

# Feeding, bioenergetics and growth in the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina*

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**ABSTRACT:** We assessed feeding and growth of the common jellyfish *Aurelia aurita* and 2 hydro-medusae, *Sarsia tubulosa* and *Aequorea vitrina*, by examining the effect of temperature, medusa size, prey concentration and prey species on feeding and growth. In growth experiments with *A. aurita* ephyrae fed different species and concentrations of prey organisms (*Artemia* sp., *Balanus* sp., *Brachionus* sp., *Rathkea octopunctata*), the specific growth rate increased with increasing prey concentration, and a maximum specific growth rate of about 0.22 d<sup>-1</sup> was obtained. For *A. aurita* medusae fed *Acartia tonsa* and *Artemia* sp., maximum growth was about 0.08 d<sup>-1</sup>. The minimum prey concentration resulting in maximum growth rate was 80 to 100 µg C l<sup>-1</sup> for ephyrae (depending on prey type), and about 100 µg C l<sup>-1</sup> for medusae. For *S. tubulosa* fed different prey concentrations of *A. tonsa* nauplii, the maximum specific growth rates were 0.32 and 0.1 d<sup>-1</sup> for 2 and 4 mm individuals, respectively, achieved at prey concentrations between 15 and 30 µg C l<sup>-1</sup>. Maximum growth rates decreased with initial size in *A. aurita* and *A. vitrina*, to become approximately constant at 0.05 to 0.06 d<sup>-1</sup>. Clearance rates ( $F, l d^{-1}$ ) of *A. aurita* offered different prey types increased as a function of the umbrella diameter ( $D, mm$ ) squared, expressed as  $F = aD^2$ , where  $a$ -value depends on prey type. Both maximum specific growth rate and clearance rate increased exponentially with temperature between 4 and 19°C for ephyrae, and between 8 and 19°C for medusae, but at higher temperatures both growth and clearance decreased markedly. From experiments with *A. aurita* (both ephyra and medusae) in which growth, ingestion and respiration were measured simultaneously, carbon budgets were constructed for individuals growing at maximum rates when feeding on different prey types. Assimilation efficiency, net growth efficiency, and minimum concentrations of prey organisms needed for sustaining maximum growth were estimated, allowing evaluation of the degree to which jellyfish realize their growth potential in the field, or whether the jellyfish are controlling the zooplankton.

**KEY WORDS:** Clearance rate · Growth of jellyfish · Effect of temperature · Carbon budget · Bioenergetics · *Aurelia aurita* · *Sarsia tubulosa* · *Aequorea vitrina*

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## INTRODUCTION

During recent decades, there has been a growing scientific interest in the trophic role of jellyfish in the marine pelagic food web (Møller 1980, Båmstedt 1990, Purcell & Grover 1990, Olesen 1995, Hansson et al. 2005). Locally high densities of jellyfish frequently exert a severe predation impact, and thus control both the abundance of zooplankton and fish larvae (Møller 1984, Schneider & Behrends 1994, Olesen 1995, Purcell 1997).

A few studies have evaluated the role of the common jellyfish *Aurelia aurita* in the field by estimating food requirements from energy budgets (Schneider 1989, Olesen et al. 1994, Uye & Shimauchi 2005). However, complete understanding of energy flux through the food web demands detailed knowledge of the bioenergetics of the organisms. Because both ingestion and respiration may vary strongly with prey type and prey concentration (Hansson et al. 2005, Møller & Riisgård 2007a), it is important that all parameters in the energy budget are determined at the same time and under the same condi-

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tions (temperature, prey species and concentrations). This was realized by Olesen et al. (1994) who constructed an energy budget for *A. aurita* ephyrae based on simultaneous measurements of actual growth, respiration and food ingestion. But, obviously, more knowledge about the bioenergetics of jellyfish is needed.

To evaluate whether a jellyfish population is food limited, or realizing its growth potential in the field, it is important to know both the potential maximum specific growth rate and the minimum prey concentration at which the maximum growth is achieved. Further, apart from constructing actual energy budgets, it is important to gain more knowledge on how different factors, such as individual size, food availability and temperature, which are fluctuating in the field, affect the different energetic parameters of the budget.

The present study deals with bioenergetics in the scyphomedusa *Aurelia aurita* and 2 hydromedusae *Sarsia tubulosa* and *Aequorea vitrina*. Both *A. aurita* and *S. tubulosa* are neritic species (Russell 1953, Kramp 1961) and are common world-wide. In Limfjorden (Denmark), *S. tubulosa* is present in the plankton during early spring together with *A. aurita* ephyrae. During summer, medusae of *A. aurita* make up the vast majority of the plankton (Hansson et al. 2005, Møller & Riisgård 2007b, this volume). Before 2004, the hydromedusa *A. vitrina* was unknown in Limfjorden, where it later became very abundant during August and September (Møller & Riisgård 2007b).

The aim of the present study was to provide data for assessing feeding and growth of *Aurelia aurita*, *Sarsia tubulosa* and *Aequorea vitrina*. This was done by examining the effects of temperature, medusa size, prey concentration and prey species on feeding and growth, and by constructing carbon budgets with data obtained in controlled laboratory experiments where feeding, growth and respiration were measured simultaneously. Such data can be used to evaluate the degree to which the jellyfish realize their growth potential in the field, and to evaluate whether they are controlling the zooplankton. Thus, in a companion paper we use the maximum growth rates obtained in the present work to evaluate whether the jellyfish realize their growth potential in Limfjorden. Further, we use the present data on minimum concentrations of prey organisms needed for sustaining maximum growth for comparison with the actual prey concentrations in Limfjorden to evaluate jellyfish-predation impact (Møller & Riisgård 2007b).

## MATERIALS AND METHODS

**Collection and storage.** Medusae were collected in Kertinge Nor (14 to 22 psu), a shallow cove in the

northern part of Fyn, Denmark, and in Skive Fjord (25 psu), an inner branch of Limfjorden in the northern part of Jutland, Denmark. Adult *Aurelia aurita* specimens were collected in Kertinge Nor during the summer of 2004 and 2005; *Aequorea vitrina* specimens were collected in Skive Fjord in August 2004. *A. aurita* ephyrae and *Sarsia tubulosa* individuals were collected at both sites during the spring of 2004 and 2005. The medusae were brought to the laboratory and kept in aquaria (15°C, 20 psu) until experiments could be performed. When stored for more than a few days, the jellyfish were fed *Artemia* sp. nauplii.

