Biomass, body elemental composition, and carbon requirement of *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in the southwestern Japan Sea

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Received 29 March 2016; Accepted 9 February 2017 Responsible Editor: Dhugal Lindsay

**Abstract:** Biomass and body elemental composition of the giant jellyfish *Nemopilema nomurai* in the southwestern Japan Sea were studied using specimens collected with mid-water trawl nets during September and October 2006, 2007, and 2009. The average biomass of *N. nomurai* was calculated as 0.26–0.93 g wet weight (WW) m⁻³. Body elemental composition of *N. nomurai* was water = 95.8% of WW, carbon = 6.6% of dry weight (DW), nitrogen = 1.7% of DW, and phosphorus = 0.14% of DW. Carbon requirements for growth and respiration were estimated in per unit area using biomass data. For growth analysis, size-frequency distributions of bell diameter (BD) were examined from specimens collected using set-nets in Wakasa Bay during August–January in 2005–2007 and the growth rate was calculated as 1.5 cm d⁻¹. For growth production, individual daily increase of total body weight derived from BD growth was summed for populations collected with mid-water trawl nets. Respiratory oxygen consumption in *N. nomurai* was estimated from electron transport system activity as 8.4 µLO₂ gWW⁻¹ h⁻¹ at 20°C. Based on these values, the carbon requirement for growth and respiration was predicted as 0.1–0.33 mgC m⁻³ d⁻¹. Biomass and carbon requirement data of *N. nomurai* were compared to the biomass of the common squid *Todarodes pacificus* and copepod production, respectively, in the Japan Sea. In the present study, it was demonstrated that when mass incidences of *N. nomurai* occurred in the Japan Sea, the biomass of *N. nomurai* was substantial and equivalent to that of the common squid. The amount of zooplankton consumed as prey by *N. nomurai* was not large enough to influence the biomass of zooplankton as a whole; however, it was critical for dense aggregations in a small area.

**Key words:** Japan Sea, jellyfish, *Nemopilema nomurai*, elemental composition, ETS activity

**Introduction**

*Nemopilema nomurai* Kishinouye, 1922 is a large rhizostome medusa that primarily inhabits the Bohai Sea, the Yellow Sea, and the northern East China Sea. However, in the Japan Sea since 2002, dense aggregations of *N. nomurai* have reached the Japanese coast and have had dire economic consequences such as reduced fish harvests owing to clogging of fishing nets (Kawahara et al. 2006). Mass occurrences of *N. nomurai* in the Japan Sea were observed in 2002–2003, 2005–2007, and 2009 (Kawahara et al. 2006, Moon et al. 2010, Kitajima et al. 2015). Prior to this, only a few mass occurrences had been recorded in 1920, 1958, and 1995 (Uye 2011). The source region of this species is still unknown; however, the coast between the Changjiang River mouth and Jiangsu Province is one plausible area (Toyokawa et al. 2012), with ephyrae believed to be released from April to June (Kawahara et al. 2006, Yoon et al. 2008, Toyokawa et al. 2012). Water discharged from the Changjiang River extends north-eastwards toward Jeju Island off the southern Korean Peninsula, entraps medusae, and transfers them to the Tsushima Warm Current (Kawahara et al. 2006, Yoon et al. 2008), which flows eastward within the Tsushima Strait and transports...
the medusae to the Japan Sea.

The number of *N. nomurai* in the Tsushima Strait peaked in July–August during the 2009 mass occurrence, with the majority of *N. nomurai* entering the Japan Sea during these months (Senjyu et al. 2013). The medusae then spread across the southern Japan Sea owing to the branching of the Tsushima Warm Current, reaching Wakasa Bay in the southwest by August (Fig. 1). Several *N. nomurai* drifted within the Tsurugis Strait from the Japan Sea to the Pacific Ocean in September, while others were retained in the Japan Sea (Kawahara et al. 2006, Japan Fisheries Information Service Center 2015). The majority of the medusae died by midwinter and their remains sank to the sea floor (Yamamoto et al. 2007).

