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Bioenergetic characterization in *Aurelia aurita* (Cnidaria: Scyphozoa) polyps and application to natural polyp populations

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ABSTRACT: Bioenergetic modeling is useful in understanding the benthic polyp population dynamics of metagenetic scyphozoan jellyfishes. We investigated the effects of environmental factors on the respiration and feeding rates of polyps of *Aurelia aurita* s.l. under controlled laboratory conditions in order to construct an empirical energy budget model for application to natural polyp populations. The carbon weight-specific respiration rate of polyps increased exponentially with increasing temperature from 8 to 28°C and was constant at salinities ranging from 15 to 33. The general functional response of polyps feeding on various zooplankton taxa was expressed by a linear increase in ingestion rate as a function of prey density, although it was affected by the size and/or swimming ability of prey organisms. Accordingly, the clearance rate was constant irrespective of prey density at a given temperature. The rate increased linearly with temperature from 8 to 26°C. Integrating these results, we constructed a carbon budget model of *A. aurita* polyps as a function of temperature and mesozooplankton prey density. An application of this model to polyps in Fukuyama Harbor, the Inland Sea of Japan, suggested that they consistently attain a positive growth (somata and offspring) rate, ranging from 0.0039 to 0.34 µg C µg C^{-1} d^{-1}. Our model allows estimation of the potential growth rates of polyps in temperate coastal waters where temperature and mesozooplankton biomass data are available, contributing to comprehensive understanding of polyp population dynamics in nature.

KEY WORDS: Asexual reproduction · Energy budget · Feeding · Mesozooplankton · Respiration

INTRODUCTION

To clarify why scyphozoan medusa populations show remarkable annual fluctuations—sometimes developing massive blooms, sometimes not—the benthic polyps (scyphistomae) have drawn special attention because of their asexual reproduction by multiple modes and their release of numerous planktonic ephyrae which develop into medusae (reviewed by Lucas et al. 2012). Previous studies have examined the effects of various environmental factors on the modes and rates of the asexual reproduction of polyps, particularly in the common jellyfish *Aurelia aurita* s.l., under controlled laboratory conditions (Ishii & Watanabe 2003, Willcox et al. 2007, Han & Uye 2010, Thein et al. 2012, Wang et al. 2015, Widmer et al. 2016). However, field studies have been confined to the clarification of the substrates and locations of polyp colonization, the seasonal changes in their numerical abundance and the timing of strobilation, because of difficulties in isolating and evaluating the effects of a given environmental factor on their eco-physiology (Willcox et al. 2008, Purcell et al. 2009, Di Camillo et al. 2010, Ishii & Katsukoshi 2010, Makabe et al. 2014). In order to elucidate the effects of various environmental factors on the population dynamics of polyps in the field, it is of fundamental value to detail their individual energetic balance and to quantify energy (or carbon flux) through the bulk biological processes: ingestion, respiration and growth.

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Bioenergetic studies have been conducted on ephyrae and medusae of *A. aurita* (Båmstedt et al. 1999, Hansson et al. 2005, Uye & Shimauchi 2005, Ishii & Tanaka 2006), but few studies have been done to date the polyp stage. To characterize bioenergetics in polyps, at least 2 physiological rates, i.e. respiration and ingestion rates, should be determined as principal indices of metabolic demand and energy acquisition, respectively. There are 2 previous studies that examined the effect of temperature on the respiration rate of *A. aurita* polyps, but the results of these studies were contradictory. Mangum et al. (1972) demonstrated an exponential increase of respiration rate with increasing temperature from 12 to 32°C, but Gambill & Peck (2014) found a sharp increase at a threshold temperature from low respiration rates at relatively low temperatures to high rates at high temperatures. Previous studies have shown that jellyfish polyps consume a wide variety of plankton, such as dinoflagellates, ciliates, rotifers, planula larvae of scyphomedusae, small hydromedusae, cladocerans, copepods, planktonic larvae of various benthic organisms, chaetognaths and fish larvae (Gröndahl 1988, Östman 1997, Kamiyama 2011, Huang et al. 2015), in addition to *Artemia* nauplii, which are a conventional food for culture of polyps. However, no attempts have been made to investigate the functional response of polyps, except for a study on ciliates as prey by Kamiyama (2011), who demonstrated a hyperbolic functional response of polyps to ciliate density.

In this study, we aimed to characterize the bioenergetics of polyps of *A. aurita* s.l. collected from temperate coastal waters of Japan. We examined the effects of temperature and salinity on carbon weight-specific respiration rates, and the effects of temperature, prey type and prey density on carbon weight-specific ingestion rates of various zooplankton (primarily mesozooplankton) taxa in the laboratory. A carbon budget model constructed from these experiments was applied to the natural polyp population in Fukuyama Harbor, Inland Sea of Japan.

MATERIALS AND METHODS

Sources of polyps

Stock-cultures of the polyps of *Aurelia aurita* s.l. were initiated in 2011 using planulae collected from 3 female medusae caught in Hakata Bay (33° 37′ N, 130° 20′ E), northern Kyushu, Japan. The polyps were maintained in plastic containers (diameter 15 cm, depth 6.5 cm) containing ca. 500 ml of filtered seawater (salinity 33) at 22°C in darkness. They were fed newly hatched *Artemia* nauplii (ca. 10 nauplii per polyp) overnight once a week, followed by replacement of the seawater. Prior to experiments, polyps bearing ≥16 tentacles were detached from the bottom of containers using forceps and transferred to new containers with 20 acrylic discs (diameter 15 mm, thickness 1 mm) on the bottom as settling substrates. Polyps attached to the discs were kept under the same conditions as the stock cultures until they were used for experiments.

Body carbon weight respiration rates, and ingestion rates of polyps

The stock-cultured polyps (range of calyx diameter 0.4 to 2.1 mm) were detached from the container bottoms and the lateral and top views of their contracted bodies were photographed with a digital camera-equipped stereomicroscope to determine their body volumes using Image J software (Ver. 1.45), assuming an ellipsoidal shape. A total of 30 samples, each consisting 5 to 21 polyps with similar body volumes, were rinsed on pre-combusted and pre-weighed Whatman GF/F glass-fiber filters (diameter 25 mm) with 5 ml of 3% isotonic ammonium formate to remove external salts. They were then dried in an electric oven at 60°C for 24 h and held in a desiccator until analysis. Dry weights of polyps were measured on a microbalance (Mettler Toledo, Tyme MT 5) to the nearest 1 µg, and their carbon contents were determined using a CHN analyzer (Perkin Elmer, CHNS/O 2400 Series II).

The effect of reduced salinity on the contracted body volumes of polyps was examined using detached polyps from the stock culture. Three lots, each consisting of 7 to 8 polyps, were kept in plastic containers (diameter 8 cm, height 2 cm) containing 30 ml of seawater at 4 different salinities (15, 20, 25, and 33) at 22°C in darkness for 4 d, followed by measurement of their body volume. Dry and carbon weights of polyps were determined following the procedures described above.

Experiments to examine the effects of temperature and salinity on the respiration rate of polyps were conducted at 8, 12, 18, 22, 26, and 28°C in a multi-incubator (Eyela MTI-202). Salinities of 15, 20, 25, and 33 were made by diluting 0.2-µm filtered seawater with distilled water at 22°C. Polyps were starved for 2 d and acclimatized to each combination of conditions for 1 d before respiration measurements. In each condition, 6 BOD bottles (volume ca. 67 ml),

each with 10 polyps on 2 or 3 acryl discs (maximum 7 polyps per disc), and 6 control bottles without polyps were incubated for 3 d. The initial and final dissolved oxygen concentrations (DOs) were measured 3 times for each bottle using a fluorescence DO meter (WTW, Multi 3410). After the measurement of final DO, the contracted body volumes of the polyps were determined and converted to carbon weight using the relationship between body volume and carbon weight (see above). Carbon weight-specific respiration rates of polyps (R, ng O_2 µg C^{-1} d^{-1}) were calculated from:

$$\frac{[(E_0 - E_t) - (C_0 - C_t)] \times V}{D \times W} \quad (1)$$

where C_0 and C_t are initial and final DO of control bottles (ng O_2 ml^{-1}), E_0 and E_t are initial and final DO of experimental bottles, V is volume of experimental BOD bottles (ml), D is duration of experiments (d) and W is carbon weight of the polyps (µg).

