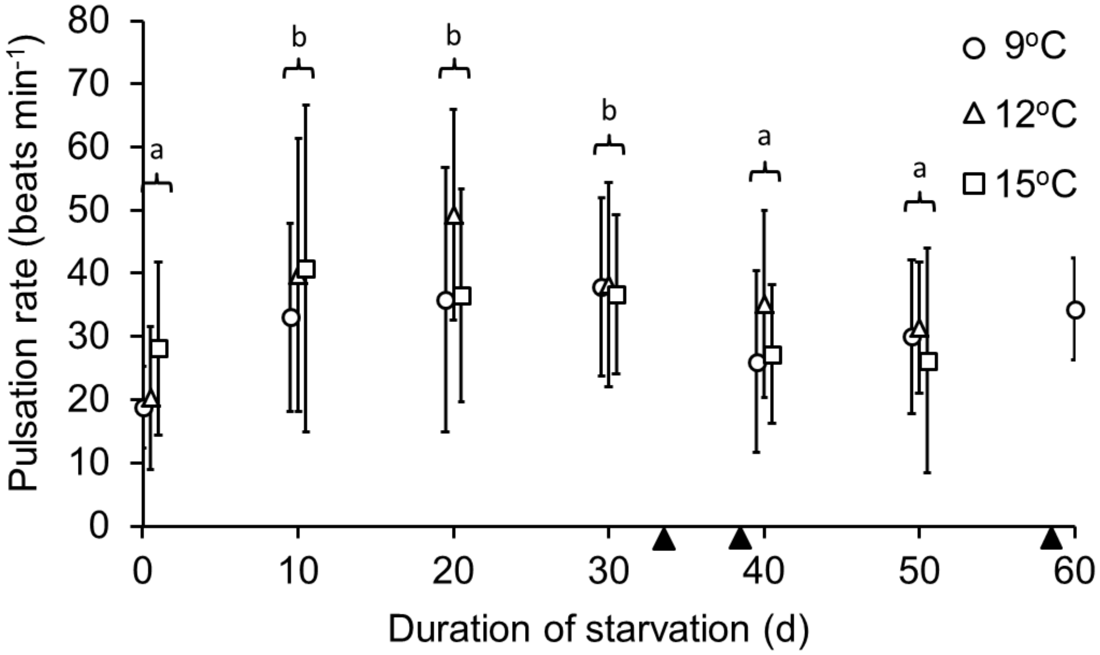

Fig. 3-3. The mean pulsation rate (contractions of umbrella per minute) of an *Aurelia aurita* ephyra kept starved for various periods at 9, 12 and 15°C. Error bars: SD. Filled triangles: PNR_{50} at 15, 12 and 9°C from left to right. Means with different letters are significantly different.

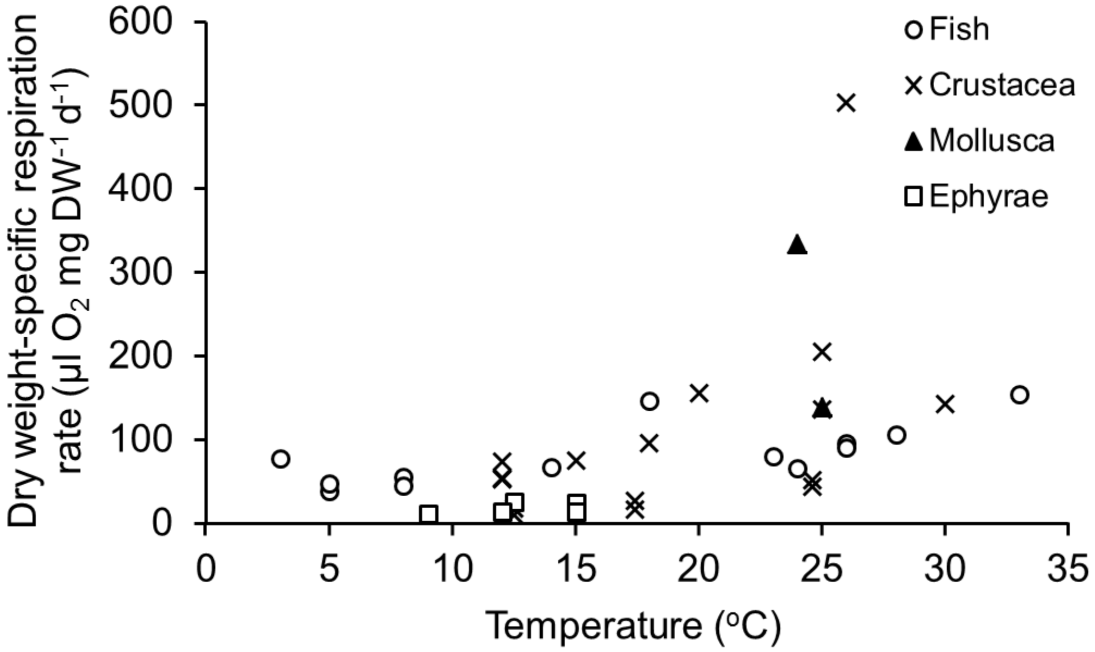

Fig. 3-4. Dry weight-specific respiration rates of newly-hatched larvae of molluscs, crustaceans and fishes, including *Aurelia aurita* ephyrae. See Table 3-1 for respective data.