The prey of *N. nomurai* in the Japan Sea is unknown at present. However, Lee (2010) successfully conducted oral arm content analysis of *N. nomurai* (bell diameter [BD]: approximately 10–60 cm, *n* = 28) in the offshore area of the Yellow Sea and discovered that calanoid copepods were the most abundant prey items (51% of 196 prey items), with *Paracalanus parvus* sensu lato (32%) the dominant species. For the majority of prey taxa, mean body width was approximately 0.5 mm. No clear feeding selectivity was discovered when comparing prey items with zooplankton composition sampled using NORPAC nets (Lee 2010). On the basis of these observations in the original habitat of *N. nomurai*, in the Japan Sea *N. nomurai* are likely to feed on zooplankton of 0.5 mm body width that are abundant in the environment, such as copepods (Hirakawa et al. 1995).

To elucidate the biological characteristics and horizontal distribution of *N. nomurai* in the Japan Sea, we have been conducting surveys using mid-water trawl nets towed by research vessels since 2006. To date, Iguchi et al. (2010) have revealed the sexual maturation processes of *N. nomurai* and Kitajima et al. (2015) have showed that the horizontal distribution patterns and variation in bell size distribution of *N. nomurai* are correlated with the course of the Tsushima Warm Current. In the present study, we focused on the abundance of *N. nomurai* drifting into the Japan Sea and the extent to which *N. nomurai* would have consumed available prey items. To clarify these characteristics, the biomass that drifted into the Japan Sea was calculated in units of wet weight (WW), carbon, and nutrients. Furthermore, we estimated food consumption rates of *N. nomurai* populations by an indirect method (carbon requirement) rather than direct laboratory measurements because of the difficulty in maintaining live *N. nomurai* in culture. Carbon requirements for growth and respiration were calculated from field sampling using set-nets and respiratory electron transport system (ETS) activity, respectively. Copepod biomass was also surveyed as potential prey for *N. nomurai* and we calculated what percentage of the production would have been consumed and assimilated by *N. nomurai*. High abundances of *N. nomurai* were obtained only in 2006, 2007, and 2009 during the mid-water trawl surveys (Kitajima et al. 2015), resulting in the current analyses only being performed for these three years.

**Materials and methods**

**Biomass**

Specimens for the determination of biomass were collected using mid-water trawl nets with 30 × 30 mm mesh and 76.5 m² mouth area (LC-net, Nichimou) from a depth of 60 m to the surface at 36–46 stations in the southwestern Japan Sea during September and October in 2006, 2007, and 2009 from the Research Vessel Shunyo-maru (Table 1). The majority of individuals were found at <40 m depth and abundances increased in shallower waters (Honda et al. 2009), hence the range of the mid-water trawls (0 to 60 m) covered the majority of their vertical distribution. The majority of *N. nomurai* were expected to enter the Japan Sea during July and August (Senjyu et al. 2013), so the timing of the surveys was designed to occur after these peak occurrences, i.e., September and October. The towing speed was 2.0–2.5 knots and the duration of hauls at each station was approximately 25–40 min. The filtered water volumes of the trawls were calculated from the initial and final location of the vessel, with the average filtered water volume being 2.0 × 10⁶ m³, assuming 100% filtration efficiency. The biomass of *N. nomurai* was expressed as per m³, and converted to units of per m² (m³ × 60 m sampling depth). The survey area in each year was calculated as the inside section of the line connecting the positions of the outermost stations (Fig. 2). Total abundance and biomass were calculated as mean density (ind. m⁻²) and biomass (kg m⁻²) for all stations × the survey area (m²).

Collections using mid-water trawl nets damaged the jellyfish, i.e., their oral arms were separated from their umbrellas by the joint part for almost all individuals, resulting in the combination between oral arms and umbrellas in the same individual being uncertain. We measured the medusa BD (cm) to the nearest 0.1 cm after complete removal of the oral arms, with the ventral side facing upwards. These
values were then converted to total body weight (kg) using equations relating BD to total body WW as described below. When the measurement of BD was impossible owing to umbrella breakage, the distance between two adjacent sensory organs (SO, cm) was measured and converted into BD using the following equation from Iguchi et al. (2010):

\[ BD = 3.157 \times SO - 8.489 \]

Iguchi et al. (2010) found no relationship between BD and maturation stage or sex, thus no separation of the data by sex or maturation stage was made in the present study.

**Body allometry and elemental composition**

Samples for body allometry (BD versus total body weight) and elemental composition (carbon, nitrogen, and phosphorus) were collected during the cruise in 2009. First, to establish the relationship between BD and umbrella weight, N. nomurai umbrellas were measured for BD (n=269) and weighed to the nearest 0.01 kg (POLS Marine Scale P15, USA). Second, to establish the relationship between umbrella weight and oral arm weight, when individuals with intact oral arms were caught (n=19) BD was measured and then the umbrella and oral arms were weighed separately.