**Feeding and growth experiments.** Experiments were done with scyphozoan *Aurelia aurita* (ephyrae and medusae) and the hydrozoans *Sarsia tubulosa* and *Aequorea vitrina*. The diameters (*A. aurita*, *A. vitrina*) or heights (*S. tubulosa*) of the medusae were measured before the jellyfish were transferred to aquaria with a known volume of filtered seawater. The jellyfish were offered different types of prey organisms in different concentrations (Table 1). The prey organisms (except *Rathkea octopunctata*) were raised in monospecific culture. Prey organisms were counted in sub-samples, and aquaria with suspensions of known prey concentrations were prepared for feeding experiments. Once a day, the medusae were transferred to an aquarium with fresh seawater containing an initial prey concentration equal to that used on the previous day. The remaining prey organisms in the old water were retained on a 80 µm filter and counted to estimate the total number of prey organisms ingested by the jellyfish during the feeding period. At the end of the experimental period, the sizes of the jellyfish were measured again so that the diameter/height of the experimental animals could be converted to body dry weight. For *A. aurita* medusae and *A. vitrina* individuals, the correlation between medusa diameter ( $D$ , mm) and dry weight ( $W$ , mg) was made by calculating the regression equation using pre-measured medusae dried at 60°C for 24 h. For ephyrae and *S. tubulosa* specimens, correlations were obtained from the literature.

The specific growth rate ( $\mu$ , d<sup>-1</sup>) was determined as:  $\mu = \ln(W_t/W_0)/t$ , where  $W_0$  and  $W_t$  are the body dry weights on Day 0 and Day  $t$ , respectively. The mean prey concentration ( $C_m$ ), ingestion rate ( $I$ ) and clearance rate ( $F$ ) were calculated by the following equations (Olesen et al. 1994):  $C_m = \exp[\ln(C_0 \times C_t)/2]$ ;  $F = V/(t \times n) \times \ln(C_0/C_t)$ ;  $I = (C_t - C_0)/(n \times t)$ , or  $I = F \times C_m$ , where  $C_0$  and  $C_t$  = prey concentration on Day 0 and Day  $t$ , respectively,  $n$  = number of animals, and  $V$  = volume of water in the aquarium. Control experiments were made with aquaria containing prey organisms, but no jellyfish. Unless otherwise indicated, the temperature in all experiments was 15°C. The experimental conditions are outlined in Table 1.

Table 1. *Aurelia aurita*, *Sarsia tubulosa*, and *Aequorea vitrina*. Experimental conditions for growth and feeding experiments. Prey type: B: *Brachionus* sp., Ar: *Artemia* sp. (1 or 3 d old), Ci: cirriped larvae (*Balanus* sp., nauplii/cypris), Co: copepods (*Acartia tonsa*), N: nauplii (*Acartia tonsa*); R: *Rathkea octopunctata*. C: approximate concentration. Experiment—GF: growth and feeding; TE: temperature effect; F: feeding. V: incubation volume; t: incubation time; n: number of medusae

Species	Prey	C (ind. l <sup>-1</sup> )	Experiment	V (l)	t (d)	n
<i>A. aurita</i> (ephyrae)	Ar (1d)	30–100	GF	4	4	6
	B	40–600	GF	4	4	8
	B	~800	TE	1–5	3	5
	Co	25–200	GF	4	4	8
	Ci	10–50	GF	4	4	8
	R	2–5	GF	3	3	5
<i>A. aurita</i> (medusae)	Ar (1 d)	30–100	GF	30–60	4	5
	Ar (1 d)	~90	TE	30–60	3	5
	Ar (3 d)	~50	F	30–60	1	4
	Co	5–110	GF	70–85	3	5
<i>S. tubulosa</i>	N	30–500	GF	2–4	4	7
<i>A. vitrina</i>	Ar (1d)	≥90	GF	15–30	4	5
	Co	~50	F	5	1	5

***Aurelia aurita*:** Feeding experiments with ephyra ( $D = 3.5$  to  $7$  mm) were carried out using *Artemia* sp. (1 d old), adult *Acartia tonsa*, *Brachionus* sp., *Balanus* sp. nauplii/cypris, and *Rathkea octopunctata* as prey organisms offered at different concentrations. Feeding experiments with medusae were carried out with individuals of known umbrella diameter ( $D = 45$  mm) offered *Artemia* sp. (1 d old), or *Acartia tonsa* (copepodites/adults) as prey in different concentrations. To estimate the maximum specific growth rate as a function of initial body size, experiments were carried out with medusae of different initial umbrella diameter ( $D_0 = 5$  to  $650$  mm) fed *Artemia* sp. (1 d old) or *A. tonsa* in surplus. In addition, clearance experiments were performed with different sizes of medusae offered *Artemia* sp. (3 d old).

***Sarsia tubulosa*:** Experiments were performed on 2 sizes of medusae ( $D = 2.3 \pm 0.04$ , and  $4.2 \pm 0.1$  mm) offered newly hatched *Acartia tonsa* nauplii in different concentrations.

***Aequorea vitrina*:** Maximum specific growth rate as a function of umbrella diameter was measured using medusae with different initial bell diameters ( $D = 6$  to  $50$  mm) fed *Artemia* sp. (1 d old) in surplus. In addition, 3 clearance experiments were done with medusae of known body dry weights ( $W = 3.3 \pm 0.2$  mg) offered adult *Acartia tonsa* as prey.

**Temperature effect.** Effects of temperature on clearance rate and maximum specific growth rate were measured for *Aurelia aurita* ephyrae and medusae (Table 1). The temperature was controlled by means of a thermostatic water bath. Ephyrae ( $D \approx$

$5$  mm) were fed *Brachionus* sp., and temperature effect was measured between  $4$  and  $26^\circ\text{C}$  and between  $4$  and  $23^\circ\text{C}$  in clearance and growth experiments, respectively. For medusae ( $D = 39.9 \pm 0.9$  mm) fed *Artemia* sp., the acute temperature effect was measured between  $8$  and  $23^\circ\text{C}$ .

**Respiration (R).** Respiration rate was measured at the end of the growth experiments when the medusae were growing at maximum specific growth rates. Respiration, measured as oxygen consumption, was recorded by means of an oxygen electrode (CellOx 325 [WTW]) connected to an oxygen measuring instrument (Oxi 197i [WTW]). The electrode was placed in a flow-through chamber connected by tubes to a respiration chamber holding the animals. Aerated filtered seawater was pumped through the chambers with a peristaltic pump. Measurements were started by closing the system so that the water was recirculated through the respiration chamber past the electrode and back

again. Each measurement was followed by a control measurement without jellyfish. The experiments were run for no longer than  $45$  min, and the oxygen saturation of the water never fell below  $80\%$ . All measurements were made at  $15^\circ\text{C}$ , unless otherwise noted. The volumes of respiration chambers used varied from  $25$  to  $400$  ml, and the number of individuals varied between  $5$  and  $15$ . The flow rate in the system was  $5$  ml  $\text{min}^{-1}$ . The electrode was calibrated in an OxiCal-SL air calibration vessel.