Zooplankton samples were collected using a NORPAC net (45 cm diameter, 100 µm mesh size) in the central Inland Sea of Japan and transported (≤1 h) to the laboratory at Hiroshima University in Higashi-Hiroshima. Three predominant taxa, i.e. *Microsetella norvegica* late copepodites and adults, *Oithona* spp. late copepodites and adults, and barnacle nauplii, were isolated with a pipette and used as prey (Table 1). Single polyps on acrylic discs (calyx diameter 1.47 ± 0.218 mm, mean ± SD), which had been starved for 7 d, were introduced into 50 ml glass bottles filled with 0.2 µm-filtered seawater (salinity 33), in which prey densities of 0.2, 0.5, 1.0, 1.5, and 2.0 prey ml^{-1} were established to allow the polyps to feed for 1 h at 22°C in darkness. At each prey density, 5 experimental and 2 control (without a polyp) bottles were prepared. To examine the effect of temperature on the feeding rate, experiments were conducted at 8, 12, 18, 22, and 26°C at a density of 1.0 prey ml^{-1} using the above-mentioned 3 zooplankton taxa. Five experimental and 2 control bottles were prepared at each temperature. Prior to the experiment, the prey and polyps had been kept at the experimental temperatures for 24 h. Additional experiments were conducted at 22°C using other 5 zooplankton types (*Acartia* sp., *Corycaeus affinis*, small copepod nauplii, large copepod nauplii and polychaeta larvae, Table 1) as prey at a density of 1.0 prey ml^{-1}, in order to evaluate the effects of prey characteristics, i.e. body length, carbon weight, cruising speed and burst speed (the latter 3 parameters were estimated from previous work, see Table 1) on polyp ingestion rates. For these prey-type experiments, 3 experimental and 2 control bottles were prepared for each prey type. After the experiments, the numbers of prey remaining in the bottles and their survival were examined, and the contracted body volumes of the polyps were determined. The clearance rates (F, ml $polyp^{-1}$ h^{-1}) and ingestion rates (I, prey $polyp^{-1}$ h^{-1}) of the polyps were calculated by: $F = V/(D \times N) \times \ln(P_0/P_t)$ and $I = (P_0 - P_t)/(D \times N)$, respectively, where N is number of predators and P_0 and P_t are initial and final prey densities (prey ml^{-1}), respectively (Båmstedt et al. 2000). These rates were also converted to carbon weight-specific rates, i.e. the carbon weight-specific clearance rate (F_C, ml µg C^{-1} h^{-1}), and the carbon weight-specific ingestion rates for prey carbon mass and number (I_C, µg C µg C^{-1} h^{-1} and I_P, prey µg C^{-1} h^{-1},

Table 1. Body length, carbon weight, cruising speed and bursting speed of various mesozooplankton used as prey for *Aurelia aurita* polyps.

Prey organisms	Body length (mean ± SD, µm)	Carbon weight (µg)	References	Cruising speed (mm s^{-1})	Burst speed (mm s^{-1})	References
Acartia sp.	570 ± 136[a]	1.1	Uye (1982)	3.9	213	Larsen et al. (2008), Buskey et al. (2002)
Corycaeus affinis	460 ± 48.2[a]	0.66	Recalculation from Uye (1982)	1.2	10	Landry & Fagerness (1988), Yen (1988)
Microsetella norvegica	357 ± 31.8[a]	0.25	Uye et al. (2002)	0.60	0.60	Koski et al. (2005)
Oithona spp.	374 ± 64.2[a]	0.38	Uye (1982)	8.0	40	Jiang & Kiørboe (2011)
Small copepod nauplii	213 ± 23.7[b]	0.17	Berggreen et al. (1988)	1.1	8.0	Titelman & Kiørboe (2003)
Large copepod nauplii	405 ± 79.5[b]	0.99	Hygum et al. (2000)	2.2	15	Titelman & Kiørboe (2003)
Barnacle nauplii	249 ± 33.1[b]	0.29	Recalculation from Uye (1982)	1.4	3.1	Lang et al. (1979), Sullivan et al. (1997)
Polychaeta larvae	362 ± 141[c]	0.30	Recalculation from Uye (1982)	1.1	1.1	Mileikovsky (1973)

[a]Prosome length. [b]Carapace length. [c]Total length

respectively), based on carbon weights of polyps and of the specific prey types using following formulae: $F_C = F/W$, $I_C = I \times PW/W$ and $I_{P\ =}\ I/W$, where PW is the carbon weight of prey (see Table 1).

A bioenergetic model and its application to a natural polyp population

The carbon budget for polyps per unit carbon weight can be expressed as: $G = A - M = I_C \times a - M$, where G, A and M are growth, assimilation and metabolic rates (µg C µg C^{-1} d^{-1}), respectively (Møller & Riisgård 2007a), and 'a' is an assimilation efficiency assuming to be 0.8 (Schneider 1989). The metabolic rate can be calculated from the respiration rate (R) as: $M = k \times R \times RQ$, where k is a conversion factor to estimate carbon mass from moles of oxygen (0.375 µg C µg O_2^{-1}, McCloskey et al. 1994), and RQ is a respiratory quotient assuming to be 0.85 for *A. aurita* medusae (Schneider 1989).

The bioenergetic model parameterized with temperature and zooplankton biomass based on the laboratory experiments was applied to the *A. aurita* polyp population in Fukuyama Harbor, where the basic parameters for the model are available (Uye & Liang 1998). The biomass of adults and copepodites of copepods and temperature have been monitored at intervals of 3 to 5 d for a year (Uye & Liang 1998). For simplification, we took monthly averages of temperature and copepod biomass and assigned them to an energy budget model for polyps in order to estimate the seasonal variations in their ingestion, assimilation, metabolic and growth rates.

Statistical analysis

All statistical analyses were conducted using R v.3.3.1 (R Core Team 2016). For the validation of respiration measurements, the differences in mean DOs between initial and final experimental bottles were tested using Welch's test. Final mean DO differences between control and experimental bottles were compared using paired *t*-tests. The differences of consumed O_2 between control and experimental bottles were also examined using paired *t*-tests.

Regression analyses for various relationships between 2 parameters, such as environmental variables and eco-physiological parameters of polyps, were performed using generalized linear models (GLMs). For relationships of polyp carbon weight versus contracted body volume and contracted body volume versus salinity, we fitted them to GLMs with a gamma distribution described as $W \sim BV$ or $BV \sim S$, where BV is the polyp contracted body volume (mm^3) and S is salinity. For the carbon weight-specific respiration rate versus temperature, and versus salinity, the models can be described as $R \sim T$ or $R \sim S$, with a gamma distribution, where T is temperature (°C). The data were fitted to exponential, linear and constant equations, and the function resulting in the lowest Akaike information criterion (AIC) was selected (Akaike 1987).

The functional responses of polyps to various zooplankton prey, that is, the relationships between polyp ingestion rates and zooplankton density, were tested by fitting linear and hyperbolic functions to confirm which function gave lower AIC and more significant probability estimates. The linear equations were analyzed with Poisson and other Tweedie error distributions for ingested prey number and carbon weight, respectively, and the hyperbolic equation was tested using the drc package in R. For the relationship between polyp clearance rate and temperature, we tested the constant, linear and exponential regression models and selected the model with the lowest AIC value.

The carbon weight-specific ingestion rates among different taxa at a density of 1 prey ml^{-1} were examined with Tukey's pairwise comparisons. The effects of prey characteristics on the rates were analyzed using model selection for the additive effects of cruising speed, burst speed and body length (Table 1) on the ingestion rates (I_P and I_C) using Poisson and gamma distributions, respectively.

RESULTS

Body volume and carbon weight relationship

W of *Aurelia aurita* s.l. was strongly and linearly correlated to BV, expressed by $W = 27.4 \times BV$ (R^2 = 0.982) (Fig. 1). This equation was used later to convert the body volumes of polyps into their carbon weights.

Respiration rates

All polyps in the experiments looked healthy, extending tentacles fully, after 4 d. There were always significant differences in mean DO between initial and final experimental bottles (Welch's test, $p < 0.05$). There were slight, but significant, differences (Welch's test, $p < 0.05$) in mean DO between initial and final

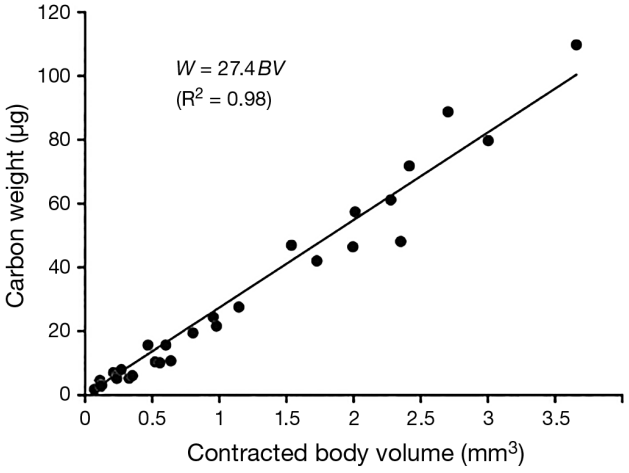

Fig. 1. Relationship between contracted body volume (*BV*) and carbon weight of polyps (*W*) of *Aurelia aurita*

control bottles, but differences in mean DO were always greater between final control and experimental bottles (paired *t*-test, $p < 0.01$). Accordingly, the amounts of O_2 consumed in the experimental bottles were always significantly larger than those in the control bottles (paired *t*-test, $p < 0.01$).

