SIZE DEPENDENT RESPIRATION AND GROWTH OF JELLYFISH, *AURELIA AURITA*

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The relationship between growth, food uptake and respiration of jellyfish, *Aurelia aurita*, was examined by means of respiration rate measurements, supplemented with laboratory growth experiments with fed and unfed medusae. *A. aurita* fed rotifers (*Brachionus*) showed daily specific growth rates of maximum 24 % d^{-1}, with a net growth efficiency of about 80 %, while unfed medusae were decreasing with a mean specific degrowth rate of –4 % d^{-1}. Indirectly estimated respiration based on the degrowth rate, and the directly measured respiration were in satisfactory agreement. The respiration rate (R, μl O$_2$ d^{-1}) of different sized unfed medusae was correlated with the body dry weight (W, mg) according to the equation R = 10.89W$^{0.86}$. No convincing difference in respiration rate was observed between fed and unfed jellyfish. An energy budget showed that the lowest prey concentration resulting in maximum growth of *A. aurita* was 68 μg C l^{-1} while the prey biomass necessary for maintaining the respiratory demand was 13 μg C l^{-1}.

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INTRODUCTION

The suspension feeding jellyfish, *Aurelia aurita*, has a considerable influence on many shallow water ecosystems all over the world by exerting a voracious predatory impact on especially the zooplankton, but also on fish larvae (MÖLLER 1980; STOECKER & al. 1987; GRÖNDAHL 1988; BÅMSTEDT 1990; SCHNEIDER & BEHRENDS 1994; BEHRENDS & SCHNEIDER 1995). The population dynamics and the effect of jellyfish on zooplankton communities have been investigated in several cases. Thus for example, in the Kiel Bight the zooplankton biomass was observed to decrease drastically after a peak in early spring due to predation by jellyfish (SCHNEIDER 1989), and in the shallow cove of Kertinge Nor up to 300 small jellyfish m^{-3} were found to control the zooplankton biomass (OLESEN & al. 1994; RIISGÅRD & al. 1995).

Previous attempts to assess the relationship between growth of jellyfish and zooplankton biomass have been made by SCHNEIDER (1989) who determined the food demands of *Aurelia aurita* in the Kiel Bight, and by OLESEN & al. (1994) who studied population density and growth of *A. aurita* in the Kertinge Nor. Using available energetic parameters OLESEN & al. (1994) set up an energy budget for *A. aurita* and estimated the minimum zooplankton concentration needed for maximum growth of jellyfish.

To qualify assessments concerning the energy budget of *Aurelia aurita* and its trophical role there is a need for data on energetic key parameters, especially respiration and filtration rates, but also growth rates at defined food levels. Size dependent filtration rate of *A. aurita* has recently been measured by OLESEN (1995) and supplemented by NIELSEN & al. (1997) while expressions for size dependent respiration rate have previously been given by LARSON (1987) and SCHNEIDER (1989). Furthermore, a number of respiration measurements, in poor agreement with previous data, have been published by OLESEN & al. (1994).

The present work deals with measurements of size dependent respiration rate, supplemented with laboratory growth experiments with fed and unfed *Aurelia aurita*. The goal was to obtain a credible connection between growth, food uptake and respiration of jellyfish.

MATERIAL AND METHODS

Medusae of *Aurelia aurita* were collected in the shallow cove Kertinge Nor (14-22 psu) located in the northern part of Fyn, Denmark (see OLESEN & al. 1994: fig. 1). Jellyfish were sampled using a 0.4 m diameter plankton net with a mesh size of 500 μm which was gently moved through the water. Medusae with visible damages to the umbrella or the tentacles were immediately discharged, and within two hours the remaining medusae were transported to the nearby Fjord Biology Laboratory, Kerteminde, where all experiments were conducted.

Growth experiments

Growth experiments were carried out with *Aurelia aurita* which were offered rotifers (*Brachionus* sp.) as food. The prey organisms were reared in a monoculture at the same temperature (15 °C) and salinity (15 psu) as used in the growth experiments in which the jellyfish were singly kept in plastic aquaria with 5 l of seawater. Fresh filtered (20 μm) seawater and food were supplied at regular intervals of 24 hours.