The oxygen concentration was plotted as a function of time, and expressed by a linear regression line. The respiration rate was calculated as  $R = b \times V/n$ , where  $b$  is the slope of the regression line,  $V$  = volume of water in the respiration vessel and tubes (l), and  $n$  = number of animals. The oxygen consumption in the control was subtracted from  $R$  to obtain the respiration rate of the jellyfish.

**Bioenergetics.** The energy (or carbon) budget of a jellyfish can be expressed as  $P = I - R - E = A - R$ , where  $P$  = production,  $I$  = ingestion,  $R$  = respiration,  $E$  = excretion (faeces and urine), and  $A$  = assimilated food. The budget can also be written as  $P = (F \times C \times AE) - R$ , where  $F$  = clearance rate,  $C$  = prey concentration, and  $AE$  = assimilation efficiency. The following definitions are used in the present study: minimum prey concentration resulting in maximum jellyfish growth,  $C_{\min} = (G_{\max} + R)/(F \times AE)$ , where  $G_{\max}$  = maximum growth rate =  $\mu_{\max} \times W$ ,  $\mu_{\max}$  = maximum specific growth rate, and  $W$  = medusa body mass; assimilation efficiency,  $AE = (G + R)/I$ ; and net growth efficiency,  $NGE = G/A = G/(G + R)$ .

**Conversion factors.** The following equations were used to estimate dry weight ( $W$ , mg) from umbrella diameter ( $D$ , mm) in *Aurelia aurita*: ephyrae:  $W = 1.913 \times 10^{-3} D^{2.998}$  (Båmstedt et al. 1999); medusae ( $\geq 20$  mm):  $W = 0.004 D^{2.7}$  (present study); and in *Aequorea vitrina*:  $W = 0.03 D^{2.3}$  (present study). For *Sarsia tubulosa* the bell height ( $H$ , mm) was converted to carbon content ( $W_C$ ,  $\mu\text{g C}$ ):  $W_C = 0.443 H^{3.10}$  (Daan 1986); 1 mg dry weight (*Sarsia* sp.) = 3.5 J = 67  $\mu\text{g C}$  (Schneider 1988, Matsakis & Conover 1991); 1 mg dry weight (ephyra) = 3.66 J = 70  $\mu\text{g C}$ ; 1 mg dry weight (medusae) = 2.24 J = 50  $\mu\text{g C}$  (Schneider 1988); 1  $\mu\text{l O}_2$  = 0.46  $\mu\text{g C}$  (Uye & Shimauchi 2005), 1 *Brachionus plicatilis* = 0.15  $\mu\text{g C}$  (Szyper 1989), 1 *Artemia* sp. = 1.16  $\mu\text{g C}$  (Szyper 1989); 1 *Acartia tonsa* (copepodite/adult, 680  $\mu\text{m}$ ) = 2.1  $\mu\text{g C}$  (Berggreen et al. 1988), 1 *A. tonsa* nauplius (280  $\mu\text{m}$ ) = 0.15  $\mu\text{g C}$  (Berggreen et al. 1988); 1 *Balanus* sp. (nauplius/cypris) = 2.46  $\mu\text{g C}$  (Möller 1979, Muxagata et al. 2004), 1 *Rathkea octopunctata* = 5  $\mu\text{g C}$  (Matsakis & Conover 1991).

## RESULTS

Fig. 1 shows the relationship between initial medusa sizes and maximum specific growth rates of *Aurelia aurita* and *Aequorea vitrina* fed *Artemia* and/or *Acartia tonsa* in surplus. The maximum specific growth rate declined with increasing initial medusa size to become approximately constant at 6 and 5%  $\text{d}^{-1}$  for *A. aurita* and *A. vitrina*, respectively.

Results from experiments carried out on 2 size groups of *Sarsia tubulosa* fed different prey concentrations of *Acartia tonsa* nauplii are depicted in Fig. 2. The maximum specific growth rates were 32 and 10%  $\text{d}^{-1}$  for  $2.3 \pm 0.04$  and  $4.2 \pm 0.1$  mm individuals, respectively. The maximum specific growth rate was achieved at a prey concentration between 15 and 30  $\mu\text{g C l}^{-1}$ , corresponding to 80 and 150 nauplii  $\text{l}^{-1}$  (Fig. 2A). In the above growth experiments, clearance rate and ingestion rate were also measured (Fig. 2B,C). The clearance rates were approximately constant at all prey concentrations, and consequently, the ingestion rate increased linearly with prey concentration in the observed interval.

Results from growth experiments with *Aurelia aurita* ephyrae fed different prey concentrations and prey species are shown in Fig. 3. The specific growth rate increased with increasing prey concentration, and a maximum specific growth rate of about 22%  $\text{d}^{-1}$  was obtained between 80 and 100  $\mu\text{g C l}^{-1}$ , corresponding to 55, 40 and 500 prey  $\text{l}^{-1}$  of *Artemia* sp., *Balanus* sp. and *Brachionus* sp., respectively. With *Rathkea octopunctata* as prey, maximum growth rate was not obtained, due to insufficient prey availability. When

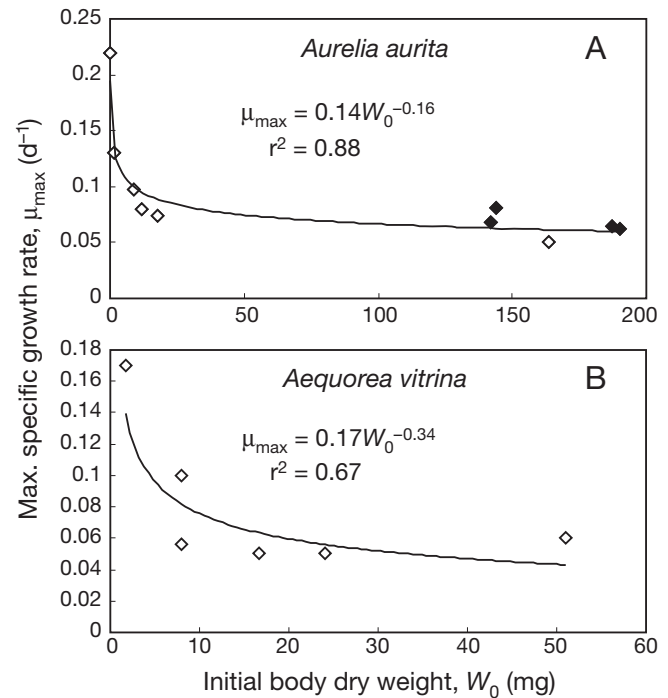


Fig. 1. Maximum specific growth rate as a function of initial dry weight for (A) *Aurelia aurita* and (B) *Aequorea vitrina* fed *Artemia* sp. ( $\diamond$ ) and *Acartia tonsa* ( $\blacklozenge$ ) in surplus. Regression lines and their equations are shown