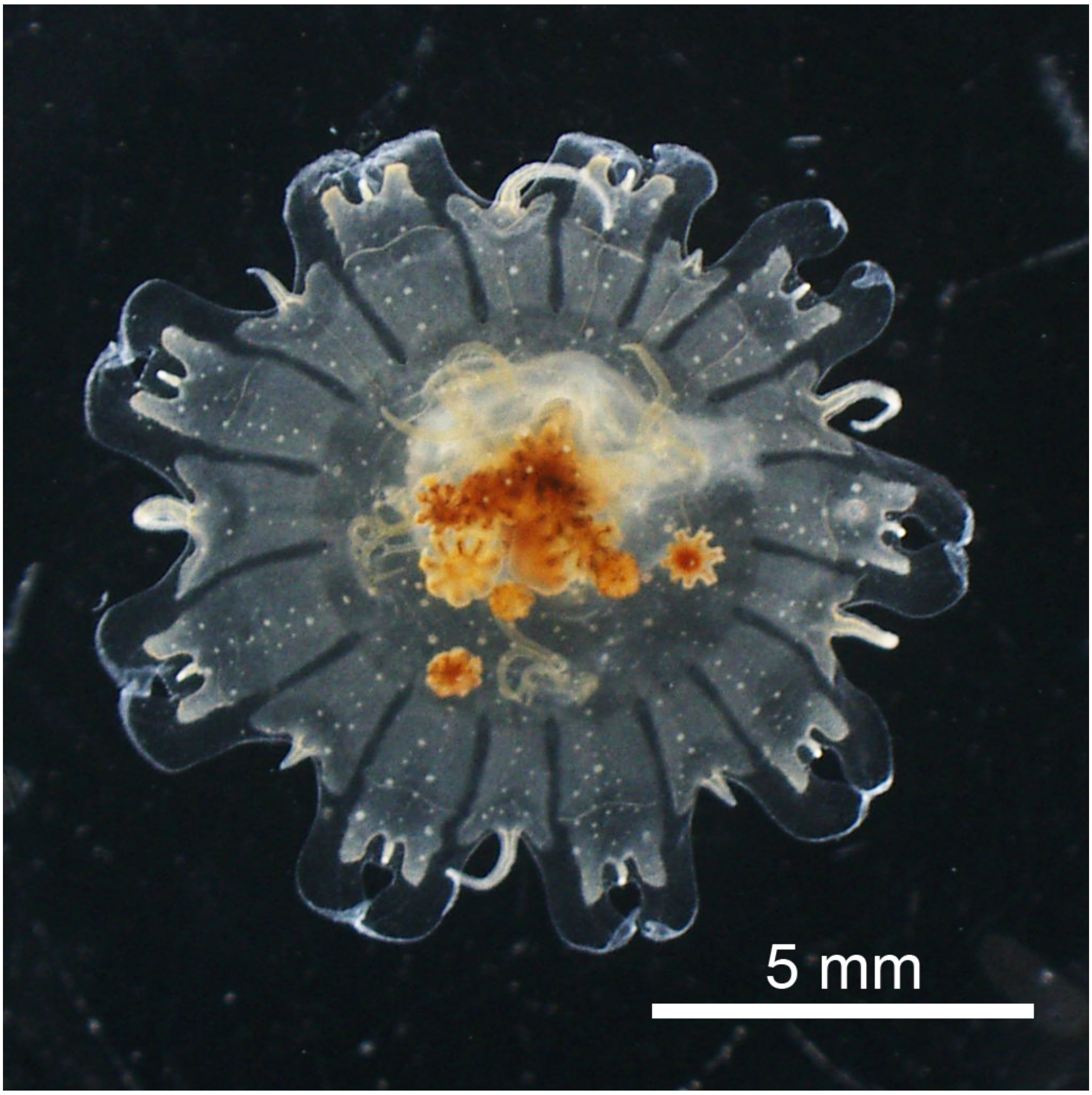

Fig. 4-1. A photograph showing ingested *Aurelia aurita* ephyrae in the gastric pouch of *Chrysaora pacifica* after the predation experiment was completed.