For determination of elemental composition, 16 umbrellas (BD=45–108 cm) and 4 oral arms were chosen arbitrarily, and then subsamples (9–1494 g) were removed by cutting and were frozen (<−20°C). After returning to the laboratory, we measured the WW of frozen subsamples and dry weights (DW) were determined after freeze-drying to the nearest 0.01 g. Carbon and nitrogen contents were measured with an elemental analyzer (PerkinElmer 2400 II CHNS/O, USA). For phosphorus measurements, specimens were digested in a H₂SO₄–HNO₃ solution and phosphorus was measured using the molybdate method.

**Respiratory carbon**

Respiratory carbon for individuals (\( \mu g C ind^{-1} h^{-1} \)) was calculated using the following equation:

\[ \text{Respiratory C} = R \times \text{total body weight} \times RQ \times 12/22.4 \]

where, R (\( \mu LO₂ gWW^{-1} h^{-1} \)) is actual respiratory oxygen consumption, RQ is the respiratory quotient induced to convert R into carbon catabolism rate by use of a conversion factor of 0.85 (Schneider 1989), and 12/22.4 is a constant for converting oxygen consumption to carbon units. In the present study, it was difficult to measure R of N. nomurai directly owing to its large body size. Thus, we measured ETS activity instead and converted this activity to R using the R/ETS ratios of Aurelia aurita sensu lato. In medusae, including A. aurita, weight-specific respiration rate is independent of body size (Larson 1986, Uye & Shimauchi 2005) and we assumed this would be applicable to both N. nomurai and A. aurita in the present study and so could be calculated as R×total body weight.

ETS activity of N. nomurai was measured based on procedures described by Owens and King (1975) for specimens collected with an LC-net on September 22–25, 2006 (n=5) and by a diver on November 16, 2006 in Toyama.
Bay, Japan Sea \( (n=4) \). The specimens collected by the diver were sampled alive and treated immediately. An eighth of the whole body was removed on the deck and a crude homogenate produced. Subsamples of the fine homogenate were stored in liquid nitrogen until analysis. The homogenates were incubated at the environmental water temperature of each jellyfish, 22°C in September and 18°C in November, and the ETS activity was adjusted using \( Q_{10} = 2.9 \) (Larson 1986).

To obtain R/ETS ratios of \( A. aurita \), specimens of live \( A. aurita \) for determination of R and ETS activity were supplied by the Niigata City Aquarium. Specimens were maintained at 20°C after being released from their polyps and fed with \( Artemia \) nauplii. The R of ten individuals was measured using the sealed chamber method and Winkler titrations based on methods described by Ikeda (2000).

Carbon requirement

Carbon assimilation by \( N. nomurai \) is defined as somatic production for growth plus respiratory carbon. Although mucus production and leakage of soluble organic matter from the bodies is almost certainly not negligible in \( N. nomurai \), because of difficulties in its quantification it was ignored in the present analysis. The sampling period of the present study (September–October) is not the active maturation season in the Japan Sea (Iguchi et al. 2010), thus we did not consider reproduction. Somatic production for growth was calculated from BD distribution data at each station. Individual daily increase of total body weight derived from BD growth was summed per population and total body weight was converted to carbon using the carbon content percentage. The respiratory oxygen consumption rate was determined and respiratory carbon was calculated using individual weight data of the populations at each station. The amount of ingested carbon was calculated by adopting an assimilation efficiency value of 80% according to Schneider (1989; i.e., Carbon requirement = (somatic production for growth + respiratory carbon)/0.8).

Copepod biomass and production

NORPAC nets (mouth diameter 0.45 m; 335 \( \mu m \) mesh) were towed to collect zooplankton samples from 150 m to the surface at the same stations as the biomass survey for \( N. nomurai \) in 2006 and 2007 (not sampled in 2009). Samples were fixed with a buffered formalin and seawater solution. Copepods were separated out using stereomicroscopes and their total WW measured to the nearest 0.001 g. WW was converted into carbon weight (CW) assuming \( CW = 0.12 \) WW (Postel et al. 2000). Copepod production was calculated based on procedures described in Huntley and Lopez (1992) using the formula:

\[
P = B \times 0.0445e^{0.111T},
\]

where, \( P \) is production (mgC m\(^{-2}\) d\(^{-1}\)); \( B \) is copepod biomass (mgC m\(^{-2}\)); and \( T \) is mean sea surface temperature (Table 1).