adult *Acartia tonsa* was used as prey, the specific growth rates remained relatively low (–2, 13 and 6%  $\text{d}^{-1}$ ), although the concentrations of prey offered were high (25, 100 and 190 copepods  $\text{l}^{-1}$ ). The clearance rate was approximately constant at all prey concentrations used, and consequently the ingestion rate increased linearly with prey concentration in the observed interval for all prey species (not shown). The average clearance rates for the different prey types are given in Table 2.

Fig. 4 shows specific growth rates as a function of prey concentration for *Aurelia aurita* medusae when preying on *Acartia tonsa* (copepodites/adults) and *Artemia* sp.  $\mu_{\text{max}}$  was about 8%  $\text{d}^{-1}$ , obtained at a prey concentration of about 100  $\mu\text{g C l}^{-1}$ . For both prey species, the clearance rate was nearly identical at all prey concentrations (not shown), thus indicating that the ingestion rate must have increased linearly with prey concentration.

Fig. 5 shows the clearance rate as a function of umbrella diameter of *Aurelia aurita* offered *Acartia tonsa* and *Artemia* sp. as prey. Clearance increased as a function of the diameter squared ( $F = aD^2$ ), but the  $a$ -values varied, indicating that clearance rate depended on prey type. Clearance rates ( $F$ ,  $\text{l d}^{-1}$ ) of the different prey can also be expressed as a function of medusa dry weight ( $W$ , mg), resulting in linear

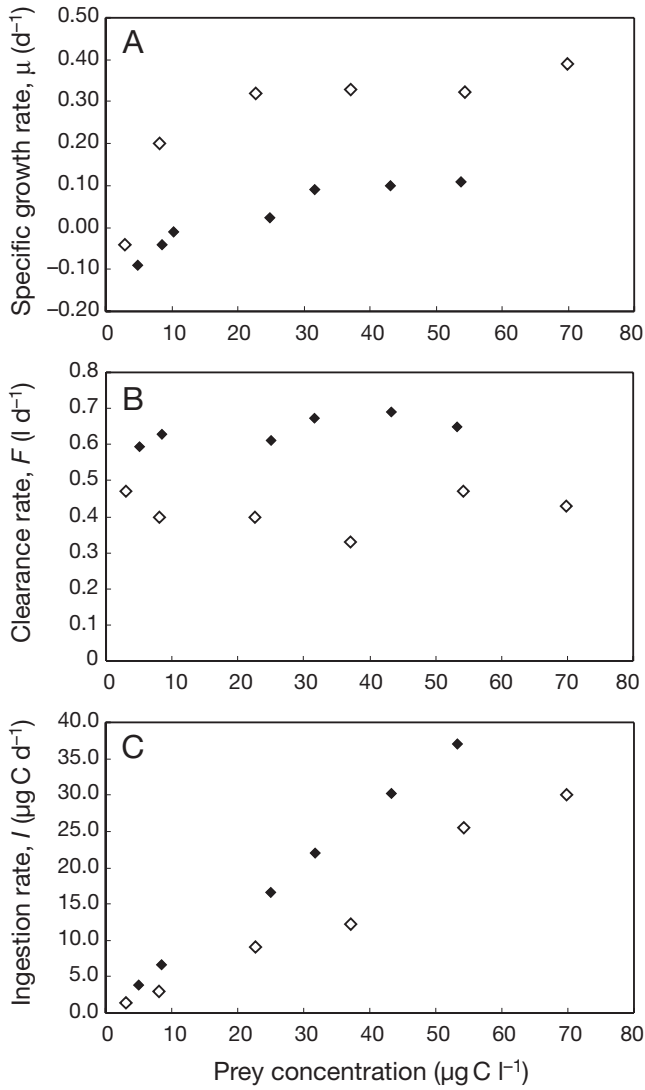


Fig. 2. *Sarsia tubulosa*. (A) Specific growth rate, (B) clearance rate, and (C) ingestion rate as a function of prey concentration for 2 size groups of medusae preying on *Acartia tonsa* nauplii. Umbrella height:  $\diamond$ :  $2.3 \pm 0.04$  mm;  $\blacklozenge$ :  $4.2 \pm 0.1$  mm

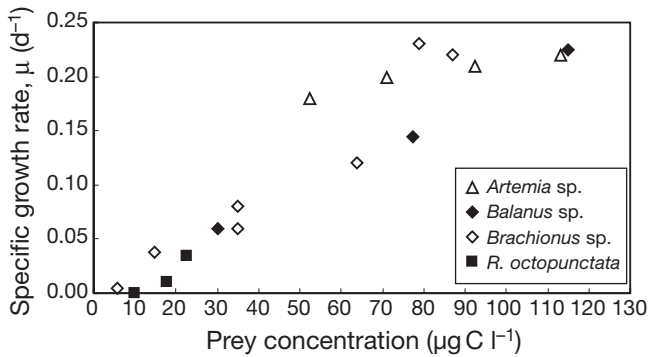


Fig. 3. *Aurelia aurita*. Specific growth rate of ephyrae as a function of concentration of different prey types (*Artemia* sp. cirripeds, rotifers, *Rathkea octopunctata*)

Table 2. *Aurelia aurita*. Clearance rate ( $F$ ) of ephyrae for different size groups ( $W$ ) during growth experiments with different prey types. B: *Brachionus* sp., Ar: *Artemia* sp., Ci: cirriped larvae (*Balanus* sp., nauplii/cypris), Co: copepods (*Acartia tonsa*); R: *Rathkea octopunctata*. Values are mean  $\pm$  SD

Prey	$W$ (mg dry wt)	$F$ (l d <sup>-1</sup> )
Ar	$0.27 \pm 0.06$	$0.26 \pm 0.03$
Ci	$0.50 \pm 0.08$	$0.45 \pm 0.05$
B	$0.25 \pm 0.03$	$0.54 \pm 0.08$
R	$0.17 \pm 0.02$	$0.21 \pm 0.05$
Co	$0.10 \pm 0.02$	$0.15 \pm 0.11$