Medusae fed *Brachionus* over a period of 4 days had an initial mean diameter of 7.5 ± 0.5 mm. The food was supplied as a suspension with a known concentration of prey organisms determined by counting the individuals in subsamples of 1 ml. The initial concentration (C_0) was between 50 and 800 prey l^{-1}. The mean food concentration (C_m, prey l^{-1}) was found as:

$$C_m = \exp(\ln(C_0 C_t)/2) \quad (1)$$

where C_t is the final concentration after 24 h when the old water was filtered through a 20 μm plankton gauze to retain the remaining prey organisms which were preserved in Lugol solution to be counted later under a microscope. At the end of the growth period the umbrella interradial diameter was measured to the nearest 0.5 mm by placing the jellyfish under a dissecting microscope with the dorsal side down. The umbrella diameter (D, mm) was converted to body dry weight (W, mg) using the equation (OLESEN & al. 1994):

$$W = 0.0017D^{2.8} \quad (2)$$

The daily specific growth rate, (μ, d^{-1}) was found using the equation:

$$\mu = [\ln(W_t/W_0)](t_t - t_0)^{-1} \quad (3)$$

where W_0 and W_t are the body dry weight at time t_0 and t_t, respectively. The net growth efficiency (NGE), defined as the growth (G = μ × W) divided by the assimilated food ration (A = G + R), was calculated according to:

$$NGE = G/A = G/(G + R) = \mu W/(\mu + R) = \mu/(\mu + R_s) \quad (4)$$

where R_s is the specific respiration rate = R/W.

Degrowth experiment

Reduction in umbrella diameter of *Aurelia aurita* due to starvation (i.e. degrowth) was recorded during a period of 25 days by keeping medusae in an aquarium with filtered seawater (25 l). On the first day the mean diameter of 25 medusae was measured, and during the following degrowth period the mean umbrella diameter was determined for subsamples of 5 medusae at different time intervals. The water was changed daily with fresh filtered (20 μm) seawater. Assuming that degrowth follows the same allometrics as growth, the mean umbrella diameter was converted to dry body weight according to Eq. (2), and the daily specific degrowth rate was afterwards estimated using Eq. (3). Finally, the degrowth rate = μ × W_t was converted to energetic equivalents to obtain an independent, indirect estimation of the respiration rate (R_{est}).

Respiration rates

The respiration rate was measured as the oxygen consumption of *Aurelia aurita* on the last day of both the growth and the degrowth periods. Furthermore, to determine the respiration rate as a function of size, a larger number of unfed medusae of different size (0.6 to 1700 mg body dry weight) were used. The oxygen consumption was recorded with an oxygen electrode (Radiometer, E 5046) and a signal amplifier (Radiometer PHM71 Mk2) connected to a recorder (Servogor S). The electrode was placed in a temperature controlled (15 °C) chamber (Radiometer D616; volume = 70 μl) through which water could be pumped by means of a peristaltic pump. The medusae were placed in a closed glass vessel filled with 100 % oxygen saturated seawater. After an appropriate time (2-6 h) the lid was opened and oxygen reduced seawater (60-70 % O_2 saturation) was pumped from the bottom of the respiration vessel to the electrode chamber via a short silicon tube. All respiration measurements were followed by a control measurement on

Table 1. *Aurelia aurita*. Jellyfish fed *Brachionus* sp. during 4 days; C_m = mean prey concentration; D_0 = initial umbrella diameter; D_t = final diameter; W_0 = initial body dry weight; W_t = final weight; R_t = respiration measured on Day t; μ = daily specific growth rate; NGE = net growth efficiency. The number of jellyfish in each experiment was 10. ± SD is indicated.