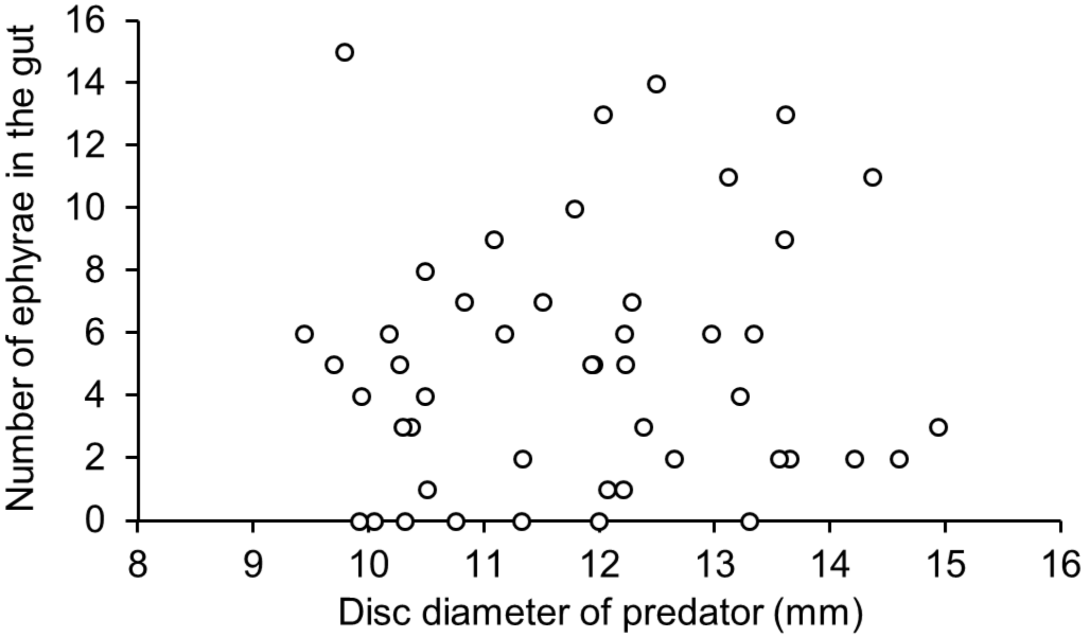

Fig. 4-2. Numbers of *Aurelia aurita* ephyrae ingested by *Chrysaora pacifica* of various disc diameters in experiments of two different prey densities, 20 and 50 ephyrae bottle^{-1}.

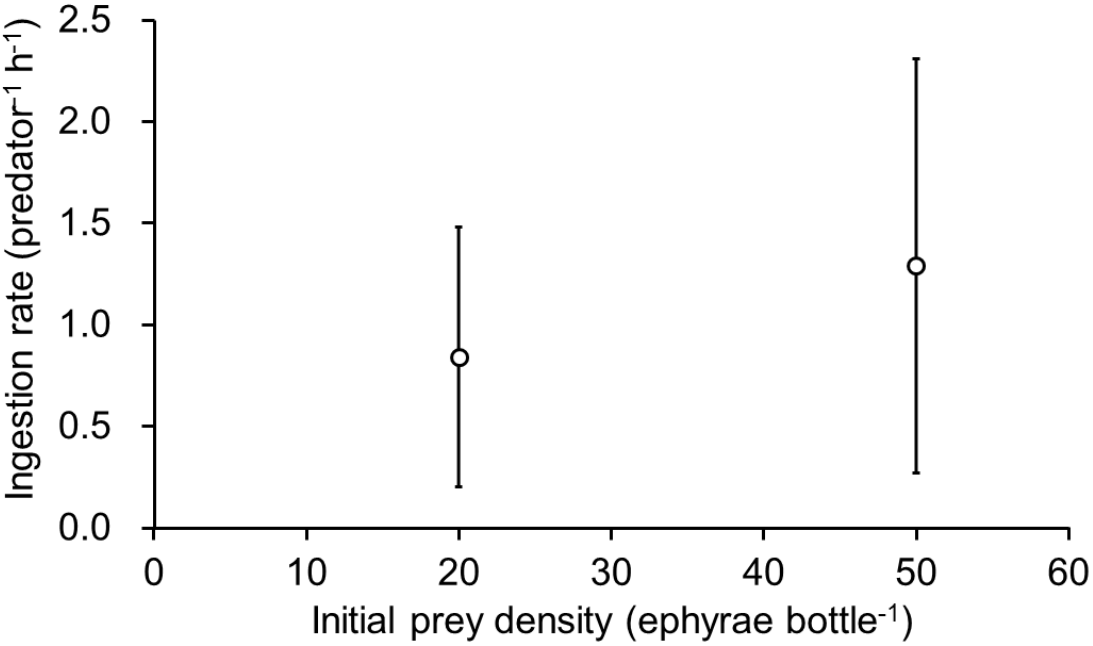

Fig. 4-3. Predation rate of *Chrysaora pacifica* on *Aurelia aurita* ephyrae at two different prey densities, 20 and 50 ephyrae bottle^{-1}. Vertical lines: SD.