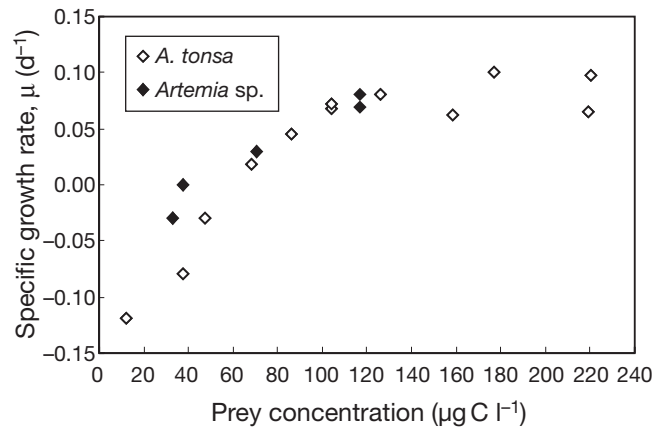


Fig. 4. *Aurelia aurita*. Specific growth rate of medusae as a function of prey concentration (*Acartia tonsa*, *Artemia* sp.)

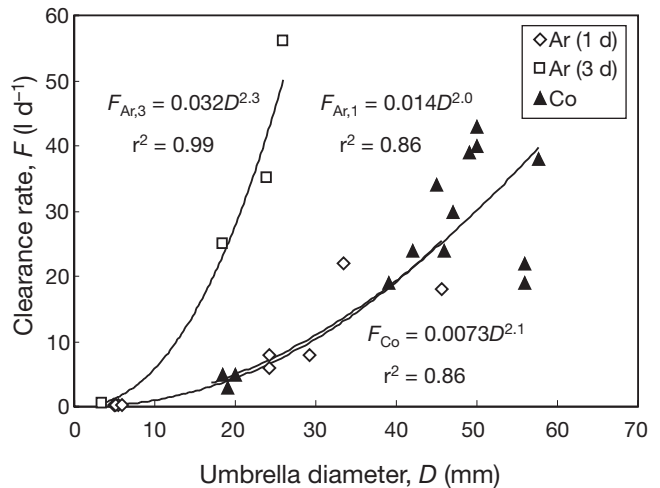


Fig. 5. *Aurelia aurita*. Clearance rate ( $F$ ) as a function of umbrella diameter when preying on *Acartia tonsa* (Co), and on 1 d (Ar,1) and 3 d (Ar,3) old *Artemia* sp. Regression lines and their equations are shown

relationships in a log–log plot, and subsequently expressed as:  $F_{Ar,1} = 0.70W^{0.74}$ ,  $F_{Ar,3} = 3.9W^{0.78}$ , and  $F_{Co} = 0.76W^{0.73}$ .

Clearance ( $F$ ,  $l\ d^{-1}$ ) as a function of dry weight ( $W$ , mg) of *Aequorea vitrina* preying on *Artemia* sp. could be expressed as a linear relationship in a log–log plot with the equation:  $F = 0.45W^{0.91}$ ,  $r^2 = 0.93$  ( $n = 4$ ). The clearance rate of *A. vitrina* preying on copepods was  $0.3\ l\ d^{-1}$  for a  $3.3 \pm 0.2$  mg dry wt individual.

The effect of temperature on maximum specific growth rates and clearance rates of *Aurelia aurita* ephyrae and medusae is shown in Fig. 6. Both maximum specific growth rate and clearance rate increased exponentially with temperature between 4 and 19°C for ephyrae, and between 8 and 19°C for medusae, but at higher temperatures both growth and clearance rates decreased markedly.

From experiments performed with *Aurelia aurita* (both ephyrae and medusae) in which growth ( $G$ ), ingestion ( $I$ ) and respiration ( $R$ ) were measured simultaneously, carbon budgets were constructed for individuals growing at maximum rates when consuming different prey types (Table 3). The values shown for  $I$ ,  $R$  and  $G_{max}$  are measured values, whereas  $AE$ ,  $NGE$  and  $C_{min}$  were estimated on basis of these values. For *A. aurita* ephyrae, the values from experiments with different prey types were similar. In general,  $AE$  was 64 to 74%, and  $NGE$  was 20 to 28%. However, in experiments where copepods were offered as prey organisms, the values were considerably lower,  $AE$  and  $NGE$  being 13 and 16%, respectively. For adult *A. aurita*, the values differed little between experiments with different prey types, and  $AE$  and  $NGE$  were 33 to 37 and 25 to 33%, respectively.  $AE$  tended to increase at lower prey concentrations (not shown). The minimum prey concentration resulting in maximum specific growth rate of medusae ( $C_{min}$ ) was calculated to be 79.1 to 114.5  $\mu\text{g C l}^{-1}$  for ephyrae (depending on prey type) and 111.2 to 118.3  $\mu\text{g C l}^{-1}$  for medusae (Table 3).

Table 3. *Aurelia aurita*. Bioenergetic parameters for medusae fed with different prey types and growing at maximum specific growth rate. B: *Brachionus* sp., Ar: *Artemia* sp., Ci: cirriped larvae, Co: copepods (*Acartia tonsa*).  $W_C$ : medusa carbon content;  $\mu_{max}$ : maximum specific growth rate;  $C$ : prey concentration;  $I$ : ingestion rate;  $R$ : respiration;  $G_{max}$ : growth rate =  $\mu_{max} W_C$ ;  $AE$ : assimilation efficiency =  $(G + R)/I$ ;  $NGE$ : net growth efficiency =  $G/(G + R)$ ;  $C_{min}$ : minimum prey concentration resulting in maximum

Stage	Prey	$W_C$ ( $\mu\text{g C}$ )	$\mu_{max}$ ( $\text{d}^{-1}$ )	$C$ ( $\mu\text{g C l}^{-1}$ )	$I$ ( $\mu\text{g C d}^{-1}$ )	$R$ ( $\mu\text{g C d}^{-1}$ )	$G_{max}$ ( $\mu\text{g C d}^{-1}$ )	$AE$ (%)	$NGE$ (%)	$C_{min}$ ( $\mu\text{g C l}^{-1}$ )
Ephyra	B	17.5	0.23	78.8	31.5	16.2	4.0	64.3	19.9	79.1
Ephyra	Ar	16.8	0.22	92.8	20.2	9.6	3.7	66.5	27.8	80.6
Ephyra	Ci	38.5	0.23	115.0	44.5	24.4	8.7	74.3	26.2	114.5
Ephyra	Co	6.3	0.13	98.0	40.6	4.5	0.8	13.0	15.5	–
Medusa	Co	8150.0	0.08	107.6	3370.4	607.3	652.0	37.4	33.1	118.3
Medusa	Ar	4800.0	0.08	116.0	2378.0	523.7	384.0	32.6	25.2	111.2