Mean values of *R* varied from 32.2 to 105 ng O_2 µg C^{-1} d^{-1} at 8 and 28°C, respectively. The effect of temperature on *R* of polyps was significant, as the AIC of a fitted exponential equation (691.0) in the GLM analysis was smaller than that for no temperature effect (738.7). *R* increased exponentially from 8 to 28°C (Fig. 2A), expressed by $R = 17.3\ e^{0.0657T}$.

Because *BV* of polyps was significantly inflated relative to *W* after exposure to lower salinities, with the mean ratios of +25, +44 and +66% at salinities of 25, 20 and 15, respectively, compared to *BV* at 33, their *W* were corrected. According to the GLM analysis, the effect of *S* on *R* was not statistically significant (AIC values of 483.2 and 485.2 for constant and exponential equations, respectively), and hence the *R* was effectively constant (mean ± SD 99.6 ± 30.2 ng O_2 µg C^{-1} d^{-1}) over a salinity range from 15 to 33 (Fig. 2B).

Feeding on mesozooplankton

Effect of prey density

Observation under illuminated conditions revealed that polyps extended their tentacles fully and started capturing prey within 2 min after being placed into the experimental bottles. In the control bottles, the prey mortality was negligible (0.4 ± 0.6%, mean ± SD). Experiments in which prey consumption was higher than 50% (maximum: 88% for barnacle nauplii) were excluded from the calculation. Mean values of *I* ranged from 2.16 to 18.7, 2.50 to 25.5 and 3.00 to 37.4 prey $polyp^{-1}$ h^{-1} for *Microsetella norvegica*, *Oithona* spp. and barnacle nauplii, respectively, at values of *P* ranging from 0.25 to 2.0 prey ml^{-1}. The GLM demonstrated that *I* of a polyp increased linearly with increasing *P* without attaining saturation below *P* = 2.0 prey ml^{-1}, expressed by $I = 8.72 \times P$ for *M. norvegica*, $I = 12.7 \times P$ for *Oithona* spp. and $I = 17.1 \times P$ for barnacle nauplii (Fig. 3A). I_C also showed a linear increase with prey carbon density (P_C, µg C ml^{-1}), expressed by $I_C = 0.225\ P_C$ for *M. norvegica*, $I_C = 0.166\ P_C$ for *Oithona* spp. and $I_C = 0.292\ P_C$ for barnacle nauplii (Fig. 3B). Accordingly, values of F_C were constant irrespective of prey density: 0.262 (range 0.214 to 0.319), 0.196 (0.160 to 0.281), and 0.364 (0.330 to 0.429) ml µg C^{-1} h^{-1} for *M. norvegica*, *Oithona* spp., and barnacle nauplii, respectively (Fig. 4A).

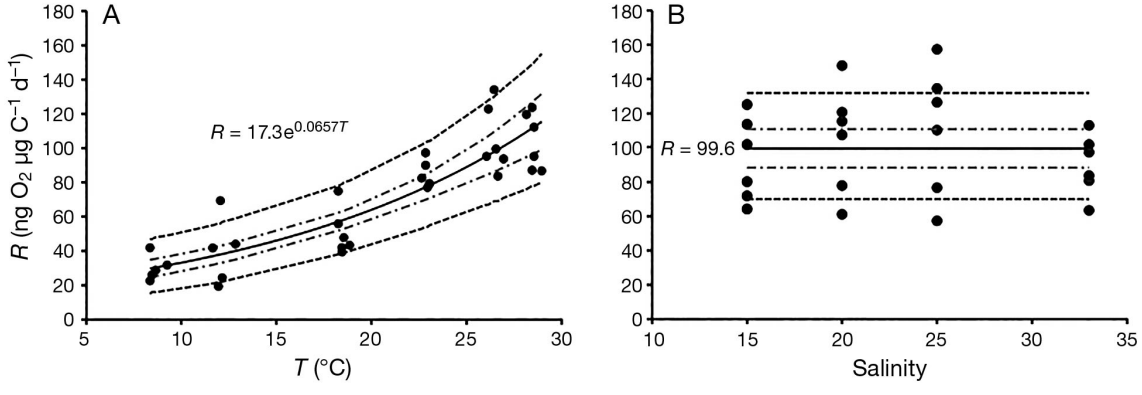

Fig. 2. Relationship between carbon weight-specific respiration rate (*R*) of *Aurelia aurita* polyps and (A) temperature (*T*) and (B) salinity. Solid line for *T* is the regression curve obtained from the generalized linear model (GLM) analyses, and for salinity indicates the mean value. Dashed lines indicate the upper and lower 95% limits of the prediction area. Dashed-dotted lines denote the upper and lower 95% confidence limits

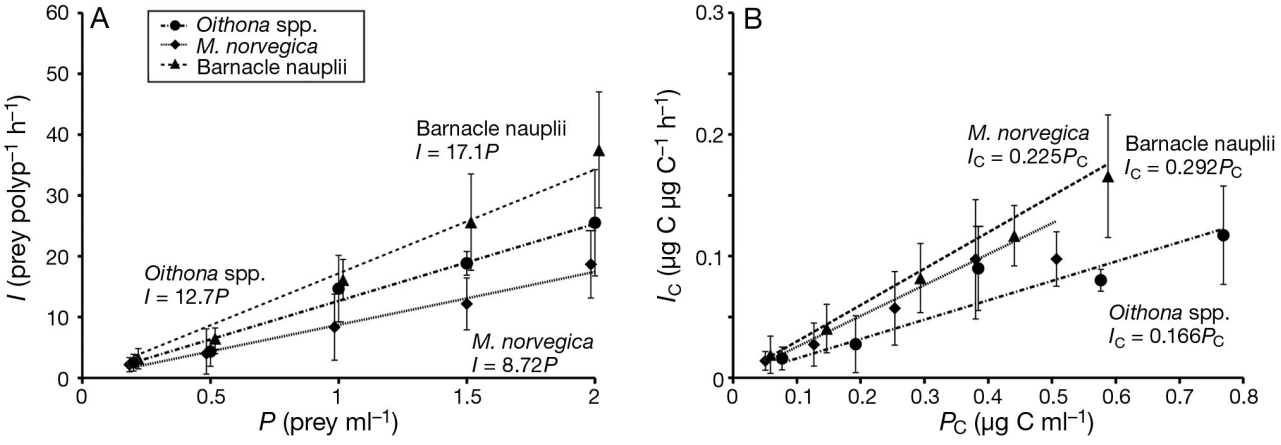

Fig. 3. Functional response of *Aurelia aurita* polyps feeding on *Microsetella norvegica* adults and copepodites, *Oithona* spp. adults and copepodites and barnacle nauplii: (A) ingestion rate in terms of prey numbers (I), (B) carbon weight-specific ingestion rate (I_C). Error bars = SD

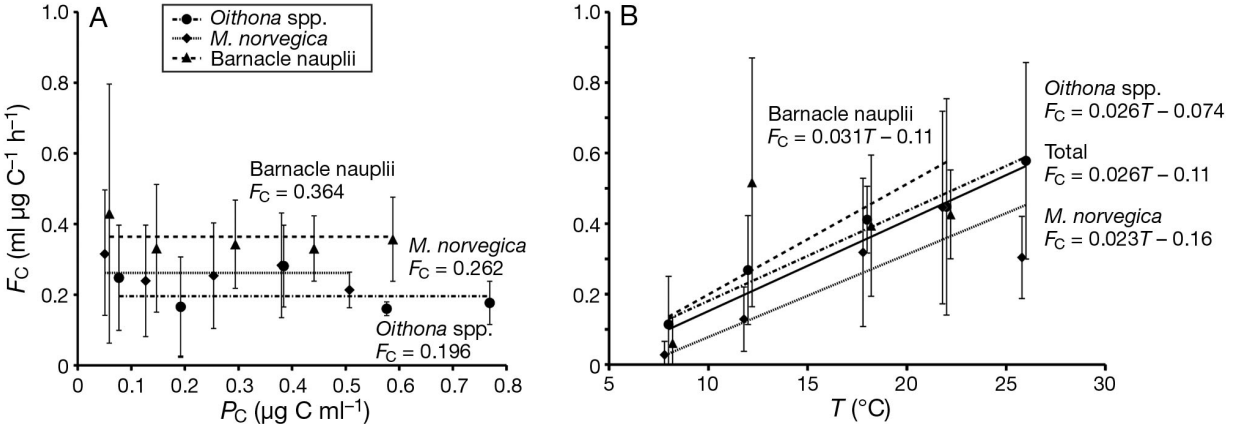

Fig. 4. Carbon weight-specific clearance rates (F_C) of *Aurelia aurita* polyps feeding on *Microsetella norvegica* adults and copepodite, *Oithona* spp. adults and copepodites, and barnacle nauplii: (A) Effect of prey density at 22°C; (B) effect of temperature (T). A solid regression line is for all prey combined. Error bars = SD