C_m (ind. l^{-1})	D_0 (mm)	D_t (mm)	W_0 (mg)	W_t (mg)	R_t (μl $O_2 d^{-1}$)	μ (%d^{-1})	NGE (%)
16 ± 8	7.5 ± 0.6	9.1 ± 1.4	0.49 ± 0.11	0.88 ± 0.39	6.6	15	77
47 ± 8	7.5 ± 0.6	9.0 ± 1.6	0.49 ± 0.11	0.86 ± 0.44	10.0	14	68
92 ± 7	7.3 ± 0.5	9.5 ± 1.4	0.45 ± 0.08	0.98 ± 0.38	6.7	19	83
186 ± 5	7.3 ± 0.5	10.1 ± 1.4	0.44 ± 0.09	1.14 ± 0.45	10.6	24	82
328 ± 16	7.4 ± 0.5	9.8 ± 1.6	0.47 ± 0.09	1.08 ± 0.47	10.9	21	78

oxygen saturated water to check the calibration. Equally, the consumption of oxygen in a vessel without medusae was tested to find the background consumption of oxygen. The calibration was always cross-checked against a self-calibrating electrode (WTW Microprocessor Oximeter OXI 196). If a difference was noticed, both electrodes were recalibrated. The volume of the different respiration vessels used ranged from 30 to 500 ml, and the number of medusae used in the experiments varied from 1 to 10, dependent on size of the medusae. The temperature and salinity were kept at 15 °C and 15 psu. The respiration rate (R, μl O$_2$ d^{-1}) was calculated as:

$$R = V(S_0 - S_t)/(nt) \qquad (5)$$

where S_0 and S_t = levels of oxygen concentration at time 0 and t, respectively; V = volume of respiration vessel; n = number of medusae. About 20 % of the respiration measurements were discarded due to failure in the calibration or other errors. The swimming behaviour of the medusae in the respiration vessel was followed visually. The bell stroke frequency was corresponding to the *in situ* Kertinge Nor or slightly increased (< 20 %)

Energy budget

To assess the growth and the predation pressure of *Aurelia aurita* a number of energetic parameters need to be known. First, the amount of ingested food (I) can be determined by the filtration rate (F) times the zooplankton biomass (C): I = F × C, where F (ml h^{-1}) as a function of jellyfish size (W, mg dry wt) may be found from (NIELSEN & al. 1997):

$$F = 16.07W^{1.01} \qquad (6)$$

Next, the growth (G) of the jellyfish can be determined as the assimilated food (A) minus the respiration (R): G = A – R, where A = I × AE, and AE = the assimilation efficiency (typically about 90 %; PURCELL 1983). The growth can thus be expressed as:

$$G = F \times C \times 0.9 - R \qquad (7)$$

which may be used in different ways, for example to estimate whether C measured in a field study is in surplus or possibly controlled by the filtration impact exerted by the jellyfish.
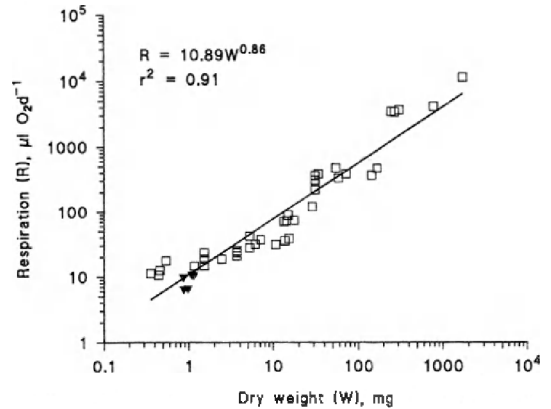

Fig. 1. *Aurelia aurita.* Respiration rate (R) as a function of body dry weight (W) in unfed (open squares) and fed (closed triangles) medusae. The regression line and its equation (R = 10.89W$^{0.86}$, r^2 = 0.91, p > 0.05) is shown for unfed jellyfish.

The following conversion factors were used: 1 mg *Aurelia aurita* body dry weight = 2.24 J (> 20 mm umbrella diameter; SCHNEIDER 1988); 1 J = 50 μl O$_2$ (ECKERT 1988); *Brachionus* = 6.7 × 10^{-3} J = 0.15 μg C.

RESULTS

The results obtained from the combined growth and respiration experiments are shown in Table 1. *Aurelia aurita* fed *Brachionus* showed daily specific growth rates of 14 to 24 % d^{-1}. The net growth efficiency (NGE) at different specific growth rates is also shown in Table 1. It is seen that NGE becomes close to 80 % at specific growth rates above 15 % d^{-1}.