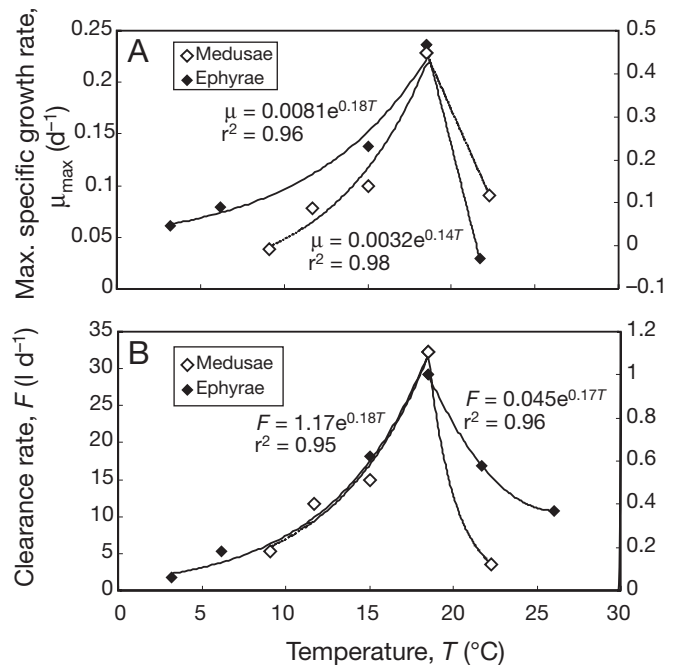


Fig. 6. *Aurelia aurita*. Effect of temperature on (A) maximum specific growth rate, and (B) clearance rate, of ephyrae (right y-axis) and medusae (left y-axis). Regression lines and their equations are shown

The net growth efficiency was found to increase with specific growth rate, becoming constant when maximum growth rate was achieved; cf. Fig. 7, which shows an example with ephyrae preying on *Brachionus* sp.

## DISCUSSION

### Growth

There have been several studies on growth rates in *Aurelia aurita* ephyrae. Generally, the maximum specific growth rate is about 24%  $\text{d}^{-1}$  at 15°C, obtained

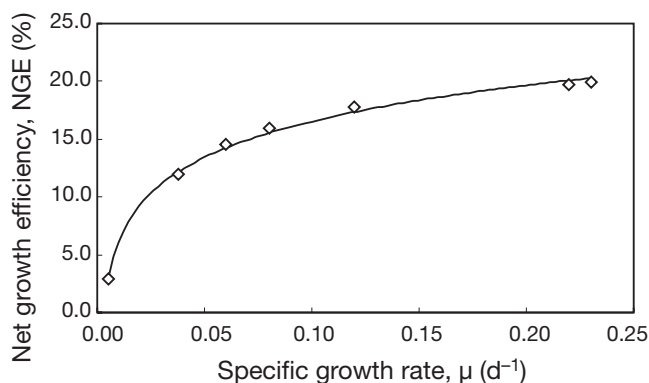


Fig. 7. *Aurelia aurita*. Net growth efficiency as a function of specific growth rate of ephyrae preying on *Brachionus* sp.

with different prey species, e.g. *Artemia* sp. (Båmstedt et al. 1999, 2001) and *Brachionus* sp. (Olesen et al. 1994, Frandsen & Riisgård 1997). In the present study, maximum specific growth rates of 22 to 24 %  $d^{-1}$  were obtained with *Brachionus* sp., *Artemia* sp. and *Balanus* sp. as prey at minimum concentrations ( $C_{min}$ ) of 80 to 100  $\mu g C l^{-1}$ , depending on prey type (Fig. 3). Olesen et al. (1994) found  $C_{min}$  to be about 60  $\mu g C l^{-1}$  when preying on *Brachionus* sp. Båmstedt et al. (2001) studied the effect of several diets on the growth of newly released *A. aurita* ephyrae and found that they did not grow well (4 to 9 %  $d^{-1}$ ) when offered adult copepods (*Calanus finmarchicus*). Båmstedt et al. (op. cit.) argued that this might be due to the nutritional quality of the copepods. This suggestion is supported by the present study, where ephyrae offered copepods (*Acartia tonsa*) also grew much less than might be expected from the number of prey ingested. With the hydromedusa *Rathkea octopunctata* as prey, maximum growth rates were not obtained, since not enough prey organisms were available, but the actual growth rates were comparable to those found for other prey species offered at similar carbon concentrations. This is the first study that reports on growth in *A. aurita* preying on hydromedusae, although several authors have suggested that hydromedusae might be an important food source for ephyrae (Matsakis & Conover 1991, Sullivan et al. 1994, 1997).

So far, little attention has been given to maximum specific growth rates in larger individuals, and in some studies it has been assumed to be constant with size (Olesen et al. 1994). In the present study, the maximum specific growth rate of *Aurelia aurita* medusae was about 8 %  $d^{-1}$ , obtained at a prey concentration of about 100  $\mu g C l^{-1}$  with adult *Acartia tonsa* and *Artemia* sp. as prey (Fig. 4). Results obtained for *Sarsia tubulosa* showed that 2 and 4 mm individuals had maximum specific growth rates of 32 and 10 %  $d^{-1}$ ,

obtained at prey concentrations of 15 and 30  $\mu g C l^{-1}$ , respectively (Fig. 2). No previous data exist on  $C_{min}$  for *A. aurita* medusae and *S. tubulosa*. The present data indicate that maximum specific growth rates in larger medusae may be lower than in smaller stages. A similar indication has been found for *S. tubulosa* offered copepods in surplus (Daan 1986).

Hansson (1997) summarized existing data on specific growth rates in *Aurelia aurita* obtained in both laboratory and field work. A plot of specific growth rate as a function of medusa size indicated a decreasing tendency, although not all growth rates were maximum values, and they were obtained under different conditions. In the present study, the medusae (*A. aurita* and *A. vitrina*) were not food limited to ensure maximum specific growth rates, which were found to decrease from initial values of about 17 to 22 %  $d^{-1}$ , stabilizing at about 5 to 6 %  $d^{-1}$  (Fig. 1). One of the explanations for this phenomenon may be, for example, the shunting of energy into gametes instead of somatic growth (Hansson 1997). To our knowledge, the only other study reporting maximum specific growth rates in adult *A. aurita* was that of Ishii & Båmstedt (1998). Individuals of 4 to 12 cm were offered prey in surplus. When plotting their (op. cit.) growth data as a function of initial medusa dry weight ( $W_0$ , mg), the trend also indicated a decreasing tendency ( $\mu_{max} = 0.34 W_0^{-0.28}$ ), and the maximum specific growth rate decreased to stabilize at about 5 %  $d^{-1}$ .