Effect of temperature

Temperature did not have an adverse effect on prey, except for barnacle nauplii, which appeared inactive at 26°C, so those data were excluded. The GLM showed that F_C increased linearly with T, expressed by $F_C = 0.023T - 0.16$ for *M. norvegica*, $F_C = 0.026T - 0.074$ for *Oithona* spp. and $F_C = 0.031T - 0.11$ for barnacle nauplii (Fig. 4B). When all the data were combined, $F_C = 0.026T - 0.11$ (Fig. 4B).

Effect of prey characters

At a density of 1.0 prey ml^{-1} of various zooplankton taxa, I_P varied from 0.091 prey µg C^{-1} h^{-1} for *Corycaeus affinis* to 0.28 prey µg C^{-1} h^{-1} for barnacle nauplii, and I_C also ranged from 0.018 µg C µg C^{-1} h^{-1} for small copepod nauplii to 0.21 µg C µg C^{-1} h^{-1} for large copepod nauplii (Fig. 5). Multiple comparisons based on the GLM analysis showed that the ingestion rates were significantly different among prey taxa (Tukey's pair-wise comparison, $p < 0.01$), showing clear separation into 2 subdivisions for the individual-based rates but indistinct for the carbon-based rates except for small copepod nauplii (Fig. 5). In the GLM analysis of the effect of prey characteristics on I_P, a model consisting of cruising and burst speeds of prey showed the lowest AIC among all models examined (Table 2). The cruising speed was positively correlated to the ingestion rates (coefficient 0.068), whereas the burst speed was negatively correlated (–0.0038). On the other hand, the GLM analysis of I_C for small and large copepod nauplii showed the lowest AIC in a model consisting of prey body length, which correlated positively (0.0027) (Table 2).

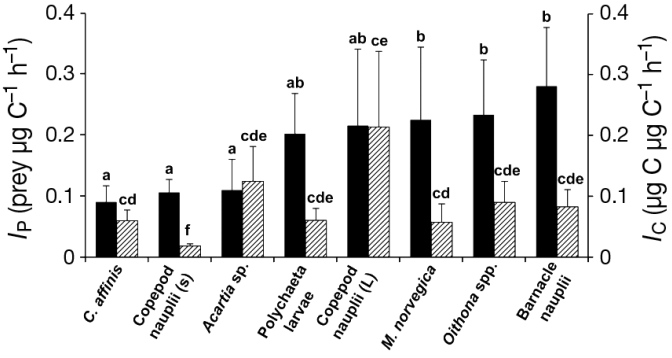

Fig. 5. Prey-specific ingestion rates (I_P) of *Aurelia aurita* polyps on various prey taxa at a density of 1.0 ind. ml^{-1}. Black bars denote the ingestion rates in terms of prey numbers per unit carbon weight, and hatched bars show the carbon weight-specific ingestion rates (I_C). Means with different letters are significantly ($p < 0.01$) different based on Tukey's pair-wise comparisons. Error bars = SD

An integration of experimental results for all prey taxa (total: 40 values) was well fit by a linear functional response of *A. aurita* polyps to mesozooplankton prey density, expressed as $I_C = 0.20 \times P_C$ (Fig. 6A), and F_C was determined as 0.26 ml µg C^{-1} h^{-1} (Fig. 6B).

Bioenergetic model

We constructed a carbon budget model of *A. aurita* polyps to simulate the basic eco-physiological rates in their natural habitat, where they are exposed to various physical (e.g. temperature and salinity) and biological (e.g. zooplankton taxonomic composition and density) conditions. For ingestion, we used the carbon weight-specific clearance rate on a composite of mesozooplanton as prey at 22°C, which was constant (F_C = 6.2 ml µg C^{-1} d^{-1}) over the range of P_C tested (Fig. 6). As F_C was affected by T (Fig. 4B), expressed in the functional relationship $F_C = 13(0.026T - 0.11)$ ml µg C^{-1} d^{-1}. Hence, I_C of wild polyps at a given P_C of wild mesozooplankton was approximated by $I_C = 13(0.026T - 0.11) \times P_C$, that of A by $10(0.026T - 0.11) \times P_C$.

Table 2. Comparison of AIC values in generalized linear model analyses of functions of multiple combinations of prey characters to individual-based and carbon weight-specific ingestion rates of polyps of *Aurelia aurita*

Characters of prey	Ingestion rate	Carbon weight-specific ingestion rate
Null	259.6	174.6
Cruising speed	255.8	173.2
Burst speed	245.9	174.4
Body length	246.7	171.0
Cruising speed + burst speed	234.6	173.9
Body length + cruising speed	240.9	171.6
Body length + burst speed	245.8	172.9
All factors	235.9	171.8

As described above, R was not affected by S, at least within a salinity range between 15 and 33, but significantly by T (Fig. 2). Therefore, M can be parameterized with T and approximated by $M = 0.0055e^{0.066T}$.

Integrating these equations, G is given by $10(0.026T - 0.11) \times P_C - 0.0055e^{0.066T}$. These relationships at 8, 18 and 26°C are representatively shown in Fig. 7.

Application of the carbon budget model to natural polyp population

We applied the carbon budget model to the polyp population in Fukuyama Harbor, where the monthly

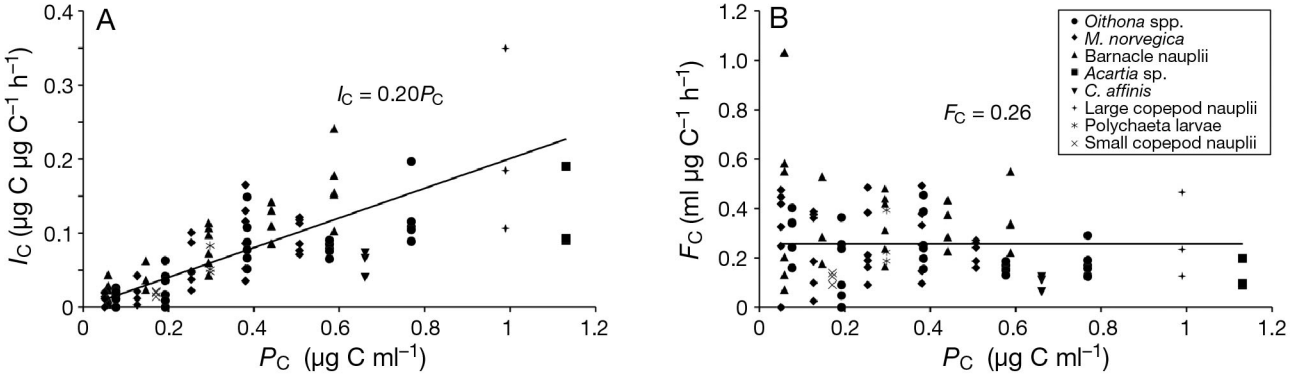

Fig. 6. Functional responses of *Aurelia aurita* polyps on various zooplankton taxa: (A) carbon weight-specific ingestion rates (I_C); (B) carbon weight-specific clearance rates (F_C). P_C: prey carbon density

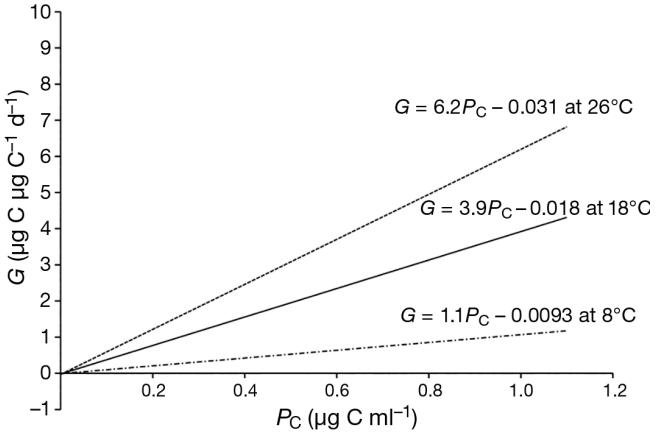

Fig. 7. Modeled relationships between prey carbon density (P_C) and the carbon weight-specific growth rate (G) of *Aurelia aurita* polyps at representative temperatures of 8, 18 and 26°C

