Bioenergetic model and specific growth rates of jellyfish *Aurelia* spp

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ABSTRACT: The common jellyfish *Aurelia* spp. often appears in large numbers in coastal regions around the world, having a considerable predation impact on zooplankton. To better understand and quantify this phenomenon, several laboratory and field studies have determined growth rates by recording umbrella diameter and/or dry weight versus time. However, there appears to be no model describing such data. Here, we use a bioenergetic model for growth of *Aurelia* spp. dry mass (W) based on ingested food minus respiration, leading to the weight-specific growth rate μ $(1/W)$ dW/d$t = aW^b$, where the constant a depends on prey concentration and the exponent is $b = -0.2$. The model is tested against *Aurelia* spp. data in several examples, some of which represent well-fed conditions that show fair agreement with the model ($b = -0.2$ to -0.4), while others depart increasingly from the model ($b < -0.4$) with increasing W, likely due to suboptimal and fluctuating prey concentrations. Based on the model and available data, it is suggested that for a given size W, the specific growth rate increases linearly with prey concentration up to about 5 to 6 *Artemia* sp. l^{-1}, where a maximal growth rate (μ_{max}) is reached which is not exceeded for higher prey concentrations.

KEY WORDS: Energy budget · Bioenergetic growth model · Specific growth rate · Jellyfish

1. INTRODUCTION

The common cosmopolitical jellyfish genus *Aurelia* has a long and confusing taxonomic history, and morphological variability in the medusae overlaps across very distant geographic localities, as described by Lawley et al. (2021) who, based on genetic data, identified 28 species of *Aurelia*. All *Aurelia* spp. are voracious filter-feeding predators of zooplankton. They occur in many coastal ecosystems where they can be very abundant and have a considerable effect on the zooplankton, thus playing an important role as a key organism in the ecosystem (Möller 1980, Bailey & Batty 1984, Båmstedt 1990, Schneider & Behrends 1994, 1998, Behrends & Schneider 1995, Lucas 1996, Uye et al. 2003, Hansson et al. 2005, Møller & Riisgård 2007a,b, Matsakis & Conover 1991).

Jellyfish population predation impact can be evaluated when the density and mean umbrella diameter of the jellyfish are known. Thus, by estimating the volume-specific population clearance rate (F_{pop} = individual clearance rate × density), the theoretical half-life of prey organisms (typically copepods) can be calculated as $t_{1/2} = \ln2/F_{pop}$ (Møller & Riisgård 2007b). If $t_{1/2}$ is short (a few days) compared to the generation time of the prey (about 3 wk for copepods), the jellyfish control the zooplankton and hence are key organisms in the ecosystem. But in ecological studies it is also important to know if the jellyfish are food limited. By repeatedly collecting jellyfish from a population, umbrella diameter can be measured and used for estimating dry weight, which can subsequently be used for estimating weight-specific growth rates (μ) in the interval between collections. The present study is focused on understanding how μ relates to body size through the bioenergetics of *Aurelia* spp. in order to make it possible to determine if jellyfish are food limited, and if so to what degree.

Growth rates of *Aurelia* spp. medusae in field studies and laboratory feeding experiments are usually estimated from changes in mean umbrella diameter and/or body dry weight with time (e.g. Lucas 1996 and references therein, Hansson 1997, Ishii & Båmstedt 1998, Goldstein & Riisgård 2016, Lüskow & Riisgård 2016). The weight-specific growth rate (d^{-1}), frequently denoted as the daily instantaneous growth rate, is calculated as $\mu = (1/W)\, dW/dt$ where $W =$ body dry weight and $t =$ time. In the case of time series data, the specific growth rate is expressed by the exponent (μ) in the regression equation for an exponential curve fit of W versus t: $W = ae^{\mu t}$, where a is a constant. A value μ determined this way is at best a mean value for a given data set because μ is not constant for jellyfish, as shown by the present study.

A bioenergetic growth model based on an energy budget and making use of near identical b exponents in the power functions for filtration rate (F) and respiration rate (R) versus W (i.e. F or $R = aW^b$) was developed for the blue mussel *Mytilus edulis*. It was found that actual growth rates in the field were generally in good agreement with the model (Riisgård et al. 2014).