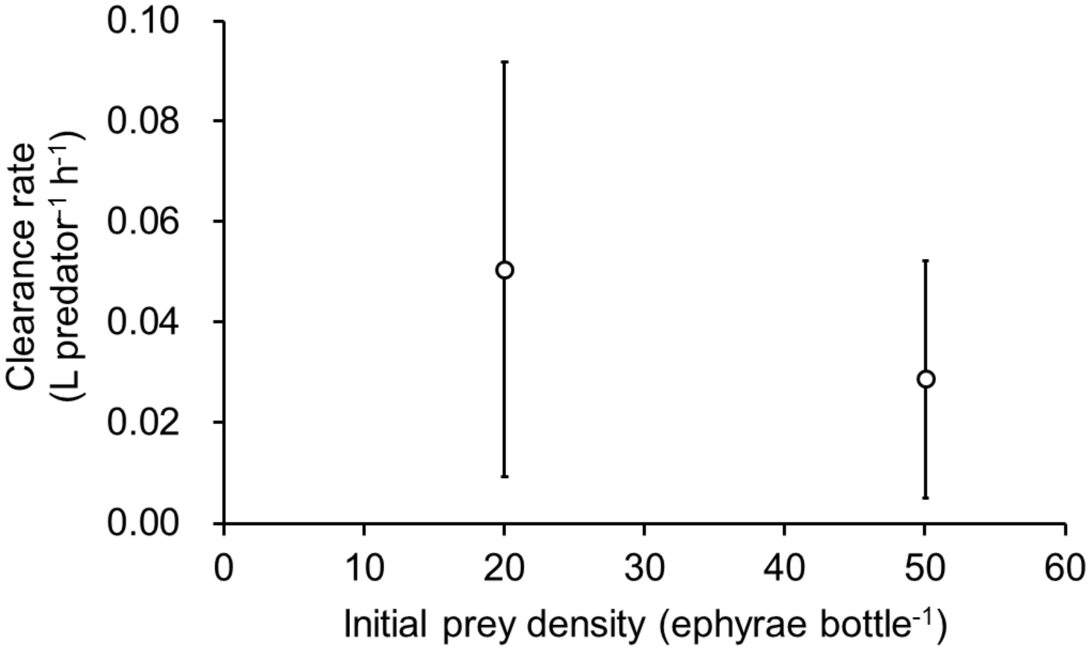

Fig. 4-4. Clearance rate of *Chrysaora pacifica* feeding on *Aurelia aurita* ephyrae at two different prey densities, 20 and 50 ephyrae bottle^{-1}. Vertical lines: SD.

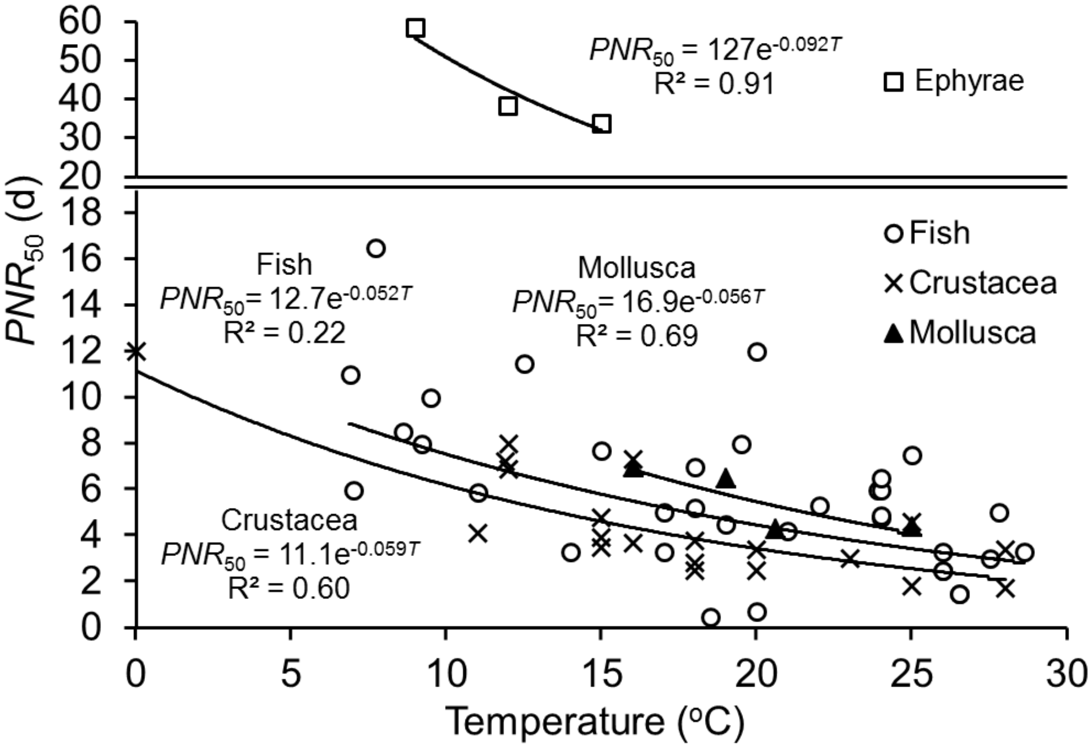

Fig. 5-1. Relationships between PNR_{50} and temperature in *Aurelia aurita* ephyrae, and larvae of molluscs, crustaceans and fishes. Note the different vertical axis scales between *A. aurita* ephyrae and the other taxa. See Table 5-1 for respective data.