Ishii & Båmstedt (1998) summarized existing data on the relation between size and reproductive maturity in jellyfish, and it appeared that when *Aurelia aurita* is food limited, it shunts energy into gamete production at an earlier stage. In Horsea Lake, England, *A. aurita* never gets larger than about 10 cm in diameter, and it matures at about 2 cm umbrella diameter. This is also the case in Kertinge Nor, Denmark, where we collected individuals for the present study. In marine areas where the medusae are not food limited, they attain larger maximum bell diameters (up to 30 to 40 cm), and they mature at a larger size. This may explain why the maximum specific growth rate declined earlier in individuals from Kertinge Nor (used in the experiments shown in Fig. 1) than in medusae from Horsea Lake (Ishii & Båmstedt 1998).

The only available data on growth in *Aequorea* sp. were reported by Arai (1980) who offered *A. victoria* *Artemia* nauplii as prey until the hydromedusa was large enough to feed on a mixed diet of the ctenophore *Pleurobrachia pileus*, *Artemia* sp. and *Phialidium* sp. Unfortunately, the concentrations were not reported, but food was always available. Specific growth rates estimated from Arai's (1980) data show a decrease with size (14 to 2 %  $d^{-1}$ ) within the same size range as that of the present study.

## Feeding

In the present study, clearance rates were obtained for *Aurelia aurita* ephyrae feeding on *Brachionus* sp., *Artemia* sp., adult *Acartia tonsa*, *Balanus* sp. larvae and the hydromedusa *Rathkea octopunctata* (Table 1). Clearance rate depended on prey type, but all rates were in the range of 150 to 540 ml d<sup>-1</sup>, which is in agreement with Båmstedt et al. (1994) who found the clearance rate for ephyrae to be in the range of 100 to 800 ml d<sup>-1</sup>, depending on prey type. Apart from these data, there have been no previous quantitative measurements on ephyrae preying on *A. tonsa* and *R. octopunctata*.

Size-dependent clearance rate ( $F$ ) in *Aurelia aurita* was described by the expression  $F = aD^b$ , with  $b$ -exponents close to 2 when related to umbrella diameter ( $D$ ). Clearance related to medusa dry weight ( $W$ ) was described by the expression  $F = aW^b$ , with  $b$ -exponents of 0.7 to 0.8. The  $b$ -exponents were quite similar in both expressions, but the  $a$ -values differed depending on prey type. Clearance rates of 1 d old *Artemia* sp. and *Acartia tonsa* were quite similar, whereas the clearance rate of 3 d old *Artemia* sp. was about 3 times higher (Fig. 5). The clearance rates obtained with *Acartia tonsa* as prey are close to those obtained by Olesen (1995) with the same prey type. He found that a 22 mm individual cleared 6.4 l d<sup>-1</sup>, which may be compared to 6.0 l d<sup>-1</sup> for an individual of the same size in the present study. That clearance rates depend on prey type was also noticed by Hansson et al. (2005), who quantified the clearance rate of *A. aurita* based both on laboratory clearance experiments using different prey organisms and on analysis of gut contents of medusae collected in the field. In general, clearance was approximately scaled to bell diameter squared, but  $a$ -values were different between prey groups. Clearance decreased in the following order: cladocerans, copepods, copepod nauplii, mussel larvae. Similar results were obtained by Hansson (2006), who estimated clearance of copepods to be about 3 times lower and 5 to 6 times higher than clearance of cladocerans and copepod nauplii, respectively. The present study shows that the clearance rate depends not only on prey type, but also on the stage/age of the prey. Thus, the clearance rate of *A. aurita* obtained with 3 d old *Artemia* sp. as prey was 3 times higher than clearance of 1 d old *Artemia* (Fig. 5).

Adult copepods and cirriped nauplii are considered to be the primary food source for *Sarsia* sp., while copepod nauplii seem to be of less importance (Purcell 1989, Costello & Colin 2002). The present study presents clearance rates of *S. tubulosa* offered copepod nauplii (Fig. 2B), but otherwise only few quantitative measurements exist. Hansson et al. (2005) reported

that the clearance rates of a 5.1 mm *S. tubulosa* offered adult *Acartia tonsa* as prey was 0.3 l d<sup>-1</sup> (11°C), which may be compared to the present study in which 2 and 4 mm individuals cleared about 0.4 and 0.5 l d<sup>-1</sup>, respectively when offered nauplii as prey (15°C). Recently, Hansson & Kiørboe (2006) measured clearance in *S. tubulosa* offered adult copepods, cirriped nauplii and larvae as prey, and they found that the clearance rate decreased in this order.

Diet and prey selection of *Aequorea victoria* and *A. aequorea* have been reported by several authors (Purcell 1989, 1991, Costello & Colin 2002). The main diet seems to comprise gelatinous zooplankton, ichthyoplankton, and to a lesser extent, crustacean prey. Purcell (2003) estimated weight-specific clearance rates from gut contents in *A. aequorea*. The clearance rates have been recalculated for a 3.3 mg dry wt individual for comparison with rates found in this study (Table 4). The present results for copepods/*Artemia* sp. are in the same range as those for copepods and cladocerans reported by Purcell (2003), but the clearance rate for larvaceans is much higher (up to 30 times higher than for copepods). As suggested by Purcell (2003), *Aequorea* sp. is presumably specialized for feeding on larger soft-bodied prey, e.g. ctenophores, which are vulnerable to predation by *Aequorea* sp. (Arai 1986).

*Aequorea victoria* has been described as a cruising-predatory medusa (Costello & Colin 2002, Colin et al. 2003). However, a recent study by Riisgård (2007) revealed that *A. vitrina* is an ambush feeder, usually remaining stationary in the water column with its very long marginal tentacles hanging down motionless, ready for ambush capture of prey organisms. Videomicroscope observations made by Riisgård (2007) revealed that *A. vitrina* is efficient in capturing brine shrimps (*Artemia salina*), less efficient in capturing rotifers (*Brachionus plicatilis*), and very inefficient at copepod (*Acartia tonsa*) capture. This is in agreement with the observations and quantitative measurements in the present study. However, it should be noted that the present clearance rates may be biased because an important prerequisite for using the clearance formula, i.e. efficient mixing of the water in the experimental aquaria, was not fulfilled (because the water was

Table 4. *Aequorea* sp. Clearance rate ( $F$ ) measured for a 3.3 mg dry wt individual offered different prey types

Predator	Prey	$F$ (l d <sup>-1</sup> )	Source
<i>A. vitrina</i>	Copepods	0.3	This study
	<i>Artemia</i> sp.	1.3	
<i>A. aequorea</i>	Copepods	2.1	Purcell (2003)
	Cladocerans	0.7	
	Larvaceans	64.5	



rather stagnant due to the usually motionless medusae). The same reservation may apply to clearance rates reported for *Sarsia tubulosa*, which is also an ambush feeder (Hansson & Kiørboe 2006).