Here, we present a bioenergetic growth model for *Aurelia aurita*, and we show that the weight-specific growth rate is not constant but decreases with size according to $\mu = a_1 W^b$ where $b < 0$. In the case of *A. aurita* feeding at optimal prey concentration, it is predicted that weight-specific growth rate will decrease with body weight as a power function with a constant exponent $b = -0.2$. This prediction for b is tested using available published data on *Aurelia* spp.

2. MATERIALS AND METHODS

Based on *Aurelia* spp. data in the literature, we first develop a growth model based on the energy budget for growth (G) by making use of near identical b exponents in the power functions for clearance rate (F) and respiration rate (R) versus body dry weight W. This development follows the earlier approach for growth of the blue mussel *Mytilus edulis* (Riisgård et al. 2014), for which F or $R = aW^{0.66}$, leading to a decrease in the weight-specific growth rate of mussels with increasing size. This weight-specific growth rate is given by $\mu = G/W = aW^{0.66-1} = aW^{-0.34}$, and showed good agreement with field data for young, non-spawning mussels during periods of growth. For *Aurelia aurita*, it has been found that $b \approx 0.8$; therefore, the model predicts the weight-specific growth rate must decrease with increasing sponge size,

which implies that growth can never be exponential. This hypothesis is supported by literature growth data obtained on *Aurelia* spp. in field experiments conducted during periods with positive growth, typically in the spring. Data were replotted from other publications using an in-house graphical program 'Gtpoints', which generates a table of data point coordinates according to the axis scales in a bitmap image of a given graph.

The change in jellyfish size over time intervals was used to estimate the specific growth rates in each interval and subsequently used for evaluation of the growth pattern. For a power-function growth pattern, the interval-specific growth rate will decrease with increasing size, and for such data a power-function fit will estimate the actual data. Thus, if an exponential curve fit is used to describe G versus time, we expect a systematic deviation between data and regression curve because μ is not constant.

From recorded experimental data, the weight-specific growth rate (μ, % d^{-1}) of *Aurelia* spp. was determined using the equation

$$\mu = \ln(W_2/W_1)/(t_2 - t_1) \times 100 \tag{1}$$

where W_2 and W_1 express the mean individual body dry mass (or body weight) of jellyfish at time t_2 and time t_1, respectively.

The corresponding average size during the time interval was estimated as

$$W_{\text{avg}} = (W_0 \times W_t)^{1/2} \tag{2}$$

leading to an experimentally determined relationship of form:

$$\mu_a = a' W_{\text{avg}}^{b'} \tag{3}$$

which may be compared to the model below expressed by Eq. (8).

The following allometric equation was used to estimate dry weight (W, mg) from umbrella diameter (d, mm) of *A. aurita* medusae (≥ 10 mm, Olesen et al. 1994):

$$W = 1.73 \times 10^{-3} \times d^{2.82} \tag{4}$$

We used 3 d old brine shrimp *Artemia* sp. as a reference prey organism because *A. aurita*'s retention efficiency for different prey organisms in clearance experiments differs from their retention efficiency for *Artemia*. Relative to *Artemia*, retention efficiency has been found to be 60% for rotifers, 35% for adult copepods, 22% for copepod nauplii, and 14% for mussel veligers (Riisgård & Madsen 2011, Table 6 therein). Therefore, we do not express prey density in µg C l^{-1}. Data employed in this study stem from publications that used the unit milligram (mg) for dry weight biomass, and we have therefore retained this

unit in all figures and tables. However, dry weight can be converted to carbon by means of the following conversion factors used in the present study: 1 mg dry weight *Aurelia* spp. = 50 µg C (Schneider 1988); 1 µl O_2 = 0.46 µg C (Uye & Shimauchi 2005); 1 *Artemia* (3 d old) = 1.16 µg C (Szyper 1989).

3. RESULTS

3.1. Bioenergetic growth model

The growth of a jellyfish can be expressed by the energy (or carbon) budget as:

$$G = I - E - R = A - R \qquad (5)$$

where G is growth (production), I is ingestion, R is respiration (total), or the sum of R_m (maintenance respiration) and R_g (growth respiration, the metabolic cost of synthesizing new biomass), E is excretion (faeces, urine, mucus), and A is assimilated food. The budget can also be written as $G = (F \times C \times AE) - (R_m + R_g)$, where F is clearance rate, C is prey concentration, and $AE = A/I$, assimilation efficiency. Thus, equating the rate of net intake of nutritional energy to the sum of various rates of consumption, the energy balance for a growing jellyfish may now be written as:

$$G = [(F \times C \times AE) - R_m]/a_0 \qquad (6)$$

where the constant a_0 follows from the experience that the metabolic cost of growth constitutes a certain amount of energy equivalent to a constant percentage of the growth (biomass production). This percentage has not been determined in jellyfish, but according to other studies on marine invertebrates it may be around 20% (Riisgård 1998). The clearance rate (F, l d^{-1}) of *Aurelia aurita* feeding on 3 d old brine shrimp *Artemia* sp. can be estimated from the dry weight (W, mg) according to $F = a_1 W^{b1}$, where $a_1 = 3.9$ and $b_1 = 0.78$ at 15°C (Møller & Riisgård 2007a). The maintenance respiratory rate (R_m, µl O_2 d^{-1}) can be estimated according to $R_m = a_2 W^{b2}$, where $a_2 = 10.89$ and $b_2 = 0.86$ at 15°C (Frandsen & Riisgård 1997). Therefore, the growth rate at 15°C may now be expressed as:

$$G = (C \times AE \times a_1 - a_2)W^{b1}/a_0 = aW^{b1} \qquad (7)$$

where $b_1 \approx b_2 = 0.8$. Thus, the resulting model for weight-specific growth rate ($\mu = G/W = aW^{b1}/W$) may be expressed as:

$$\mu = aW^b \qquad (8)$$

where $b = 0.8 - 1 = -0.2$. According to Eq. (8), the weight-specific growth of *A. aurita* fed a constant concentration of prey will decrease as a power function with the exponent $b = -0.2$. This prediction for the exponent is tested here using published experimental data shown in the Supplement at www.int-res.com/articles/suppl/m688p049.pdf. However, it should be mentioned that shunting of energy to production of gametes to be subsequently released by sexually mature jellyfish is not included in the growth model.

3.2. Weight-specific growth rate

Verification of the present growth model can be made using brine shrimp *Artemia* sp. as reference prey. The number n_m of *Artemia* (3 d old) needed to cover the maintenance of an *A. aurita* so that it does not starve and lose weight ($G = 0$), can according to Eqs. (5) & (7) be expressed as: $G = I - E - R_m = A - R_m = (C \times AE \times a_1 - a_2)W^{b1} = (1.16 \times n_m \times 0.9 \times 3.9/50 - 5.01/50)W^{b1} = (n_m \times 0.0814 - 0.1002)W^{b1} = 0$; hence $n_m = 0.1002/0.0814 = 1.23$ ind. l^{-1}. From this it appears that for any value n of 3 d old *Artemia*, Eq. (8) can be written as:

$$G = (n \times 0.08 - 0.10)W^{b1}/a_0 \qquad (9)$$

where $b_1 = 0.8$ and $a_0 = 1.20$, and the specific growth rate becomes

$$\mu = G/W = (n \times 0.07 - 0.08)W^{-0.2} \qquad (10)$$

where units are μ: d^{-1}, n: number l^{-1} of 3 d old *Artemia* of 1.16 µg C each, and W: mg dry weight *A. aurita*. It should be emphasized that Eq. (10) with suggested $AE = 90\%$ (Pitt et al. 2009) is only valid for *A. aurita* with $d \geq 10$ mm in the range of 1 to 6 *Artemia* l^{-1} equivalent to about 1 to 6 µg C l^{-1}, and that AE will be increasingly reduced at increasingly higher (superfluous) prey concentrations (see Fig. 1) as it would for other prey through the retention efficiency mentioned above. It should also be mentioned that influence of temperature is not addressed in the model, and finally that the reference prey organism, brine shrimp *Artemia* sp., is not among the natural zooplankton species in the sea. Brine shrimp only inhabit salt lakes and hypersaline coastal ponds but are an easily available food for cultured predatory organisms and therefore frequently used as food source for e.g. jellyfish kept in the laboratory for experimental purposes (Shields 2001, Sorgeloos et al. 2001, Riisgård et al. 2015). The 3 d old reference *Artemia* used here have no escape behavior and are
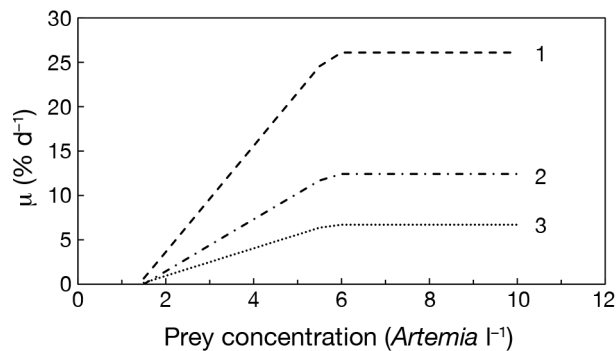
Fig. 1. Estimated specific growth rate (μ,% d^{-1}) of *Aurelia aurita* as a function of reference prey (*Artemia*) concentration using Eq. (10). Series 1: small jellyfish (d = 12.7 mm, W = 2.2 mg); Series 2: larger jellyfish (d = 56.9 mm, W = 154 mg); see Examples 1 & 2. Series 3: large jellyfish (d = 115 mm, W = 1887 mg); see Example 3. The figure shows that μ increases linearly with prey concentration, but actual data (Tables S1–S5 in the Supplement) indicate that maximum possible specific growth rates (μ_{max}) are about 20–25% d^{-1} and 10–12% d^{-1} for small and larger jellyfish, respectively, but decrease to 6–7% d^{-1} for large jellyfish. This indicates that Eq. (10), with AE = 90%, could be expected to be valid only in the range of about 1 to 6 *Artemia* l^{-1} and that at higher prey concentrations $AE < 90\%$

captured by jellyfish with about 2 times higher efficiency than other prey such as copepods (Møller & Riisgård 2007a, Fig. 5 therein). The a_1 value in the equation for clearance rate used in Eq. (7) does not apply to natural zooplankton prey, but when the retention efficiency of other prey organisms relative to *Artemia* and their carbon content is known, the present growth model may easily be modified to apply to such prey (Riisgård & Madsen 2011).

3.3. Test of bioenergetic growth model and predicted power-function exponent

The following examples serve to test the model and the predicted exponent $b = -0.2$.

Example 1. Here, the concentration of prey to constitute a fully-fed condition is unknown, so we chose 4 times the above *Artemia* maintenance concentration, implying the number $n = n_m \times 4 = 1.23 \times 4 = 4.92$ ind. l^{-1}. This is essentially the steady-state concentration of 4.9 ± 2.0 *Artemia* l^{-1} used by Lüskow & Riisgård (2016). For the specific case of an *A. aurita* (d = 56.9 mm, W = 154 mg), using Eq. (10) it is found that $\mu = (4.92 \times 0.07 - 0.08)W^{-0.2} = 0.264 W^{-0.2} = 0.264 \times 154^{-0.2} = 0.264 \times 0.365 = 0.10$ d^{-1} or 10% d^{-1}, which agrees fairly well with the experimentally measured 11.3% d^{-1} at 11.8°C in Lüskow & Riisgård (2016, Table 3 therein). This suggests a prey concentration

4 times that of maintenance closely mimics the condition of fully-fed specimens. This value is tested in the next example.

Example 2. To check if the model $\mu \sim W^{-0.2}$ can predict observed data, we use the case of a small (d = 12.7 mm) *A. aurita* (W = 2.2 mg) fed 4 times above the *Artemia* maintenance concentration. Eq. (10) gives $\mu = (4.92 \times 0.07 - 0.08)W^{-0.2} = 0.264 W^{-0.2} = 0.264 \times 2.2^{-0.2} = 0.264 \times 0.854 = 0.23$ d^{-1} or 23% d^{-1}, which is in fairly good agreement with the measured 24.4% d^{-1} at 17.1°C in Lüskow & Riisgård (2016, Table 4 therein).