Results

Biomass

In each survey year, the majority of jellyfish were horizontally distributed between approximately 132–134°E and remained in the survey area (Fig. 2). Mean abundance and biomass in 2006, 2007, and 2009 ranged from 0.98 to 4.32 \( \times 10^{-5} \) ind. m\(^{-3}\) and from 0.26 to 0.93 gWW m\(^{-3}\), respectively, with abundance and biomass highest in 2009.
Total individual abundance and biomass in each survey area over the sampling periods ranged from $0.43 \times 10^8$ to $2.58 \times 10^8$ ind. and from $1.12 \times 10^9$ to $5.58 \times 10^9$ kg, respectively (Table 1). Using the conversion factors in the elemental composition, jellyfish populations contained $0.31–1.55 \times 10^7$ kg C, $0.80–3.98 \times 10^6$ kg N, and $0.66–3.28 \times 10^5$ kg P (Table 1).

Minimum and maximum individual total body weights were 0.8 and 155.8 kg, respectively (mean: 24.1 kg, n = 264) in 2006, 3.2 and 68.1 kg, respectively (mean: 25.8 kg, n = 90) in 2007, and 1.4 and 68.1 kg, respectively (mean: 20.9 kg, n = 317) in 2009 (Fig. 3). Maximum weight decreased each year during the study period and the mean weight in 2009 was lower than that in 2006 (Tukey–Kramer comparison, $p < 0.05$).

**Body allometry and elemental composition**

The relationship between umbrella weight ($W_1$, kg) and BD (cm) of *N. nomurai* (Fig. 4) can be expressed as the following equation, which was obtained after logarithmic conversion of the data:

$$W_1 = 7.574 \times 10^{-5} BD^{2.650} \quad (r^2 = 0.907, n = 269, p < 0.01)$$

The range of specimens used to establish the equation was 43.7–134.5 cm for BD and 1.65–33.88 kg for $W_1$. The weight of oral arms ($W_2$) ranged from 2.60 to 25.15 kg and can be expressed as a function of $W_1$ or of BD (Fig. 4):

$$W_2 = 0.317 + 1.044 W_1 \quad (r^2 = 0.889, n = 19, p < 0.01)$$

or

$$W_2 = 1.606 \times 10^{-4} BD^{2.501} \quad (r^2 = 0.828, n = 19, p < 0.01)$$

The slope of the equation for $W_1$ was 1.044, indicating that the weight of the oral arms was approximately equivalent to that of the umbrellas. The relationship between total body weight ($W_1 + W_2$) and BD was defined as:

$$W_1 + W_2 = 0.317 + 1.548 \times 10^{-4} BD^{2.650}$$

Water content (%WW) of *N. nomurai* ranged from 95.1 to 97.0 (mean: 95.8, Fig. 5). Ranges of carbon, nitrogen, and phosphorus composition (%DW) were 1.9–12.8 (mean: 6.6), 0.6–2.9 (mean: 1.7), and 0.03–0.28 (mean: 0.14), respectively. All carbon, nitrogen, and phosphorus compositions (%DW) increased with increasing BD ($r = 0.481–0.634, p < 0.10$) and decreased with increasing water content ($r = -0.620$ to $-0.641, p < 0.01$). The water, carbon,
nitrogen, and phosphorus contents of jellyfish umbrellas were not significantly different to the oral arms (t-test, p > 0.3).

Growth

Size frequency BD distributions were generally broad in all samples; therefore, it was not possible to trace growth as a single population (Fig. 6). However, mode classes of frequency distribution revealed a temporal trend to larger size classes in the initial sampling period of 2005, i.e., from 55 to 105 cm between August 28 and September 27, 2005; therefore, we calculated growth rate using a simple linear regression as 1.462 cm per day (Fig. 6). The growth exponent \(k\) based on WW (\(W_t = W_0 e^{kt}\)) was calculated as 0.05. For this calculation, BD on August 28 and September 27 were derived from the linear regression and then converted into total WW using the equations for body allometry.

During other seasons and years, determination of the growth rate was impossible. \(N.\) nomurai drift between various areas, so different populations merge in the Yellow Sea and East China Sea as well as in the Japan Sea, which results in the wide range of BD, especially later sampling period in the season. On the other hand, there is the possibility of no growth or negative growth (shrinking BD) in Wakasa Bay. We adopt the growth exponent \(k\) as 0.05 for calculations. However, the percentage of carbon requirement that decreases if no growth occurred was also shown in the carbon requirement results.