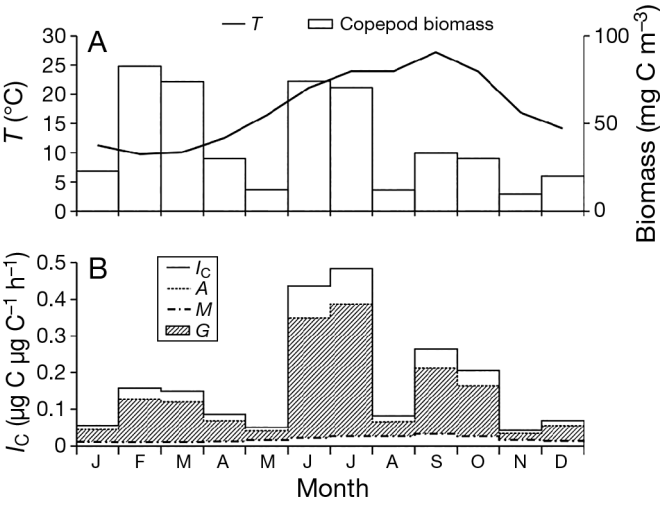

Fig. 8. (A) Monthly changes in average temperature and copepod biomass in Fukuyama Harbor calculated from the data obtained by Uye & Liang (1998). (B) Simulated carbon budget of an *Aurelia aurita* polyp population. Columns denote, from the top: ingestion (I_C), assimilation (A) and metabolic (M) rates. Hatched area indicates the polyp growth rate (G)

average temperature ranged from 9.7 to 27.2°C and copepod biomass ranged from 9.7 to 82.7 mg C m^{-3} (Fig. 8A). Our simulation suggests that the polyps likely have a large seasonal variation in both I_C (range: 0.043 to 0.48 µg C µg C^{-1} d^{-1}) and A (range: 0.034 to 0.39 µg C µg C^{-1} d^{-1}) rates, with the latter always greater than M (range 0.010 to 0.033 µg C µg C^{-1} d^{-1}), sustaining positive growth rates (with values of G ranging from 0.017 to 0.36 µg C µg C^{-1} d^{-1}). G is lowest in November and highest in July (Fig. 8B).

DISCUSSION

Respiration rates

As R of fed *Aurelia aurita* s.l. polyps was 4 times as high as that of starved ones (for 14 d at 20°C) due to specific dynamic action (Shick 1975), feeding condition is one of important factors influencing the respiration rates. Hence, we standardized the feeding condition of polyps by starving them for 2 d (plus 1 d for acclimation) prior to the measurement of R, which was the same starvation period used in previous studies (Mangum et al. 1972, Gambill & Peck 2014). Because the respiration rates at 20°C of 0.07 and 0.06 µg O_2 µg C^{-1} d^{-1} in Mangum et al. (1972) and this study, respectively, were almost equivalent to that of 14-d starved polyps (0.05 µg O_2 µg C^{-1} d^{-1}) in Shick (1975), we speculate that the 2-d starved polyps respire at close to the basal rate. The respiratory response of polyps to temperature was rapid in our experiment because of the 1-d acclimation period, which was the same in Mangum et al. (1972), but different from the slow response of polyps acclimated for 2–5 wk in Gambill & Peck (2014). Our preliminary experiments (data not shown) showed no significant differences in values of R between 1-d and 7-d acclimated polyps at each value of T between 8 and 28°C (Welch's test, $p > 0.05$), and therefore our respiration rates determined at different temperatures (Fig. 2A) were not affected by the acclimation period, at least within 7 d.

Mangum et al. (1972) reported that the respiration rate of *A. aurita* polyps increased exponentially with increasing temperature from 12 to 32°C for polyps from Chesapeake Bay, USA. On the other hand, Gambill & Peck (2014) found that the rate remained at a steady minimum in lower temperature conditions and increased markedly above a temperature threshold, which was between 12 and 15°C for polyps from the Baltic Sea and between 10 and 12°C for polyps from the North Atlantic. Our polyps from Hakata Bay exhibited exponentially increasing oxygen consumption with temperature (Fig. 2), conforming to the result in Mangum et al. (1972). The differences in the respiratory responses of polyps to temperature may be attributed to the different thermal windows at the sites of geographic origin, as speculated by Gambill & Peck (2014). Compared to the boreal North Atlantic and Baltic Sea, with cooler and narrower thermal ranges (2 to 17°C; Gambill & Peck 2014), our polyps in Hakata Bay are exposed to much wider thermal fluctuations (annual range 6 to 32°C;

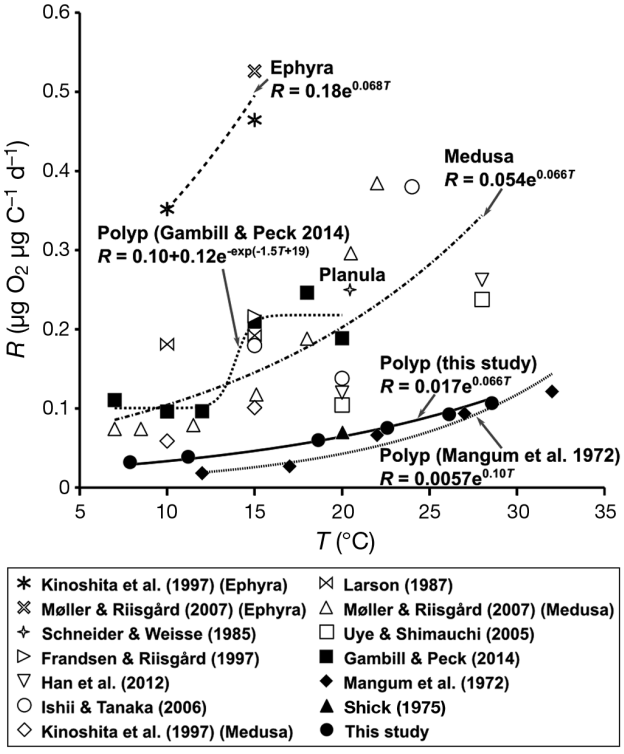

Fig. 9. Relationships between carbon weight-specific respiration rate (R) and temperature (T) in *Aurelia aurita* polyp, ephyra, medusa and planula stages. An exponential regression curve is fitted for each stage, except for polyp respiration rates reported by Gambill & Peck (2014) where the Gompertz curve is applied

Shikata et al. 2008) as are those in Chesapeake Bay (1.9 to 29°C; Mangum et al. 1972).

The body volume of polyps increased by osmotic uptake of ambient water with decreasing salinity, as was found by Webb et al. (1972) and Weiler & Black (1991). Weiler & Black (1991) also demonstrated that the amino acid incorporation rate of polyps sharply increased immediately after the salinity change but became stable at a new rate in 9 h. Hence, our acclimation period (1 d) may be enough for polyps to acclimate to each salinity condition. Constant R over a wide range of S (15 to 33; Fig. 2B) suggests that *A. aurita* polyps spend no energy for osmoregulation, i.e. they are osmocomformers (Weiler & Black 1991), which facilitates their euryhaline character (Ishii & Katsukoshi 2010, Thein et al. 2012, Widmer et al. 2016). The relationship between R and T can be compared among different life stages (i.e. polyp, ephyra, medusa, and planula) of *A. aurita* (Fig. 9). For polyps, R can be converted from the rates measured by Shick (1975), Mangum et al. (1972) and Gambill & Peck (2014) by assuming a polyp's specific density (i.e. wet weight/contracted body volume) to be 1.0 and the dry-to-carbon weight conversion to be 0.11 ± 0.03 (authors' unpubl. data). Rates of ephyrae are converted from the measurements by Kinoshita et al. (1997) and Møller & Riisgård (2007b), assuming the dry-to-carbon weight conversion to be 0.07 (Møller & Riisgård 2007b). The rates in medusae are converted from those in previous studies (Larson 1987, Frandsen & Riisgård 1997, Kinoshita et al. 1997, Ishii & Tanaka 2006, Uye & Shimauchi 2005, Møller & Riisgård 2007b, Han et al. 2012), using conversion factors from wet weight and dry weight to carbon weight to be 0.0012 and 0.048, respectively (Han et al. 2009). A rate for planulae is estimated using a dry-to-carbon weight conversion to be 0.39 (Schneider & Weisse 1985). In the polyp stage, values of R from Mangum et al. (1972) range from 0.018 to 0.094 µg O_2 µg C^{-1} d^{-1} at 12 and 27°C, respectively, which are nearly comparable to our results, i.e. 0.029 and 0.11 µg O_2 µg C^{-1} d^{-1} at 12 and 27°C, respectively (Fig. 9). On the other hand, the rates reported by Gambill & Peck (2014) ranged from 0.096 to 0.11 µg O_2 µg C^{-1} d^{-1} at ≤12°C and from 0.19 to 0.25 µg O_2 µg C^{-1} d^{-1} at ≥15°C, which are much higher than our results (Fig. 9). In the ephyra stage, the mean rates are 0.35 and 0.49 µg O_2 µg C^{-1} d^{-1} at 10 and 15°C, respectively, ca. 10 times higher than those of our polyps. In the medusa stage, the rates range from 0.027 to 109 µg O_2 µg C^{-1} d^{-1} at 8 and 28°C, respectively, ca. 3 times higher than those of our polyps. The respiration rate of planulae is 0.25 µg O_2 µg C^{-1} d^{-1} at 20°C (Schneider & Weisse 1985; Fig. 9). From these facts, we speculate that the sedentary polyp stage has lower metabolic requirements per unit body carbon weight than do the swimming planula, ephyra and medusa stages.