The degrowth experiment (Table 2) showed that the body mass of the medusae was decreasing with a mean specific degrowth rate of –4 % d^{-1}. The indirectly estimated respiration, R$_{est}$, and the directly experimentally measured respiration (R$_t$) were fairly concordant, the mean estimated value being 73 % of the measured.

The respiration rate (R, μl O$_2$ d^{-1}) of the different sized unfed medusae (open squares in Fig. 1) was highly

Table 2. *Aurelia aurita.* Degrowth of jellyfish in a 25 d starvation experiment. D$_t$ = umbrella diameter; W$_t$ = dry body weight; μ = specific growth rate; R$_{est}$ = estimated respiration rate = –W$_t$ × μ × (2.24 × 50); R$_t$ = measured respiration rate. ± SD and the number of jellyfish (n) are indicated.

Time (d)	D$_t$ (mm)	W$_t$ (mg dry wt)	μ (d^{-1})	R$_{est}$ (μl O$_2$ d^{-1})	R$_t$ (μl O$_2$ d^{-1})	R$_{est}$/R$_t$ (%)
0	42.0 ± 1.9 (25)	62.9 ± 8.0			383	
2	40.0 ± 2.2 (5)	57.3 ± 8.6	–0.05	321	354	91
6	39.0 ± 2.8 (5)	51.5 ± 9.8	–0.03	173	323	54
9	36.6 ± 0.8 (5)	42.6 ± 2.6	–0.04	191	274	70
25	26.2 ± 3.7 (5)	17.5 ± 6.8	–0.05	98	127	77
		Mean ± SD	–0.04 ± 0.01			73 ± 15

correlated with dry body weight (W, mg). Regression analysis showed that the respiration rate increases with increasing body weight according to the equation $R = 10.89W^{0.86}$. No difference between fed (closed triangles in Fig. 1 representing respiration values in Table 1) and unfed medusae was revealed.

DISCUSSION

The maximum specific growth rate of small *Aurelia aurita* fed *Brachionus* has previously been measured by OLESEN & al. (1994) to be 21 ± 2 % for concentrations above 160 and up to 12,940 prey l⁻¹. The specific growth rates of 24 and 21 % for *A. aurita* fed a mean concentration of 186 and 328 *Brachionus* l⁻¹ in the present work (Table 1) is thus in reasonably good agreement with previous work.

However, the maximum net growth efficiency of only 35 % obtained by OLESEN & al. (1994) is low compared to the present maximum NGE ~ 80 % (Table 1). A closer inspection of the respiration values given by OLESEN & al. (1994: table 3) reveals considerable disagreement, because the values of the present work are 7 times lower. It is believed that insufficient mixing in the respiration chamber used in the previous work caused the erroneously high respiration rates (interpretation made by K.T.F. who carried out the respiration measurements in both cases). In addition, the independent estimation of the respiration rate from the degrowth experiment (Table 2) supports the corrected respiration values. The systematically lower estimated respiration rates ($R_{est}/R_t < 100$ %; Table 2) is presumably due to a somewhat inexact conversion factor (for 1 mg body dry weight to joule) which changes from 2.24 J for < 20 mm umbrella diameter to 3.5 J for > 20 mm umbrella diameter (SCHNEIDER 1988). Furthermore, the relationship between size and respiration found in the present work is in agreement with several other measurements on *Aurelia aurita* made by other workers, see Table 3.

The specific growth rate of 24 % d⁻¹ (Table 1) is presumably close to the highest possible for *Aurelia aurita*,

see Table 4 which places together a number of maximum values reported in the literature. The growth rates are high compared with other invertebrates, for instance: 9 % d⁻¹ for the blue mussel *Mytilus edulis* (RIISGÅRD & POULSEN 1981; CLAUSEN & RIISGÅRD 1996) and 7 % d⁻¹ for the polychaete *Nereis diversicolor* (NIELSEN & al. 1995). Apparently, scyphomedusae have a unique ability to grow fast. Thus, 30 % d⁻¹ has recently been found for *Chrysaora quinquecirrha* fed rotifers, and as high as 70 % d⁻¹ when ctenophore larvae were offered (OLESEN & al. 1996). Another striking phenomenon is the high degrowth rate of –4 % d⁻¹ in *A. aurita* (Table 2) which is about 10 times higher than found in similar starvation experiments with *M. edulis* (RIISGÅRD & RANDLØV 1981). This shows that the oxygen dependent metabolic expenditure in jellyfish may not be substantially reduced during starvation. This contrasts with the mussel which closes its shells during periods without phytoplankton thus efficiently reducing its oxygen uptake (RIISGÅRD & RANDLØV 1981).