Respiratory carbon

For live \(A.\) aurita (0.7–1.9 g WW, \(n=10\)), actual R was 4.3–9.1 \(\mu\)LO2 gWW\(^{-1}\) h\(^{-1}\) (mean±SD: 5.9±1.4) and ETS activity was 4.2–12.2 \(\mu\)LO2 gWW\(^{-1}\) h\(^{-1}\) (7.1±2.6), which yields an R/ETS ratio of 0.5–1.4 (0.9±0.3) for each individual.

For \(N.\) nomurai, ETS activity adjusted to 20°C ranged between 1.4 and 16.6 \(\mu\)LO2 gWW\(^{-1}\) h\(^{-1}\) (8.1±5.6) for specimens collected using the LC-net (BD: 36–94 cm, \(n=5\)) and between 4.7 and 15.6 (11.1±4.9) for those collected by the diver (BD: 106–118 cm, \(n=4\)). No significant difference was obtained between the two (t-test, p>0.4), so total mean ETS activity of \(N.\) nomurai (9.4±5.2) was converted into R using a R/ETS ratio of 0.9 (8.4 \(\mu\)LO2 gWW\(^{-1}\) h\(^{-1}\)). There was no significant difference in ETS activity between \(N.\) nomurai and \(A.\) aurita (t-test, p>0.2).

Carbon requirement

Because a growth curve for the wide range of BD could not be obtained, we calculated somatic production using a \(k\) of 0.05, i.e., assuming that \(N.\) nomurai grows with a constant weight-specific growth rate. Daily weight increase was converted to carbon units with a water content of 95.8% WW and a CW of 6.6% DW. Respiratory carbon for the populations was calculated by adopting an R of 8.4 \(\mu\)LO2 gWW\(^{-1}\) h\(^{-1}\) at 20°C, which was then adjusted to the sea surface temperature at each station (Table 1) using a Q\(_{10}\) of 2.9. The populations in the southwestern Japan Sea during September–October (biomass 0.71–2.56 mgC m\(^{-3}\)) required 0.10–0.33 mgC m\(^{-3}\) d\(^{-1}\) to meet their somatic production (0.04–0.13 mgC m\(^{-3}\) d\(^{-1}\)) and respiratory carbon (0.04–0.13 mgC m\(^{-3}\) d\(^{-1}\)) requirements in 2006, 2007, and 2009 (Table 2). Calculated carbon requirements (mgC m\(^{-3}\) d\(^{-1}\)) of \(N.\) nomurai were 0.26 in 2006, 0.10 in 2007, and 0.33 in 2009, and in the case of no growth (see Growth in Results), these values decreased by 43% in 2006, 50% in 2007, and 50% in 2009 (Table 2).

Maximum biomass of \(N.\) nomurai was observed as 7.37 gWW m\(^{-3}\) (20.4 mgC m\(^{-2}\)) at one station in 2009 (Table 1 and Fig. 1). Carbon requirement calculated for the maximum biomass population was 2.65 mgC m\(^{-3}\) d\(^{-1}\) (159.0 mgC m\(^{-2}\) d\(^{-1}\)).

Copepod biomass and production

Copepod biomass ranged from 82 to 2042 mgC m\(^{-2}\) (mean±SD: 605±376, \(n=47\)) in 2006 and 189 to
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862 mgC m$^{-2}$ (366±143, n=35) in 2007. Copepod production was calculated from mean biomass as 315 and 253 mgC m$^{-2}$ d$^{-1}$ in 2006 and 2007, respectively. Carbon requirement by *N. nomurai* (15.8 and 6.0 mgC m$^{-2}$ d$^{-1}$, Table 2) revealed that the populations consumed 5.0% and 2.4% of the copepod production per day in 2006 and 2007, respectively.

Carbon requirement for the maximum biomass population observed at one station in 2009 was 159.0 mgC m$^{-2}$ d$^{-1}$, which was equivalent to 50.6% and 62.9% of the copepod production in 2006 and 2007, respectively.