Functional response

The functional responses of *A. aurita* polyps fed *Microsetella norvegica*, *Oithona* spp., and barnacle nauplii (Fig. 3) were similar in pattern to that of all mesozooplankton taxa combined: a constant clearance rate irrespective of prey density and a linear increase of ingestion rate with prey availability (Fig. 6). Values of I never attained saturation below a density of 1.1 µg C ml^{-1} (1100 mg C m^{-3}), the highest density tested. Such an extraordinary density would, however, scarcely be encountered by polyps in the field, since the reported annual maxima of mesozooplankton biomass fall in the range 100 to 300 mg C m^{-3} in highly productive coastal waters, such as Nar-

ragansett Bay and Chesapeake Bay, USA (Durbin & Durbin 1981, Roman et al. 2005), and the Inland Sea of Japan and Honjo Area, Japan (Uye & Shimazu 1997, Han et al. 2009). Although our experimental setup (i.e. 1 h feeding duration, using starved polyps) might lead to higher ingestion rates, their actual feeding capacity appears to be extremely high; they are capable of consuming as much carbon daily as 5 times their own body carbon content when eating large copepod nauplii (Fig. 6A), prey commonly available in the field.

All zooplankton types used in this study were captured and ingested by *A. aurita* polyps, although the characteristics of each type greatly affected the ingestion rate (Fig. 5, Table 2). The ingestion rates in terms of number of prey per unit polyp carbon weight were higher for prey with faster cruising speeds, corroborating a theoretical encounter model, in which faster swimmers encounter a predator more frequently (Rothschild & Osborn 1988). I_P were lower for prey with higher burst speeds, which may be attributed to their better ability to escape from entanglement by sticky polyp tentacles, as typically represented by *Acartia* sp. (Table 1). Further, there was a positive correlation between prey body length and I_C suggesting that larger prey with more carbon content more efficiently provide ingestable carbon. Thus, the most appropriate prey for polyps are characterized by relatively larger body sizes and lower burst speeds, particularly as represented by large copepod nauplii (Table 1).

Ciliated protozoa, major components of microzooplankton, can also be prey for *A. aurita* polyps. Kamiyama (2011) conducted feeding experiments using 3 ciliate species (*Favella ehrenbergii*, *Strombidium* sp. and *Myrionecta rubra*) at various densities up to ca. 1.4 µg C ml^{-1} at 20°C. The functional response of polyps (mean carbon content 38.1 µg) was hyperbolic with a plateau above a ciliate density of 0.5 µg C ml^{-1}. The I_C and A estimated in Kamiyama's experiments were 0.21 and 0.17 µg C µg C^{-1} d^{-1}, respectively, much higher than the metabolic demand (0.021 µg C µg C^{-1} d^{-1}). However, the high ciliate densities established in the experiments would be unrealistic in natural waters, as the highest reported microzooplankton biomass was ca. 300 mg C m^{-3} in Nueces Estuary, USA (Buskey 1993), and the annual average microzooplankton biomass generally ranges from 3 to 30 mg C m^{-3} (Revelante & Gilmartin 1983, Dolan & Coats 1990, Leakey et al. 1992, Uye & Shimazu 1997). That is slightly less than the average mesozooplankton biomass which ranges roughly from 10 to 50 mg C m^{-3} in many coastal waters (Durbin & Durbin 1981, Buskey 1993, Uye & Shimazu 1997, Roman et al. 2005).

There is still an open question: What are the major foods for scyphozoan polyps in nature? Here, we compare the ingestion rates of *A. aurita* polyps at 20°C of microzooplankton (according to experiments by Kamiyama 2011) and of mesozooplankton (based on our results) at densities equivalent to their annual average biomasses in the Inland Sea of Japan, i.e. 4.0 and 19.5 mg C m^{-3} for microzooplankton and mesozooplankton, respectively (Uye et al. 1996, Uye & Shimazu 1997). The estimated A of microzooplankton is 0.0018 µg C µg C^{-1} d^{-1}, equivalent to only 9% of their M, whereas for mesozooplankton it could be as much as 0.09 µg C µg C^{-1} d^{-1}, or 420% of their M. Therefore, we conclude that mesozooplankton accounts for the majority of polyp diets in the field, with the microzooplankton contribution a supplement.

Dissolved organic carbon (DOC) is another possible source of energy for *A. aurita* polyps, as indicated by Shick (1973, 1975). According to Shick (1975), the incorporation rate, being dependent on temperature as well as surrounding DOC concentration, at the annual average DOC concentration in the Inland Sea of Japan (ca. 1.6 mg C l^{-1}; Akane et al. 2004), varies from 0.008 to 0.050 µg C µg C^{-1} d^{-1} at 12 and 32°C, respectively. This estimation demonstrates that the DOC incorporation rates of polyps are higher than their M, resulting in net growth when they experience temperatures >18°C. However, our polyps kept in 0.2-µm filtered seawater from the Inland Sea of Japan for 8 wk did not grow, but rather gradually shrank and/or formed podocysts, as was also observed by Han & Uye (2010) and Thein et al. (2012). Therefore, the role of DOC in the energetic balance of scyphozoan polyps needs to be re-examined.

Bioenergetics of *A. aurita* polyp populations in the field

Enclosure with concrete walls, large numbers of floating piers and buoys, and the recurrent occurrence of massive blooms of *A. aurita* medusae in adjoining offshore waters, which have severely damaged local seine-net fisheries for anchovy larvae (Hashirijima Fisheries Cooperative, Fukuyama, pers. comm.), are factors that likely make Fukuyama Harbor a major habitat of seeding polyps supplying numerous medusae, like other harbors with a similar physical structure in the Inland Sea of Japan (Makabe et al. 2014). The presence of copepod biomass

that would provide suitable prey for polyps was detected in Fukuyama Harbor in 1986 and 1987 (Uye & Liang 1998), years when bloom-level phytoplankton and associated benthic anoxia were prominent in summer (Uye et al. 1984). Since similar eutrophic and polluted conditions persist, at least until the first decade of this century as reported by Takata et al. (2011), we speculate that zooplankton taxonomic composition and biomass in Fukuyama Harbor have not changed appreciably over the last 3 decades. Hence, the growth rates of polyps computed here (Fig. 8B) may also represent present-day conditions, suggesting that this harbor has long been a suitable habitat for *A. aurita* polyps. If non-copepod mesozooplankton, which were excluded from the prey biomass estimates of Uye & Liang (1998), were to be incorporated in our simulation, the growth rate of polyps would be even greater.