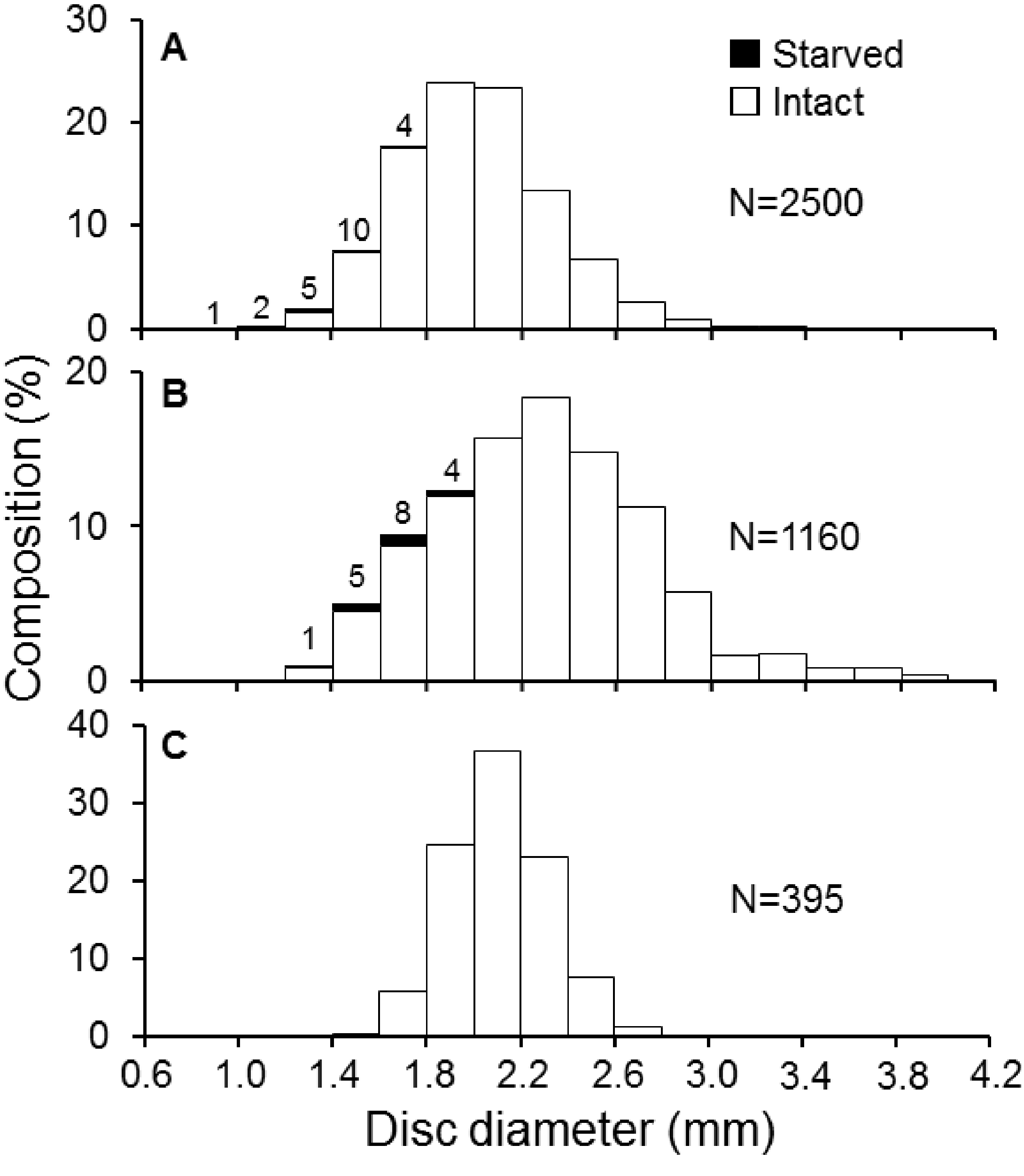

Fig. 5-2. Frequency distributions of disc diameters of *Aurelia aurita* ephyrae sampled in (A) Hiroshima Bay and (B) Harima Nada, the Inland Sea of Japan, and of (C) ephyrae newly released in the laboratory cultures. Numerals show the numbers of ephyrae exhibiting starvation-derived morphology in each DD range. Data for (A) and (B) are from Makabe et al. (unpulished) by permission.

Table 1-1. List of cnidarian jellyfish species in Chinese seas. + means occurrence (From Zheng et al. 1991, Gao et al. 2002 Hong & Lin 2010, and Dong et al. 2010).

Species	Geographical distribution			
	Bohai Sea	Yellow Sea	East China Sea	South China Sea
Class Cubozoa				
Order Carybdeidae				
Carybdea rastoni Haeckel			+	+
C. sivickisi Stiasny			+	+
Tamoya alata Reynaud			+	+
Class Hydrozoa				
Subclass Hydroidolina				
Order Anthoathecata				
Sarsia nipponica Uchida		+		+
Ectopleura dumortieri van Beneden	+	+	+	+
Euphysa aurata Forbes		+	+	
Ephysora bigelowi Maas		+	+	+
Velella velelle Linnaeus			+	+
Zanclea costata Gegenbaur		+	+	+
Cytaeis tetrastyla Eschscholtz			+	+
Turritopsis nutricula McCrady	+	+	+	+
Rathkea octopunctata M. Sars	+	+	+	
Podocoryne minina Trinci		+		
Bougainvillia britannica Forbes	+	+	+	+
B. ramosa van Beneden	+	+	+	+
Nemopsis bachei Agassiz				+
Koellikerina constricta Menon			+	+
Amphinema dinema Peron et Lesueur	+	+	+	+
Leuckartiara hoepplii Hsu	+	+	+	+
Heterotiara minor Vanhoffen				+
Order Leptothecata				
Laodicea undulata Forbes et Goodsir			+	+
Phialidium chengshanense Ling	+	+	+	+
P. hemisphaericum Linnaeus	+	+	+	+
Eucoeilota menoni Kramp			+	+
Lovenella assimilis Browne		+	+	+
Phialucium carolinae Mayer		+	+	+
Octophialucium indicum Kramp		+	+	+
Eirene ceylonensis Browne	+	+	+	+