**Table 2.** Carbon requirement (mgC m$^{-2}$) of *Nemopilema nomurai* populations per day in the southwestern Japan Sea in September–October 2006, 2007, and 2009. Figures in parentheses show data expressed in m$^{-2}$.

|          | 2006          | 2007          | 2009          |
|----------|---------------|---------------|---------------|
| Mean biomass | 2.31 (138.6)  | 0.71 (42.6)  | 2.56 (153.6)  |
| Somatic production for growth (SP) | 0.12 (7.2)    | 0.04 (2.4)    | 0.13 (7.8)    |
| Respiratory carbon (RC) | 0.09 (5.4)    | 0.04 (2.4)    | 0.13 (7.8)    |
| Assimilation (A=SP+RC) | 0.21 (12.6)   | 0.08 (4.8)    | 0.26 (15.6)   |
| Carbon requirement (CR=A/0.8) | 0.26 (15.8)   | 0.10 (6.0)    | 0.33 (19.5)   |

**Discussion**

The biomass measured in the present study (ranging between 13.0 and 55.8 gWW m$^{-2}$ in 2006, 2007, and 2009, Table 1) was similar to the mean *N. nomurai* biomass of their original habitat, the southern Yellow Sea (20.4 gWW m$^{-2}$), which was previously measured by Zhang et al. (2012). However, the collection methods differed between these two studies, with the samples from the latter study collected using a bottom trawl net. Biomass data in the present study was compared with biomass of...
the common squid Todarodes pacificus (Steenstrup, 1880), which migrates between the East China Sea and the Okhotsk Sea during its one-year lifespan (Okutani 1983), with its main habitat being the Japan Sea. The importance of T. pacificus to fisheries as well as its short lifespan makes it reasonable to compare this species with the biomass of N. nomurai even though T. pacificus is not a competitor for food with N. nomurai. Studies on the feeding habits of T. pacificus in the Japan Sea reported that hyperiid Themisto japonica (Bovallius, 1887) and small fish Mauroides japonicus Ishikawa, 1915 were their main diet (Okiyama 1965). The abundances of T. pacificus in Japanese fishing grounds within the Japan Sea have been assessed as being 0.313–0.421 million tons (Murata 1989), which can be converted to 2.5–3.4×10⁷ kgC assuming DW is 18.82% WW and CW is 42.70%DW as determined from the congener T. sagittatus (Lamarck, 1798) (Clarke et al. 1985). Therefore, the biomass (kgC) of N. nomurai in the Japan Sea (Table 1) was 38–52% in 2006, 9–12% in 2007, and 46–62% in 2009 that of T. pacificus.

Calculation of mean carbon requirement by N. nomurai revealed that the populations consumed 5.0% and 2.4% of the copepod production per day in 2006 and 2007, respectively. On the other hand, dense aggregations in small areas (maximum biomass at a station) would have consumed a much greater percentage (50.6% and 62.9% in 2006 and 2007, respectively). In the Tsushima Strait, N. nomurai populations ingested 28% of the total micro- and mesozooplankton biomass per day (Uye 2014). The higher calculated ingestion rates would be due to the higher biomass reported in the Tsushima Strait (40.5 mgC m⁻³) than the maximum biomass recorded in the present study (20.4 mgC m⁻³). When mass occurrences of N. nomurai occurred, the biomass of N. nomurai was substantial and equivalent to that of the common squid in the Japan Sea. The amount of zooplankton consumed as prey by N. nomurai was not great enough to influence zooplankton biomass in the Japan Sea as a whole; however, dense aggregations of N. nomurai in small areas would lead to some competition for food resources with planktivorous pelagic fish and carnivorous zooplankton that ingest copepods, such as the Japanese anchovy Engraulis japonicus Temminck & Schlegel, 1846, Japanese jack mackerel Trachurus japonicus (Temminck & Schlegel, 1844) (Tanaka et al. 2006), and the pelagic chaetognath Zonosagitta nagae (Alvariño, 1967) (Nagasawa and Marumo 1972).

Kawahara et al. (2006) showed that the growth exponents of N. nomurai were 0.11 for 20–48 day old jellyfish in the laboratory and 0.02 based on field observations from August to December in the southwestern Japan Sea. The growth exponent of 0.05 derived from the BD distribution pattern during August–September, 2005 in the present study was intermediate between these results, although our result was derived from a small data set and growth was not detected in 2006 and 2007. In the East China Sea, the BD of N. nomurai increases to 40–50 cm in June and 80 cm or more by September. Their growth then stagnates, with numbers decreasing from mid-October and medusae disappearing until early December (Cheng et al. 2004). Based on this information, in the Japan Sea, N. nomurai would be unable to grow after October (Fig. 6), which is a possible explanation for no clear growth observed during 2006 and 2007 in the present study with further verification of growth patterns in this area required. When no growth was observed, the calculated carbon requirement (i.e., respiratory carbon only) decreased to 43–50%, which did not result in a drastic drop in carbon requirement. Even under no-growth conditions, respiration should always be greater than 0.