Eco-physiological conditions or life cycle traits of *A. aurita* polyps change on a seasonal basis in temperate Japanese waters (Ishii & Watanabe 2003, Han & Uye 2010, Thein et al. 2012), as in other temperate coastal waters (Willcox et a. 2007, Pascual et al. 2015, Wang et al. 2015). During warm seasons, when temperature is generally >15°C, well-fed adult polyps reproduce asexually—primarily by budding (Han & Uye 2010, Thein et al. 2012)—expanding the population. Podocyst production, another form of asexual reproduction, is carried out when adult polyps are kept starved or fed little (Han & Uye 2010, Thein et al. 2012). During cold seasons (≤15°C), some physiological changes occur perhaps in preparation for metamorphosis into strobilae (Spangenberg 1965, Berking et al. 2005). Budding and podocyst formation greatly diminish, but somatic growth nonetheless persists and strobilation progresses (Willcox et al. 2007, Han & Uye 2010). Thus, the seasonal polyp population dynamics in Fukuyama Harbor can be surmised as follows. During warm months from May to November, owing to higher growth rates (mean 0.15 µg C µg C^{-1} d^{-1}), the polyps are capable of expanding their populations by budding and subsequent somatic growth of budded polyps. In addition, polyps also increase through the settlement of planulae as a result of sexual reproduction in the medusa stage. Podocyst production may be limited because of relatively high ingestion rates. During cold months (December to April), when mean growth rate is 0.075 µg C µg C^{-1} d^{-1}, the majority of ingested carbon may be incorporated into somatic growth to produce larger polyps which can then metamorphose into strobilae with more discs so they can release more ephyrae (Ishii & Watanabe 2003, Wang et al. 2015). In the field, however, the polyp populations are threatened by several factors, including predation by natural enemies (Hernroth & Gröndahl 1985, Takao et al. 2014), and by space and food competition with other sessile animals (Willcox et al. 2008, Ishii & Katsukoshi 2010). Therefore, the potential rates of population increase predicted by our model may not always be accomplished by the population in nature.

The moon jellyfish, formerly known as *A. aurita*, is now a species complex which consists of at least 8 cryptic species in addition to *A. aurita* s.s., according to molecular phylogenetics (Dawson & Jacobs 2001). If the seasonal life cycle and physio-ecological characteristics of these species are similar to our *A. aurita*, tentatively designated as *Aurelia* sp. 1 (Dawson & Jacobs 2001), our bioenergetic model may be applicable to the polyp populations in any temperate coastal waters having an annual thermal range similar to that of Hakata Bay. Our model predicts that oligotrophic areas in which the mesozooplankton biomass is always less than the minimum requirement for metabolism (4.6 to 8.6 mg C m^{-3} within the seasonal thermal range of 8 to 28°C) do not constitute polyp habitat.

As the growth rate of polyps increases with the increase of mesozooplankton biomass, eutrophication very likely is a major driving force for the increase of polyp populations (Richardson et al. 2009, Purcell 2012, Duarte et al. 2013), together with other factors such as global warming and the increase of artificial structures, which can lead to extensive medusa blooms. For comprehensive understanding of *A. aurita* polyp population dynamics in the field, intensive monitoring of polyp colonies, which commonly attach to the undersurfaces of artificial structures (Willcox et al. 2008, Purcell et al. 2009, Makabe et al. 2014), together with parameters affecting the eco-physiology of polyps (e.g. temperature, salinity, DO, zooplankton biomass, predators, and sessile animals), is essential. However, methodological difficulties (e.g. SCUBA underneath piers, enumeration of polyps attached to 3-dimensional substrates) constrain such monitoring, so few such studies have been conducted (Willcox et al. 2008, Di Camillo et al. 2010, Makabe et al. 2014). In any case, our model will be useful for estimating the potential population dynamics of *A. aurita* polyps in temperate coastal waters from the viewpoint of bioenergetics.

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LITERATURE CITED

Akaike H (1987) Factor analysis and AIC. Psychometrika 52: 317–332

Akane S, Makino S, Hashimoto N, Yatsuzuka Y, Kawai Y, Takeda K, Sakugawa H (2004) Hydrogen peroxide in the sea water of Hiroshima Bay, Japan. Oceanogr Jpn 13: 185–196 (in Japanese with English abstract)

Båmstedt U, Lane J, Martinussen MB (1999) Bioenergetics of ephyra larvae of the scyphozoan jellyfish *Aurelia aurita* in relation to temperature and salinity. Mar Biol 135:89–98

Båmstedt U, Gifford DJ, Irigoien X, Atkinson A, Roman M (2000) Feeding. In: Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley M (eds) ICES zooplankton methodology manual, Academic Press, San Diego, CA, p 297–399

Berggreen U, Hansen B, Kiørboe T (1988) Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. Mar Biol 99:341–352

Berking S, Czech N, Gerharz M, Herrmann K and others (2005) A newly discovered oxidant defence system and its involvement in the development of *Aurelia aurita* (Scyphozoa, Cnidaria): reactive oxygen species and elemental iodine control medusa formation. Int J Dev Biol 49:969–976

Buskey EJ (1993) Annual pattern of micro- and mesozooplankton abundance and biomass in a subtropical estuary. J Plankton Res 15:907–924

Buskey EJ, Lenz PH, Hartline DK (2002) Escape behavior of planktonic copepods in response to hydrodynamic disturbances: high speed video analysis. Mar Ecol Prog Ser 235:135–146

Dawson MN, Jacobs DK (2001) Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria, Scyphozoa). Biol Bull 200:92–96

Di Camillo CG, Betti F, Bo M, Martinelli M, Puce S, Bavestrello G (2010) Contribution to the understanding of seasonal cycle of *Aurelia aurita* (Cnidaria: Scyphozoa) scyphopolyps in the northern Adriatic Sea. J Mar Biol Assoc UK 90:1105–1110

Dolan JR, Coats DW (1990) Seasonal abundances of planktonic ciliates and microflagellates in mesohaline Chesapeake Bay waters. Estuar Coast Shelf Sci 31:157–175

Duarte CM, Pitt KA, Lucas CH, Purcell JE and others (2013) Is global ocean sprawl a cause of jellyfish blooms? Front Ecol Environ 11:91–97

Durbin AG, Durbin EG (1981) Standing stock and estimated production rates of phytoplankton and zooplankton in Narragansett Bay, Rhode Island. Estuaries 4:24–41

Frandsen K, Riisgård H (1997) Size dependent respiration and growth of jellyfish, *Aurelia aurita.* Sarsia 82:307–312

Gambill M, Peck MA (2014) Respiration rates of the polyps of four jellyfish species: potential thermal triggers and limits. J Exp Mar Biol Ecol 459:17–22

Gröndahl F (1988) Interactions between polyps of *Aurelia aurita* and planktonic larvae of scyphozoans: an experimental study. Mar Ecol Prog Ser 45:87–93

Han CH, Uye S (2010) Combined effects of food supply and temperature on asexual reproduction and somatic growth of polyps of the common jellyfish *Aurelia aurita* s.l. Plankton Benthos Res 5:98–105

Han CH, Kawahara M, Uye S (2009) Seasonal variations in the trophic relationship between the scyphomedusa *Aurelia aurita* s.l. and mesozooplankton in a eutrophic brackish-water lake, Japan. Plankton Benthos Res 4: 14–22

Han C, Chae J, Jin J, Yoon W (2012) Estimation of the minimum food requirement using the respiration rate of medusa of *Aurelia aurita* in Sihwa Lake. Ocean Sci J 47: 155–160

Hansson LJ, Moeslund O, Kiørboe T, Riisgård HU (2005) Clearance rates of jellyfish and their potential ingestion impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). Mar Ecol Prog Ser 304: 117–131

Hernroth L, Gröndahl F (1985) On the biology of *Aurelia aurlta* (L.): 2. Major factors regulating the occurrence of ephyrae and young medusae in the Gullmar Fjord, western Sweden. Bull Mar Sci 37:567–576

Huang X, Huang B, Zeng Y, Li S (2015) Effect of dinoflagellates and diatoms on the feeding response and survival of *Aurelia* sp. polyps. Hydrobiologia 754:179–188

Hygum BH, Rey C, Hansen BW (2000) Growth and development rates of *Calanus finmarchicus* nauplii during a diatom spring bloom. Mar Biol 136:1075–1085

Ishii H, Katsukoshi K (2010) Seasonal and vertical distribution of *Aurelia aurita* polyps on a pylon in the innermost part of Tokyo Bay. J Oceanogr 66:329–336

Ishii H, Tanaka F (2006) Respiration rates and metabolic demands of *Aurelia aurita* in Tokyo Bay with special reference to large medusae. Plankton Benthos Res 1:64–67

Ishii H, Watanabe T (2003) Experimental study of growth and asexual reproduction in *Aurelia aurita* polyps. Sessile Organisms 20:69–73

Jiang H, Kiørboe T (2011) The fluid dynamics of swimming by jumping in copepods. J R Soc Interface 8:1090–1103

Kamiyama T (2011) Planktonic ciliates as a food source for the scyphozoan *Aurelia aurita* (s.l.): feeding activity and assimilation of the polyp stage. J Exp Mar Biol Ecol 407: 207–215

Kinoshita J, Hiromi J, Kadota S (1997) Do respiratory metabolic rates of the scyphomedusa *Aurelia aurita* scale isometrically throughout ontogeny in a sexual generation? Hydrobiologia 347:51–55

Koski M, Kiørboe T, Takahashi K (2005) Benthic life in the pelagic: aggregate encounter and degradation rates by pelagic harpacticoid copepods. Limnol Oceanogr 50: 1254–1263