Example 3. To our knowledge the longest and best time series of *A. aurita* bell diameter as a function of time was reported by Ishii & Båmstedt (1998, Figs. 2 & 4 therein) in tank experiments conducted at 12 to 15°C with food in excess. Based on recalculation of their data, we have made 2 plots. Fig. 2A shows the dry weight of jellyfish as a function of time in the well-fed tank feeding experiment. The exponential curve fit suggests a constant specific growth rate of
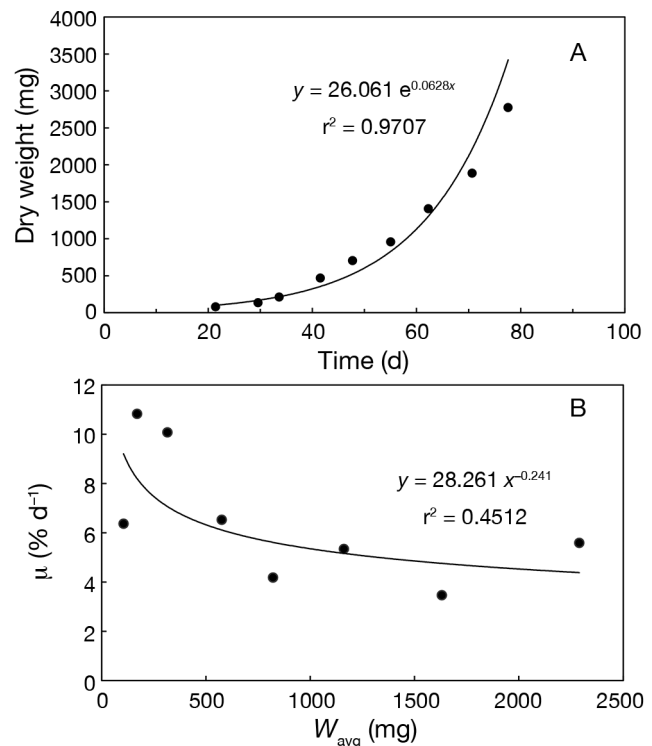

Fig. 2. (A) Dry weight of *A. aurita*. as a function of time in the well-fed condition of a tank feeding experiment. The exponential curve fit suggests a constant specific growth rate of 6.28% d^{-1}. (B) Weight-specific growth rate (μ) as a function of average size (W_{avg}) of jellyfish in the same feeding experiment. The power-function curve with $b = -0.24$ shows that the weight-specific growth rate decreases with size. Data from Table S1 based on Ishii & Båmstedt (1998)

$\mu = 6.28\%$ d^{-1}. However, Fig. 2B shows that the weight-specific growth rate as a function of average dry weight is a power-function curve, with $b = -0.24$ in good agreement with the predicted exponent of -0.2 in Eq. (8). This shows that the weight-specific growth rate is not constant but decreasing with size. In both Fig. 2A & 2B, there is data scattering, but in Fig. 2A there is a systematic deviation between data and regression curve, which clearly shows that μ is not constant, and that the regression equation under-estimates the dry weight in the first half of the growth period and overestimates it in the second half. How-ever, the exponential fit with $\mu = 6.28\%$ d^{-1} can be considered a good way to find a mean value of μ over the period of a time series $W(t)$. For comparison, the algebraic mean value of μ in Fig. 2B is 6.55% d^{-1} (Table S1). The growth data were reported for the period of late May to mid-July, during which the temperature increased from about 12°C to a maximum of 15°C.

Example 4. In an earlier study, Møller & Riisgård (2007a, Fig. 1A therein) found the relationship be-tween *A. aurita* medusa size (W, mg) and specific growth rate (μ, d^{-1}) when fed *Artemia* and/or *Acartia tonsa* in surplus at 15°C could be described by the power function $\mu = 0.1W^{-0.16}$, which is close to the ex-ponent -0.2 predicted in Eq. (8). Further, Møller & Riisgård (2007a, Fig. 1B therein) reported that the maximum weight-specific growth rate of the hydrom-edusae *Aequorea vitrina* fed in surplus was comparable to that of *A. aurita* and followed the same trend.

The above model tests and the observed power-function exponents close to $b = -0.2$ inspire confi-dence in the bioenergetic growth model. From these examples, it may be stated that the maximum spe-cific growth rates in larger medusae are always lower than in smaller stages, and the rate of decrease of μ with increasing size becomes smaller for larger sizes, i.e. showing an increasingly negative slope. Accord-ing to the model, growth of jellyfish is never expo-nential. However, during suboptimal conditions the b exponent may decrease below -0.2, as is shown in the following examples.