In the present study, mean actual R (directly measured) of live A. aurita (2.0 µLO₂ gDW⁻¹ h⁻¹ using DW/WW=0.03 from Larson 1987 and 5.9 µLO₂ gWW⁻¹ h⁻¹) was similar to that obtained in other studies (0.1–0.3 µLO₂ gDW⁻¹ h⁻¹ at 13–29°C, Larson 1987). After the ETS activity measurement in A. aurita, we obtained an R/ETS ratio of 0.9, which is greater than the theoretical R/ETS of 0.5 based on Michaelis-Menten kinetic assumptions, but within the range of 0.5–1.0 proposed for in vivo marine zooplankton (Hernández-León & Gómez 1996, Hernández-León & Ikeda 2005). We obtained an R of 8.4 µLO₂ gWW⁻¹ h⁻¹ at 20°C for N. nomurai. Purcell et al. (2010) reported respiration equations for live N. nomurai and the combined equation for small and large N. nomurai produced an R of 22.9 µLO₂ gWW⁻¹ h⁻¹ at 24°C. Active swimming of rhizostome medusae during measurement (Purcell et al. 2010) is one possible cause for the differences obtained, and the low ETS activity from the present study would reflect deteriorating health since N. nomurai drifted from its original habitat to another environment and sampling was conducted after September. Nevertheless, confirmation of the metabolic characteristics of N. nomurai requires further data accumulation, including R/ETS ratios. The ETS method requires calibration of ETS activity with R for each species and using the R/ETS ratio of A. aurita in the present study might have caused errors in the calculations.

Acknowledgements

We are grateful to A. Yamato for providing live A. aurita, and T. Yasuda for the support for set-net sampling. Assistance at sea from the captain and crew aboard the Research Vessel Shunyo-maru is greatly appreciated. We thank everyone who participated in the surveys for collecting and analyzing medusae. The present study was supported by the Fisheries Agency, Government of Japan.

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Data Appendix. Summary of LC net sampling data for *Nemopilema nomurai* in the southwestern Japan Sea.