E. hexanemalis Goette	+	+	+
Helgicirraha malayensis Stiasny	+	+	+
Eutima (*Octorchis*) *gegenbauri* Haeckel	+	+	
E. levuka Agassiz et Mayer		+	+
Aequorea australis Uchida	+	+	+
A. parva Browne		+	+
Order Siphonophore			
Physalia physalis Linnaeus		+	+
Rhizophysa filiformis Forskal		+	+
Agalma okeni Eschscholtz		+	+
A. elegans Sars	+	+	+
Halistemma rubrum Vogt		+	+
Nanomia bijuga Chiaje		+	+
N. cara Agassiz			+
Nectalia loligo Haeckel			+
Bargmannia elongata Totton			+
Physophora hydrostatica Forskal	+	+	+
Forskalia edwardsi Kolliker		+	+
Amphicaryon acaule Chun		+	+
A. peltifera Haeckel		+	+
A. ernesti Totton		+	+
Rosacea plicata Quoy et Gaimard		+	+
Praya reticulata Bigelow		+	+
Hippopodius hippopus Forskal		+	+
Vogtia serrata Moser		+	+
V. spinosa Kefferstein et Ehlers		+	+
V. pentacantha Kolliker		+	+
V. kuruae Alvarino			+
V. glabra Bigelow		+	+
V. microsticella Zhang		+	+
Sulculeolaria monoica Chun		+	+
S. quadrivalvis Blainville	+	+	+
S. brintoni Alvarino		+	+
S. turgida Gegenbaur		+	+
S. biloba Sars		+	+
S. angusta Totton		+	+
S. chuni Lens et van Riemsdijk		+	+
S. bigelowi Sears			+
S. tropica Zhang		+	+
S. xishanensis Hong et Zhang		+	+
Diphyes dispar Chamisso et Eysenhardt		+	+
D. bojani Eschscholtz		+	+

D. chamissonis Huxley	+	+	+	+
Lensia subtiloides Lens et van Riemsdijk		+	+	+
L. subtilis Chun			+	+
L. leloupi Totton			+	+
L. campanella Moser			+	+
L. fowleri Bigelow			+	+
L. challengeri Totton			+	+
L. hotspur Totton			+	+
L. cossack Totton			+	+
L. meteori Leloup			+	+
L. tottoni Daniel A. et Daniel R.			+	+
L. conoides Kefferstein et Ehlers			+	+
L. cordata Totton				+
L. havock Totton				+
L. multicristata Moser			+	+
L. multicristatoides Zhang et Lin				+
Muggiaea atlantica Cunningham	+	+	+	+
M. delsmani Totton			+	+
Dimophyes arctica Chun			+	+
Chelophyes appendiculata Eschscholtz		+	+	+
C. contorta Lens et van Riemsdijk			+	+
Eudoxides spiralis Bigelow			+	+
E. mitra Huxley			+	+
E. macra Totton			+	+
Chuniphyes multidentata Lens et van Riemsdijk			+	+
C. moserae Totton				+
Clausophyes ovata Kefferstein et Ehlers				+
C. galeata Lens et van Riemsdijk			+	+
Sphaeronectes gracilis Claus			+	+
Ceratocymba sagittata Quoy et Gaimard			+	+
C. leuckarti Huxley			+	+
C. dentata Bigelow			+	+
C. intermedia Sears				+
Abyla trigona Quoy et Gaimard			+	+
A. carina Haeckel				+
A. schmidti Sears			+	+
A. haeckeli Lens et van Riemsdijk			+	+
A. tottoni Sears				+
A. brownia Sears				+

A. bicarinata Moser			+	+
Abylopsis tetragona Otto		+	+	+
A. eschscholtzi Huxley		+	+	+
Bassia bassensis Quoy et Gaimard			+	+
Enneagonum hyalinum Quoy et Gaimard			+	+
E. searsae Alvarino			+	+
Subclass Trachylina				
Order Limnomedusae				
Tiaricodon coeruleus Browe		+		+
Gonionemus vertens A. Agassiz		+	+	
Proboscidactyla ornata McCrady		+	+	+
Order Narcomedusae				
Aegina citrea Eschschooltz				+
Aeginura grimaldii Maas		+	+	+
Solmundella bitentaculata Quoy et Gaimard		+	+	+
Order Trachymedusae				
Rhopalonema velatum Gegenbaur			+	+
Aglaura hemistoma Peron et Lesueur		+	+	
Amphogona apsteini Vanhoffen			+	+
Geryonia proboscidalis Forskal				+
Liriope tetraphylla Chamisso et Eysenhardt		+	+	+
Class Scyphozoa				
Order Coronatae				
Atolla wyvillei Haeckel			+	+
A. arcturi Bigelow				+
A. subglobosa Vanhoffen				+
A. vanhoeffeni Bigelow				+
Linuche draco Haeckel				+
Nausithoe punctata Kolliker			+	+
Periphylla periphylla Peron et Lesueur			+	
Subclass Discomedusae				
Order Semaeostomeae				
Cyanea capillata Linnaeus		+		
C. ferruginea Eschscholtz		+	+	
C. nozakii Kishinouye	+	+	+	+
C. purpurea Kishinouye			+	
Chrysaora helvola Brandt			+	+
Pelagia noctiluca Forskal			+	+