3.4. Growth under suboptimal conditions

Example 5. Here, we use data for growth reported by Lüskow & Riisgård (2016, Tables 3 & 4 therein, shown here in Tables S2 & S3). The weight-specific growth rate as a function of average dry weight in 2 series of feeding experiments at a maintained con-stant prey concentration of 5 *Artemia* l^{-1} at 2 temper-

atures is shown in Fig. 3. The power-function expo-nents -0.49 (Series #1, 11.8°C) and -3.4 (Series #2, 17.1°C) are considerably lower than the predicted b of -0.2. This may reflect a problem keeping the prey concentration constant, as the jellyfish increased in size during the long experimental period. For Series #1, there is a clear and systematic deviation between data and the regression curve, showing a shift from small negative exponent (b) for smaller W to an even smaller negative exponent for larger W. Regression analysis shows Series #1 data fit an approximately linear relation, $\mu = c - d \times W$, so the exponent b in $\mu = aW^b$ will depend on W as follows: $d\mu/dW = abW^{-1} = -d$, or $b \sim -(d/a)W$. Hence b becomes more and more negative as W increases in the data range of the experiment (240 to 580 mg). This may be a typical trend for cases of under-fed species, while b would remain rather constant for cases of well-fed species.

Example 6. The low exponents of -0.43 and -0.66 found for *A. aurita* during the growth period in Kertinge Nor and Mariager Fjord, respectively (Fig. 4), may reflect decreasing zooplankton concen-trations due to the predation impact of jellyfish, with prey half-life of only a few days or less, until jellyfish growth becomes negative (degrowth) due to starva-tion (Lüskow & Riisgård 2016). During sampling in 2015, the temperature increased from 5.3 to 22.4°C in Kertinge Nor, and during sampling in 2014 and 2015, the temperature increased from 9.8 to 16.8 and from 6.8 to 19.7°C, respectively, in Mariager Fjord.

Example 7. Table 3 in Olesen et al. (1994) shows the instantaneous specific growth rate of 4 mm *A. aurita* in 10 d feeding experiments using rotifers *Brachionus plicatilis* as the prey organism. The spe-cific growth rate $\mu = 20\%$ d^{-1} at initial prey concen-
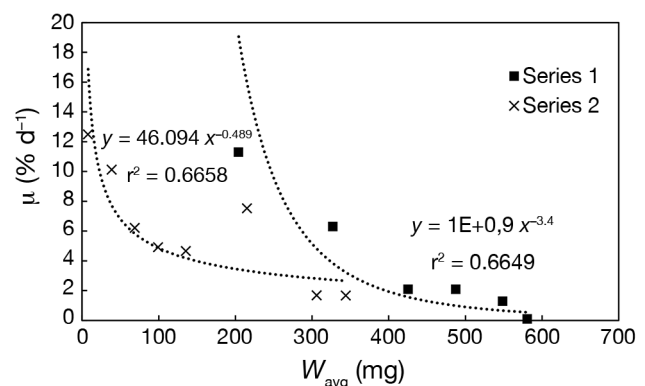

Fig. 3 Weight-specific growth rate (μ) as a function of average size (W_{avg}) for *A. aurita* in 2 series of feeding ex-periments with maintained constant food concentration at 2 temperatures. Data from Table S2 based on Lüskow & Riisgård (2016)
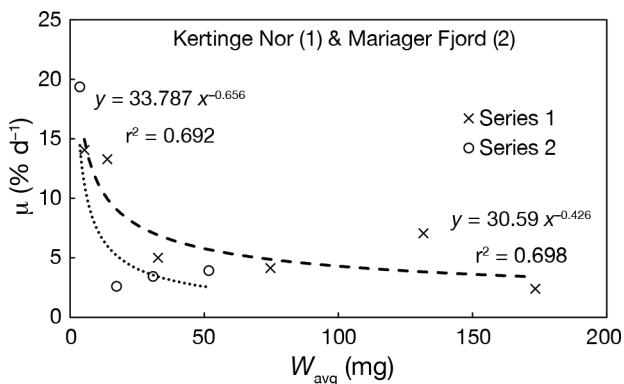
Fig. 4. Weight-specific growth rate (μ) as a function of average size (W_{avg}) for *A. aurita* in Kertinge Nor and Mariager Fjord in 2015. Data from Table S3 based on Lüskow & Riisgård (2016)

trations of 160 prey l^{-1} (equivalent to 160 × 0.15 μg C/1.16 = 21 *Artemia* l^{-1}) did not increase at higher prey concentrations up to 12 940 prey l^{-1}. At these high prey concentrations, the guts of *A. aurita* were 'completely filled up with prey organisms', and further that parts of the captured rotifers 'were apparently rejected instead of being digested', resulting in superfluous feeding and overestimation of the actual ingestion rate (Olesen et al. 1994, p. 14).