Landry MR, Fagerness VL (1988) Behavioral and morphological influences on predatory interactions among marine copepods. Bull Mar Sci 43:509–529

Lang WH, Forward RB, Miller DC (1979) Behavioral responses of *Balanus improvisus* nauplii to light intensity and spectrum. Biol Bull 157:166–181

Larsen PS, Madsen CV, Riisgård HU (2008) Effect of temperature and viscosity on swimming velocity of the copepod *Acartia tonsa,* brine shrimp *Artemia salina* and rotifer *Brachionus plicatilis.* Aquat Biol 4:47–54

Larson RJ (1987) Respiration and carbon turnover rates of medusae from the NE Pacific. Comp Biochem Physiol A 87:93–100

Leakey RJG, Burkill PH, Sleigh MA (1992) Planktonic ciliates in Southampton Water: abundance, biomass, production, and role in pelagic carbon flow. Mar Biol 114: 67–83

Lucas CH, Graham WM, Widmer C (2012) Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. Adv Mar Biol 63:133–196

Makabe R, Furukawa R, Takao M, Uye S (2014) Marine

artificial structures as amplifiers of *Aurelia aurita* s.l. blooms: a case study of a newly installed floating pier. J Oceanogr 70:447–455

Mangum CP, Oakes MJ, Shick JM (1972) Rate-temperature responses in scyphozoan medusae and polyps. Mar Biol 15:298–303

McCloskey LR, Muscatine L, Wilkerson FP (1994) Daily photosynthesis, respiration, and carbon budgets in a tropical marine jellyfish (*Mastigias* sp.). Mar Biol 119:13–22

Mileikovsky SA (1973) Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. Mar Biol 23:11–17

Møller LF, Riisgård HU (2007a) Feeding, bioenergetics and growth in the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina*. Mar Ecol Prog Ser 346:167–177

Møller LF, Riisgård HU (2007b) Respiration in the scyphozoan jellyfish *Aurelia aurita* and two hydromedusae (*Sarsia tubulosa* and *Aequorea vitrina*): effect of size, temperature and growth. Mar Ecol Prog Ser 330:149–154

Östman C (1997) Abundance, feeding behaviour and nematocysts of scyphopolyps (Cnidaria) and nematocysts in their predator, the nudibranch *Coryphella verrucosa* (Mollusca). Hydrobiologia 355:21–28

Pascual M, Fuentes V, Canepa A, Atienza D, Gili J, Purcell JE (2015) Temperature effects on asexual reproduction of the scyphozoan *Aurelia aurita* s.l.: differences between exotic (Baltic and Red seas) and native (Mediterranean Sea) populations. Mar Ecol 36:994–1002

Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Annu Rev Mar Sci 4:209–235

Purcell JE, Hoover RA, Schwarck NT (2009) Interannual variation of strobilation by the scyphozoan *Aurelia labiata* in relation to polyp density, temperature, salinity, and light conditions *in situ*. Mar Ecol Prog Ser 375:139–149

R Core Team (2016). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Revelante N, Gilmartin M (1983) Microzooplankton distribution in the Northern Adriatic Sea with emphasis on the relative abundance of ciliated protozoans. Oceanol Acta 6:407–415

Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol Evol 24:312–322

Roman M, Zhang X, McGilliard C, Boicourt W (2005) Seasonal and annual variability in the spatial patterns of plankton biomass in Chesapeake Bay. Limnol Oceanogr 50:480–492

Rothschild BJ, Osborn TR (1988) Small-scale turbulence and plankton contact rates. J Plankton Res 10:465–474

Schneider G (1989) Estimation of food demands of *Aurelia aurita* medusae populations in the Kiel Bight/Western Baltic. Ophelia 31:17–27

Schneider G, Weisse T (1985) Metabolism measurements of *Aurelia aurita* planulae larvae, and calculation of maximal survival period of the free swimming stage. Helgol Meeresunters 39:43–47

Shick JM (1973) Effects of salinity and starvation on the uptake and utilization of dissolved glycine by *Aurelia aurita* polyps. Biol Bull 144:172–179

Shick JM (1975) Uptake and utilization of dissolved glycine by *Aurelia aurita* scyphistomae: temperature effects on the uptake process; nutritional role of dissolved amino acids. Biol Bull 148:117–140

Shikata T, Nagasoe S, Matsubara T, Yoshikawa S and others (2008) Factors influencing the initiation of blooms of the raphidophyte *Heterosigma akashiwo* and the diatom *Skeletonema costatum* in a port in Japan. Limnol Oceanogr 53:2503–2518

Spangenberg BD (1965) A study of strobilation in *Aurelia aurita* under controlled conditions. J Exp Zool 160:1–10

Sullivan BK, Suchman CL, Costello JH (1997) Mechanics of prey selection by ephyrae of the scyphomedusa *Aurelia aurita*. Mar Biol 130:213–222

Takao M, Okawachi H, Uye S (2014) Natural predators of polyps of *Aurelia aurita* s.l. (Cnidaria: Scyphozoa: Semaeostomeae) and their predation rates. Plankton Benthos Res 9:105–113

Takata N, Takahashi H, Ukita S, Yamasaki K, Awahihara H (2011) Ecology of *Polydora cornuta* Bosc, 1802 (Spionidae: Polychaeta) in the eutrophic port of Fukuyama, with special reference to life cycle, distribution, and feeding type. J Water Environ Technol 9:259–275

Thein H, Ikeda H, Uye S (2012) The potential role of podocysts in perpetuation of the common jellyfish *Aurelia aurita* s.l. (Cnidaria: Scyphozoa) in anthropogenically perturbed coastal waters. Hydrobiologia 690:157–167

Titelman J, Kiørboe T (2003) Motility of copepod nauplii and implications for food encounter. Mar Ecol Prog Ser 247: 123–135

Uye S (1982) Length–weight relationships of important zooplankton from the Inland Sea of Japan. J Oceanogr Soc Jpn 38:149–158

Uye S, Liang D (1998) Copepods attain high abundance, biomass and production in the absence of large predators but suffer cannibalistic loss. J Mar Syst 15:495–501

Uye S, Shimauchi H (2005) Population biomass, feeding, respiration and growth rates, and carbon budget of the scyphomedusa *Aurelia aurita* in the Inland Sea of Japan. J Plankton Res 27:237–248

Uye S, Shimazu T (1997) Geographical and seasonal variations in abundance, biomass and estimated production rates of meso-and macrozooplankton in the Inland Sea of Japan. J Oceanogr 53:529–538

Uye S, Yoshiya M, Ueda K, Kasahara S (1984) The effect of organic sea-bottom pollution on survivability of resting eggs of neritic calanoids. Crustaceana Suppl 7:390–403

Uye S, Nagano N, Tamaki H (1996) Geographical and seasonal variations in abundance, biomass and estimated production rates of microzooplankton in the Inland Sea of Japan. J Oceanogr 52:689–703

Uye S, Aoto I, Onbé T (2002) Seasonal population dynamics and production of *Microsetella norvegica*, a widely distributed but little-studied marine planktonic harpacticoid copepod. J Plankton Res 24:143–153

Wang N, Li C, Liang Y, Shi Y, Lu J (2015) Prey concentration and temperature effect on budding and strobilation of *Aurelia* sp. 1 polyps. Hydrobiologia 754:125–134

Webb KL, Schimpf AL, Olmon J (1972) Free amino acid composition of scyphozoan polyps of *Aurelia aurita*, *Chrysaora quinquecirrha* and *Cyanea capillata* at various salinities. Comp Biochem Physiol B 43:653–663

Weiler KS, Black RE (1991) Immediate decrease in apparent translation rate caused by salinity change in scyphistomae of *Aurelia aurita* (Linnaeus). Comp Biochem Physiol A 99:199–202

Widmer CL, Fox CJ, Brierley A (2016) Effects of temperature

and salinity on four species of northeastern Atlantic scyphistomae (Cnidaria: Scphozoa). Mar Ecol Prog Ser 559:73–88

Willcox S, Moltschaniwskyj N, Crawford C (2007) Asexual reproduction in scyphistomae of *Aurelia* sp.: effects of temperature and salinity in an experimental study. J Exp Mar Biol Ecol 353:107–114

Willcox S, Moltschaniwskyj N, Crawford C (2008) Population dynamics of natural colonies of *Aurelia* sp. scyphistomae in Tasmania, Australia. Mar Biol 154:661–670

Yen J (1988) Directionality and swimming speeds in predator-prey and male-female interactions of *Euchaeta rimana*, a subtropical marine copepod. Bull Mar Sci 43: 395–403

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