Sanderia malayensis Goette			+	+
Aurelia aurita Linnaeus	+	+	+	
Order Rhizostomeae				
Cassiopea andromeda Forskal			+	+
Acromitus flagellatus Maas			+	+
A. hardenbergi Stiasny				+
A. rabanchatu Aunandate				+
A. tankahkeei Light			+	
Catostylus townsendi Maas			+	
Cephea conifera Haeckel			+	
Netrostoma setouchianum Kishinouye			+	
N. coerulescnsens Maas			+	
Lobonema smithi Mayer			+	+
Lobonemodies gracilis Light			+	+
Lychnorhiza arubae Stiasny				+
L. malayensis Stiasny				+
Mastigias papua Lesson			+	+
M. ocellatus Modeer			+	+
Nemopilema nomurai Kishinouye	+	+	+	
Rhopilema esculentum Kishinouye	+	+	+	+
R. hispidum Vanhoffen			+	+
R. rhopalophorum Haeckel			+	
Thysanostoma flagellatum Haeckel				+
Class Staurozoa				
Order Stauromedusae				
Stenoscyphus inabai Kishinouye		+		
Haliclystu auricula Ciark		+		
H. steinegeri Kishinouye		+		
H. sinensis Ling		+		
Sasakiella cruciformis Okubo		+		
S. tsingtaoensis Ling		+		
Kishinouyea nagatensis Oka			+	

Table 1-2. Major jellyfish fishing grounds and seasons in China (From Dong et al. 2013).

Province	Fishing grounds	Fishing seasons	Maximum annual catches (tons wet weight)	Depth of water (m)
Liaoning Province	Northern Yellow Sea	Mid August-mid October	35,000	5~20
	Liaodong Bay	Late August-mid October	290,000	5~15
Hebei Province	Bohai Sea	Mid August-mid October	40,000	5~15
Shandong Province	Bohai Sea and Yellow Sea	Mid August-late October	65,000	5~20
Jiangsu Province	Lvsi fishing ground	Early June-mid October	145,000	5~15
Zhejiang Province	Zhoushan fishing ground	Late June-mid October	350,000	5~30
	Wentai fishing ground	Early August-late October	-	5~15
Fujian Province	Mindong fishing ground	Mid June-mid July	127,000	7~15
	Minnan fishing ground	Early April-late May	-	7~15
Guangdong Province	Yuedong fishing ground	Early April-early July	-	-
	Coastal water of south Guangdong Province	April-July	-	-

Table 1-3. Effects of stock enhancement of *Rhopilema esculentum* in Liaodong Bay from 2005 to 2010 (From Dong et al. 2013).

Year	Number of recaptured medusae ($\times 10^6$)	Recapture rate (%)	Recapture catches ($\times 10^4$ tons wet weight)	Value (10^6 million Yuan)
2005	5.02	3.20	1.25	75
2006	8.07	3.13	1.60	72
2007	5.27	2.11	0.32	30
2008	3.06	1.02	0.28	22.7
2009	2.14	0.67	1.08	100
2010	1.68	0.46	0.32	34.7
Total	22.54	1.77	4.85	334.4

Table 1-4. Production of *Rhopilema esculentum* in Liaodong Bay during from 2005 to 2012 (From Dong et al. 2013).

Year	Production ($\times 10^4$ tons wet weight)	Number of fishing boats	Price (Yuan kg^{-1})	Value (million Yuan)
2005	9.1	ca.10000	6	546
2006	3.09	10367	7	216
2007	3.36	11469	7	235
2008	1.75	10427	10.8	186
2009	2.35	9461	10	235
2010	1.57	6156	11	173
2011	0.10	2061	16.6	17
2012	0.13	2020	15.3	19

Table 3-1. Dry weight-specific respiration rates of newly-hatched larvae of molluscs, crustaceans and fishes, including *Aurelia aurita* ephyrae.

Taxonomic groups and species	Respiration rate (µl O_2 mg DW^{-1} d^{-1})	Temperature (°C)	References
Molluscans			
Grassostrea gigas Thunberg	139.2	25	Gerdes (1983)
Perna perna Linnaeus	333.8	24	Lemos et al. (2003)
Crustaceans			
Cancer productus Randall	17.9	12.5	Belman & Childress (1973)
	17.0	17.4	
	43.9	24.6	
Carcinus meanas Linnaeus	73.9	12	Dawirs (1983)
	96.0	18	
	205.9	25	
Hyas araneus Linnaeus	54.1	12	Anger & Jacobi (1985)
H. araneus Linnaeus	52.6	12	Anger (1986)
H. coarctatus Leach	53.0	12	Jacobi & Anger (1985)
Farfantepenaeus paulensis Pérez-Farfante	504.0	26	Lemos et al. (2003)
Macrobrachium holthuisi Genofre & Lobão	75.6	15	Moreira et al. (1980)
	155.8	20	
	136.8	25	
	142.3	30	
Panulirus interruptus Randall	9.6	12.5	Belman & Childress (1973)
	27.1	17.4	
	52.1	24.6	
Fish			
Anchoa mitchilli Linnaeus	96.0	26	Houde & Schekter (1983)
Chaos chanos Forsskål	80.1	23	Walsh et al. (1991)
	91.4	26	Swanson (1996)
	107.1	28	Walsh et al. (1991)
	154.1	33	Walsh et al. (1991)
Clupea harengus Linnaeus	55.7	8	Kiørboe & Møhlenberg (1987)

	44.9	8	Holliday et al. (1964)
Gadus morhua Linnaeus	39.0	5	Davenport & Lönning (1980)
Pleuronectes platessa Linnaeus	47.8	5	Davenport & Lönning (1980)
Sardinops caerulea Girard	67.2	14	Lasker & Theilacker (1962)
Sciaenops ocellatus Linnaeus	66.7	24	Torres et al. (1996)
Scomber japonicus Houttuyn	146.4	18	Hunter & Kimbrell (1980)
Theragra chalcogramma Pallas	78.1	3	Porter (2001)
Cnidarians			
Aurelia aurita ephyra	22.1-27.6	15	Møller & Riisgård (2007a)
	26.4	10-15	Kinoshita et al. (1997)
	11.7	9	This study
	14.5	12	This study
	14.6	15	This study