In all feeding experiments in the present study, the ingestion rate increased linearly with prey concentration, and consequently, the clearance rate must have been constant, in agreement with a number of previous studies on *A. aurita* (Båmstedt et al. 1994, 2001, Olesen et al. 1994, Olesen 1995) and on *S. tubulosa* (Daan 1986). Hansson et al. (2005) found that the clearance rate of *S. tubulosa* was constant up to ca. 130 copepods l<sup>-1</sup>, above which it decreased. This indicates that jellyfish may be well adapted to feed in patches of food, always being able to exploit their clearance capacity. However, Hansson & Kiørboe (2006) recently observed that *S. tubulosa* may apparently be food-saturated at considerably lower copepod concentrations.

### Temperature effect

Little is known about the effect of temperature on feeding and growth of jellyfish. We found that an exponential increase in both clearance and maximum specific growth rates with temperature apply to both *Aurelia aurita* ephyrae and medusae (Fig. 6A,B). Olesen (1995) studied the effect of temperature on the clearance rates of *Aurelia aurita* between 5 and 20°C and found that clearance increased from 200 ml h<sup>-1</sup> at 5°C to 400 ml h<sup>-1</sup> at 10°C, above which it apparently became constant. Unfortunately, this experiment was made with only one medusa. Temperature effects (between 5 and 19°C) on specific growth rates in *A. aurita* medusae were studied by Hansson (1997), who found that specific growth rates increase up to about 17°C, above which rates became constant. The results showed considerable variation at a given temperature, probably because not all individuals were growing at the maximum rate. Furthermore, the initial sizes of the medusae varied, and since specific growth rates decline with size (Fig. 1), this also affected the result. In the present study the effect of temperature was isolated by using the same initial sizes and by feeding the individuals in surplus to ensure maximum growth.

Recently, Widmer (2005) studied the relation between maximum specific growth rate and temperature in *Aurelia labiata* ephyrae (Fig. 8). The pattern was similar to that found in the present work, although the maximum specific growth rate (40% d<sup>-1</sup>) was obtained at a higher temperature (21°C) which is probably due to higher temperatures in California (15 to 22°C) where *A. labiata* was studied. Båmstedt et al. (2001) mea-

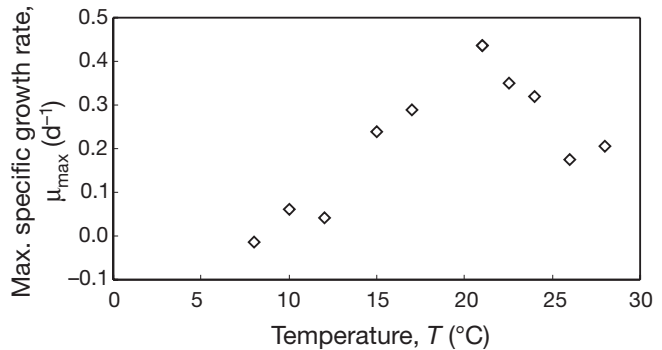


Fig. 8. *Aurelia labiata*. Maximum specific growth rate of ephyrae as a function of temperature (data from Widmer 2005)

sured growth in *A. aurita* ephyrae fed in surplus at both 15 and 18°C, and the rates measured (20 and 40% d<sup>-1</sup>, respectively) are in agreement with the present growth rates measured at the same temperatures.

### Budgets

In the present study, NGE for *Aurelia aurita* was about 20 to 30% (Fig. 7, Table 3), indicating that 70 to 80% of the assimilated energy may have been used for respiration. This is in fairly good agreement with Olesen et al. (1994) who made an energy budget for *A. aurita* ephyrae ( $D = 9$  mm) and found that respiration constituted 66% of assimilated energy. Uye & Shimauchi (2005) constructed a budget for *A. aurita* medusae and found that respiration constituted 61% of the assimilated energy. However, respiration was probably underestimated in the laboratory feeding studies made by Olesen et al. (1994) and Uye & Shimauchi (2005). Thus, Møller & Riisgård (2007a) showed that the weight-specific respiration is up to 4 times higher in well fed and fast growing individuals compared to starving individuals. Hence, the respiration rate rapidly decreases to the starvation level within a few hours without food. In the present study, respiration was measured quickly after the last feeding period.

The present budgets were constructed by estimating the lowest concentration resulting in maximum growth as:  $C_{\min} = (G_{\max} + R_t)/(F \times AE)$ , which should fit the actual data of maximum specific growth (Figs. 3 & 4). The unknown factor is the assimilation efficiency,  $AE$ , which has so far been assumed to be 85 to 90% (e.g. Olesen et al. 1994, Uye & Shimauchi 2005). The present study shows, however, that to balance the budget,  $AE$  should be lower than 80 to 90%.  $AE$  estimated for *Aurelia aurita* ephyrae was 75 to 85%, close to the assumed values, but  $AE$  for adult *A. aurita* was low

(32 to 37 %). The low *AE* values might be due to several reasons. The actual production may be underestimated by assuming that the total production is equal to the growth measured as an increase in umbrella diameter, which does not include all production, e.g. mucus production and released larvae (reproduction). It is assumed that no dissolved organic carbon (DOC) is lost from the medusae, which is unrealistic. Hansson & Norrman (1995) estimated DOC release to account for 2.5 to 7 % of assimilated carbon in *A. aurita*. Kremer & Reeve (1989) found that DOC release accounted for 8 % of assimilated energy in the ctenophore *Mnemiopsis* sp.

Another factor that may explain a decreasing *AE* with size is that the jellyfish also keep feeding at high rates at high prey concentrations by displacing partially digested material, as found in the ctenophore *Mnemiopsis mccradyi* (Reeve et al. 1989). Reeve et al. (1978) found that *AE* in the ctenophore *Pleurobrachia* sp. decreased from 74 to 19 % when fed 10 and 100 copepods l<sup>-1</sup>, respectively. This could be true also in the present study, especially since there was a tendency for higher *AE* at lower prey concentrations.

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