The maximum NGE ~ 80 % for well fed *Aurelia aurita* (Table 1) is somewhat high compared with e.g. the above mentioned representatives for 'other invertebrates', but the level is theoretically realistic (KIØRBOE & al. 1985). However, it should be noted in this connection that the respiration of fed jellyfish did not differ from the unfed (Fig. 1). This indicates that expected higher respiration values for the fed jellyfish, due to energy cost of growth (SDA, see e.g. WIESER 1994; NIELSEN & al. 1995), failed to appear (possibly due to a relatively rapid decline of SDA during the up to 6 h measurement). A higher respiration rate in fed medusae would tend to decrease the maximum NGE. The unsolved problem illustrates the limit of the respiration vessel used in the present work and the built-in problem of obtaining both a short measuring time and ensuring suitable space for the jellyfish to swim and feed.

It is notable that the exponents for $R = aW^b$ (Fig. 1) and $F = aW^b$ (Eq. (6)) are quite alike, $b \sim 1$. This implies that the amount of water filtered as related to the oxygen consumed (i.e. the water processing capacity) must be a

Table 3. *Aurelia aurita*. Regression constants of respiration rate (R, µl O_2 d⁻¹ or ml O_2 d⁻¹) on body weight (W, mg dry wt or g wet wt): $R = aW^b$.

W (mg dry wt)	a (µl O_2 d⁻¹)	b	r^2	p <	Source
0.6-1700	10.86	0.86	0.91	0.05	This work
13-3400	9.36	0.91	0.91	0.05	LARSON (1987)

W (g wet wt)	a (ml O_2 d⁻¹)	b	r^2	p <	Source
30-150	0.103	0.94	0.72	0.001	SCHNEIDER (1989)

Table 4. *Aurelia aurita*. Maximum specific growth rates (µ) calculated from growth data obtained by different workers.

µ (% d⁻¹)	Location	Source
24	Laboratory	This work
25	Laboratory	OLESEN & al. (1994)
20	Kiel Bight, Germany	SCHNEIDER (1989)
28	Southampton, England	LUCAS & WILLIAMS (1994)
23	Gullmar Fjord, Sweden	HERNROTH & GRØNDAHL (1983)

near constant ratio for jellyfish of different size: $F/R = (16.07/10.89)24 = 35$ l of water filtered per ml of oxygen consumed. This value is within the range of high water processing capacities measured in various groups of marine invertebrate (herbivorous) suspension feeders: polychaetes, bivalves, ascidians and copepods (see e.g. RIISGÅRD & LARSEN 1995; THOMASSEN & RIISGÅRD 1995).

In the present work the lowest prey concentration resulting in maximum growth of *Aurelia aurita* was 186 *Brachionus* l^{-1} for a 10 mm (1.07 mg dry wt) medusa (Table 1). Using Eqs (6) and (7) the minimum zooplankton (*Brachionus*) biomass necessary for maximum growth ($\mu_{max} = 24$ %, cf. Table 4) may also be found as: $C_{max} = (G + R)/(F \times 0.9) = (0.24 \times 1.07 \times 3.5 + 11.54/50)/(0.41 \times 0.9) = 3.05$ J $l^{-1} = 456$ *Brachionus* $= 68$ µg C l^{-1}.

Likewise, the zooplankton biomass necessary for just maintaining the respiratory demand may be found as: $C_{main} = R/F = 0.23/0.41 = 0.56$ J $l^{-1} = 84$ *Brachionus* $l^{-1} = 13$ µg C l^{-1}. If the small difference in b-values for the size dependent F and R equations ($1.01 - 0.86 = 0.15$) is real this would of course imply that the above estimated C_{max} and C_{main} biomasses will tend to decrease with increasing jellyfish size. Therefore, the values should only be regarded as guiding and not as definitive constants to be used uncritically. The same remark applies to the above-mentioned figure for water processing capacity.

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