Table 5-1. Point-of-no-return (PNR_{50}) of newly-hatched larvae of molluscs, crustaceans and fish collated from previous works

Species	PNR_{50} (d)	Temperature (^{o}C)	Reference
Molluscans			
Gastropoda			
Neogastropoda			
Babylonia formosae habei Altena et al.	4.4	25	Zheng et al. (2005)
Bivalvia			
Veneroida			
solen marginatus Pulteney	6.5	19	Da Costa et al. (2012)
Ruditapes philippinarum Adams & Reeve	4.3	20.6	Yan et al. (2009)
Pteriomorphia			
Ostrea edulis Linnaeus	7.0	16	Labarta et al. (1999)
Crustaceans			
Isopoda			
Idotea baltica Pallas	3.7	16	Gutow et al. (2007)
I. metallica Bosc	7.3	16	Gutow et al. (2007)
Ephausiacea			
Euphausia superba Dana	12.0	0	Ross & Quetin (1989)
Decapoda			
Pleocyemata			
Caridea			
Crangon crangon Linnaeus			
Winter larvae	4.8	15	Paschke et al. (2004)
Summer larvae	3.5	15	
Astacidae			
Homarus americanus Edwards	3.0	23	Anger et al. (1985)
Achelata			
Panulirus cygnus George	4.6	25	Liddy et al. (2003)
P. japonicus Von Siebold	3.4	28	Mikami et al. (1995)
Thenus sp.	1.7	28	Mikami et al.

			(1995)
Anomura			
Pleuroncodes monodon Edwards	4.1	11	Yannicelli & Castro (2013)
Petrolisthes laevigatus Guérin	7.2	11.9	Gebauer et al. (2010)
	3.9	15	
Brachyura			
Carcinus maenas Linnaeus	3.8	18	Dawirs (1984)
	6.9	12	
Maja brachydactyla Balss	2.8	18	Guerao et al. (2012)
Chasmagnathus granulata Dana	2.5	18	Giménez (2002)
Hyas araneus Linnaeus	8.0	12	Anger and Dawirs (1981)
Neohelice granulata Dana	2.5	20	Bas et al. (2008)
	3.4	20	
Sesarma cinereum Bosc	1.8	25	Staton & Sulkin (1991)
Fish			
Clupeiformes			
Anchoa mitchilli Linnaeus	2.5	26	Houde (1974)
Clupea harengus Linnaeus	8.0	9.2	Yin & Blaxter (1987)
	7.5	25	Blaxter & Hempel (1963)
Engraulis japonicus Temminck & Schlegel	6.0	23.9	Wan et al. (2007)
E. mordax Girard	16.5	7.7	Lasker et al. (1970)
Gonorhynchiformes			
Chanos chanos Forsskål	3.3	28.6	Bagarinao (1986)
Gadiformes			
Gadus morhua Linnaeus	11.0	6.9	Yin & Blaxter (1987)
Melnogrammus aeglefinus Linnaeus	6.0	7	Laurence & Roger (1976)
Theragra chalcogramma Pallas	8.5	8.6	Bailey & Stehr (1986)
Atheriniformes			
Leuresthes tenuis Ayres	12.0	20	May (1971)
Gasterosteiformes			
Hippocampus kuda Bleeker	4.8	24	Sheng et al.

			(2007)
H. trimaculatus Leach	4.9	24	Sheng et al. (2007)
Perciformes			
Archosargus rhomboidalis Linnaeus	2.5	26	Houde (1974)
Auxis spp.	1.5	26.5	Margulies (1993)
Epinephelus fuscoguttatus Forsskål	3.0	27.5	Ching et al. (2012)
Euthynnus lineatus Kishinouye	1.5	26.5	Margulies (1993)
Lates calcarifer Bloch	5.0	27.8	Kailasam et al. (2007)
Miichthys miiuy Basilewsky	6.0	24	Shan et al. (2009)
Oplegnathus fasciatus Temminck & Schlegel	5.3	22	Shan et al. (2008)
Scomber Japonicus Houttuyn	4.5	19	Hunter & Kimbrell (1980)
Scomberomorus niphonius Cuvier	0.5	18.5	Shoji et al. (2002)
Sparus aurata Linnaeus	8.0	19.5	Yúfera et al. (1993)
Pleuronectiformes			
Achirus lineatus Linnaeus	3.3	26	Houde (1974)
Kareius bicoloratus Basilewsky	5.9	11	Oozeki et al. (1989)
	3.3	14	
	3.3	17	
	0.7	20	
Paralichthys californicus Ayres	7.0	18	Gisbert et al. (2004)
P. dentatus Linnaeus	11.5	12.5	Bisbal & Bengtson (1995)
P. olivaceus Temminck & Schlegel	7.7	15	Dou et al. (2002, 2005)
	5.0	17	
	5.2	18	
	4.2	21	
Platichthys flesus Linnaeus	10.0	9.5	Yin & Blaxter (1987)
Tetraodontiformes			
Takifugu obscurus T. Abe	6.5	24	Yang (2007)