Example 8. According to Møller & Riisgård (2007a), their Fig. 4 shows maximum μ = 8% reached for *A. aurita* medusae of size W = 96 mg at *Artemia* prey concentrations up to 100 *Artemia* l^{-1}. To match the present growth model, a very low AE ~ 3.5% would be the only possibility, which could be a result of superfluous feeding.

4. DISCUSSION

In feeding experiments by Lüskow & Riisgård (2016; see Examples 1 & 2) it was found that *Aurelia aurita* fed *Artemia* 4 times above the maintenance prey concentration resulted in specific growth of 25% for small (12.7 mm diameter) jellyfish and 11% for larger (56.9 mm diameter) jellyfish. According to the model (Eq. 10), it may be hypothesized that the weight-specific growth rate of a given size of *A. aurita* increases linearly with increasing prey concentration above n_m = 1.23 *Artemia* l^{-1} and that for any constantly maintained prey concentration the weight-specific growth rate will be proportional to $W^{-0.2}$. The latter has been demonstrated using case studies, but the former remains to be demonstrated for several prey concentrations. However, such predictions have previously been made for filter-feeding

blue mussels *Mytilus edulis*. In this example the power function exponents for filtration and respiration versus body dry weight were nearly identical 0.66 resulting in a weight-specific growth rate μ = $G/W = aW^{0.66}/W = a'W^{-0.34}$ (Riisgård et al. 2014). Experimental field data for μ versus W_{avg} in a log–log plot showed *b* values close to the predicted −0.34, while the predicted *a'* values varied linearly with the actual measured food level, expressed as μg chl *a* l^{-1} (Riisgård et al. 2014, Fig. 5 therein). While the chlorophyll *a* concentration in certain areas may be relatively constant over the mussel growth season, decreasing or boom–crash zooplankton prey concentrations may be the normal case for *A. aurita*, which makes it difficult to apply the bioenergetic growth model to field data. However, during periods with steady growth, resembling exponential growth, it should be noticed that the weight-specific growth rate of *A. aurita* is not constant but decreases with increasing size, as explained by the present bioenergetic growth model. This insight also helps to understand why Hansson (1997, Fig. 7 therein) found the specific growth rate of *A. aurita* based on data from the literature and their own study 'appears to decrease with size' (Hansson 1997, p. 150).

A general picture emerges when μ versus W for *Aurelia* spp. living in various marine localities is plotted in a log-log plot (Fig. 5, Table 1). All *b* exponents

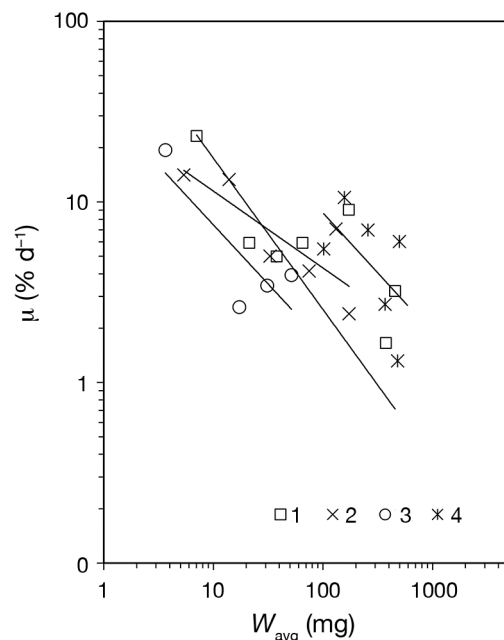Fig. 5. Weight-specific growth rate (μ) as a function of average size (W_{avg}) for *Aurelia* spp. in the 4 marine localities listed in Table 1 (Kagoshima Bay, Kertinge Nor, Mariager Fjord, and Vågsbøpollen) along with the power-function regression equations

Table 1. Parameters of power function regression lines $\mu = aW^b$ shown in Fig. 5