| Station number | Latitude (°N) | Longitude (°E) | LC net start day and time | Volume of water filtered individuals/haul (×1000 m³) per haul (kg) | Total Volume of water filtered individuals/haul (×1000 m³) per haul (kg) |
|---------------|--------------|---------------|--------------------------|---------------------------------------------------------------|---------------------------------------------------------------------|
| 1             | 38.50        | 136.50        | Sep 21 7:53              | 289 0.0 0.0                                                    | -                                                                   |
| 2             | 38.00        | 136.50        | Sep 24 12:35             | 223 1 21.7                                                     | -                                                                   |
| 3             | 37.50        | 136.50        | Sep 21 16:24             | 165 0.0 0.0                                                    | -                                                                   |
| 4             | 37.00        | 136.50        | Sep 22 06:38             | 165 0.0 0.0                                                    | -                                                                   |
| 5             | 36.50        | 136.13        | Sep 22 10:33             | 195 5 136.1                                                    | -                                                                   |
| 6             | 36.00        | 135.75        | Sep 22 14:32             | 193 2 80.1                                                     | -                                                                   |
| 7             | 35.50        | 135.75        | Sep 22 18:54             | 140 3 101.0                                                    | -                                                                   |
| 8             | 37.00        | 135.75        | Sep 23 7:08              | 198 1 25.5                                                     | -                                                                   |
| 9             | 37.50        | 135.75        | Sep 23 11:23             | 197 0.0 0.0                                                    | -                                                                   |
| 10            | 38.00        | 135.75        | Sep 23 15:37             | 230 0.0 0.0                                                    | -                                                                   |
| 11            | 38.00        | 135.00        | Sep 24 7:16              | 202 3 81.8                                                     | -                                                                   |
| 12            | 37.50        | 135.00        | Sep 24 10:06             | 227 3 33.6                                                     | -                                                                   |
| 13            | 37.00        | 135.00        | Sep 24 15:07             | 222 4 27.9                                                     | -                                                                   |
| 14            | 36.50        | 135.00        | Sep 25 18:35             | 212 10 281.1                                                   | -                                                                   |
| 15            | 35.75        | 134.25        | Sep 25 7:15              | 189 6 313.8                                                    | -                                                                   |
| 16            | 35.60        | 134.25        | Sep 25 10:50             | 125 7 202.4                                                    | -                                                                   |
| 17            | 36.00        | 134.25        | Sep 25 14:14             | 286 4 24.8                                                     | -                                                                   |
| 18            | 37.00        | 134.25        | Sep 25 18:26             | 268 7 115.8                                                    | -                                                                   |
| 19            | 37.50        | 134.25        | Sep 26 7:05              | 168 8 116.9                                                    | -                                                                   |
| 20            | 37.00        | 133.50        | Sep 26 10:50             | 125 7 202.4                                                    | -                                                                   |
| 21            | 37.00        | 133.50        | Sep 26 16:05             | 172 9 145.5                                                    | -                                                                   |
| 22            | 36.50        | 133.50        | Sep 27 6:43              | 196 7 143.8                                                    | -                                                                   |
| 23            | 34.50        | 133.50        | Sep 27 12:51             | 214 5 755.3                                                    | -                                                                   |
| 24            | 35.67        | 133.50        | Sep 27 13:07             | 243 11 174.2                                                   | -                                                                   |
| 25            | 36.57        | 132.75        | Sep 27 15:43             | 114 4 56.7                                                     | -                                                                   |
| 26            | 36.00        | 132.75        | Sep 27 18:08             | 156 13 633.2                                                   | -                                                                   |
| 27            | 37.75        | 132.75        | Sep 30 6:42              | 153 1 546.7                                                    | -                                                                   |
| 28            | 37.00        | 132.75        | Sep 30 10:15             | 119 7 484.6                                                    | -                                                                   |
| 29            | 37.50        | 132.75        | Sep 30 13:58             | 177 4 92.2                                                     | -                                                                   |
| 30            | 36.50        | 132.00        | Oct 1 7:00               | 141 6 181.6                                                    | -                                                                   |
| 31            | 36.00        | 132.00        | Oct 1 10:50              | 140 8 404.6                                                    | -                                                                   |
| 32            | 35.50        | 132.00        | Oct 1 14:20              | 182 11 290.2                                                   | -                                                                   |
| 33            | 35.00        | 132.00        | Oct 1 18:03              | 126 2 62.1                                                     | -                                                                   |
| 34            | 34.58        | 131.25        | Oct 1 2:26               | 130 1 19.8                                                    | -                                                                   |
| 35            | 35.00        | 131.25        | Oct 1 6:26               | 159 10 246.8                                                   | -                                                                   |
| 36            | 35.50        | 131.25        | Oct 1 9:22               | 219 10 246.8                                                   | -                                                                   |
| 37            | 36.00        | 131.25        | Oct 1 12:21              | 237 6 119.3                                                   | -                                                                   |
| 38            | 36.00        | 131.25        | Oct 1 17:28              | 283 7 190.0                                                    | -                                                                   |
| 39            | 35.42        | 130.50        | Oct 3 6:35               | 159 3 123.4                                                   | -                                                                   |
| 40            | 35.00        | 130.50        | Oct 3 9:20               | 188 2 79.2                                                    | -                                                                   |
| 41            | 34.50        | 130.50        | Oct 3 12:34              | 128 0.0 0.0                                                   | -                                                                   |
| 42            | 34.00        | 130.50        | Oct 3 15:07              | 227 2 22.2                                                    | -                                                                   |
| 43            | 34.00        | 129.75        | - - - - - - - - - - - - - | - - - - - - - - - - - - - | - - - - - - - - - - - - - |
| 44            | 34.50        | 129.75        | Oct 5 6:29               | 182 0.0 0.0                                                   | -                                                                   |
| 45            | 35.00        | 129.75        | Oct 5 17:12              | 215 6 59.0                                                    | -                                                                   |
| 46            | 34.72        | 129.13        | Oct 4 13:24              | 124 0.0 0.0                                                   | -                                                                   |
| 47            | 34.27        | 128.90        | Oct 4 10:11              | 108 0.0 0.0                                                   | -                                                                   |
| 48            | 33.82        | 129.18        | Oct 4 6:31               | 167 0.0 0.0                                                   | -                                                                   |