Line	a	b	r^2	Locality	Reference
1	120.22	−0.84	0.359	Kagoshima Bay	Miyake et al. (1997)
2	30.59	−0.43	0.698	Kertinge Nor	Lüskow & Riisgård (2016)
3	33.79	−0.66	0.692	Mariager Fjord	Lüskow & Riisgård (2016)
4	185.20	−0.66	0.322	Vågsbøpollen	Ishii & Båmstedt (1998)

are <−0.2; in comparison, the b exponent for well-fed *A. aurita* (Fig. 2) is −0.24, which is close to the model-predicted value of −0.2 for jellyfish experiencing constant prey concentration. It can therefore be concluded that growth in the field is generally fluctuating and frequently suboptimal, which is reflected in the fact that weight-specific growth rate decreases with size at a rate faster than for $b = -0.2$. Growth in the field is usually uneven due to increases and decreases in zooplankton concentrations. In Kertinge Nor, for example, jellyfish growth is strongly affected by density-driven water exchange caused by new Great Belt water entering with zooplankton, while a fraction of the jellyfish in Kertinge Nor are washed out into the Great Belt. Thus, the remaining jellyfish temporarily get more food until the newly-arrived zooplankton have been consumed (Nielsen et al. 1997, Goldstein et al. 2018).

Finally, we examine the effect of temperature on *A. aurita* growth rate G (Eq. 7) and thus the weight-specific growth rate $\mu = G/W$ (Eq. 8) where both F and R have been measured at 15°C. We then discuss possible practical applications of the growth model.

In Eq. (7) both a_1 (weight-specific clearance rate) and a_2 (weight-specific respiration rate) are sensitive to temperature, while a_0 (cost of growth) is constant. The effect of temperature on clearance rate (F) of *A. aurita* was measured by Møller & Riisgård (2007a, Fig. 6B therein), who found an increase in temperature from 5 to 15°C may result in a 5× increase in clearance rate. Further, the weight-specific respiration rate was measured in Møller & Riisgård (2007c, Fig. 2 therein) and from this it appears that an increase in temperature from 5 to 15°C results in a 3× increase in respiration rate (R). Because $b \approx b_1 \approx b_2$ in the power functions for F and $R = aW^b$, this implies that a change of F and R with temperature is determined by the change of a_1 and a_2. Thus, the greater increase in F (and thus ingestion) than in R with temperature will result in an increase in μ with temperature if prey concentration is constant. According to Møller & Riisgård (2007a, Fig. 6A therein), an increase in temperature from 5 to 15°C may result in a

4× increase in the weight-specific growth rate.

The present bioenergetic growth model may help biologists to understand if *Aurelia* spp. are food limited in, for example, enclosed or semi-enclosed marine areas in which the jellyfish population is stable, without input of jellyfish from other areas. The following may serve as an example. By making 2 or more collections of jellyfish with a time interval of about 7 to 10 d, the measured umbrella diameter (d, mm) can be used to estimate the dry weight (W, mg; Eq. 4) at the collection time and subsequently used for estimating the weight-specific growth rate (μ, % d^{-1}; Eq. 1) in each of the consecutive time intervals in which both temperature and prey concentration are likely to be near constant. The estimated μ may then be compared to the maximum possible weight-specific growth rate (μ_{max}, Fig. 1) for that size of jellyfish. If the temperature is about 15°C and the size (W) of jellyfish is close to one of the 3 modeled series for different sizes shown in Fig. 1, it can be determined whether $\mu < \mu_{max}$ and thus if the jellyfish are food limited and to what degree, by comparing the actual weight-specific growth rate with the linear phase of the weight-specific growth curve.

5. CONCLUSIONS

For consistently well-fed *Aurelia* spp., the growth model shows reasonable agreement with $\mu = aW^b$, $b \sim -0.2$ to -0.4 during growth with increasing W. At lower prey concentrations there is a trend of increasingly negative slopes of the $\mu(W)$ curve, i.e. more and more negative values of the exponent b for increasing values of W. The explanation for this may be that with decreasing and suboptimal prey concentrations, larger jellyfish will, during a given period of time, deplete the population of prey within their reach more quickly than smaller jellyfish and therefore ingest relatively less food, a process probably affected by the mixing conditions in laboratory tank experiments and in the field. Based on the model Eq. (10) and available data, it is hypothesized that for a given size W the specific growth rate increases linearly with prey concentration n up to about 5 to 6 *Artemia* l^{-1} where a maximal growth rate μ_{max} is reached. This maximal value is not exceeded for higher prey concentrations (Fig. 1). The model may be used as a tool to evaluate if *Aurelia* spp. are food limited in the field, and if so to what degree.

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