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Superfluous Feeding and Growth of Jellyfish *Aurelia aurita*

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Abstract: According to a recently presented bioenergetic model for the weight-specific growth rate of jellyfish, *Aurelia aurita*, fed brine shrimp, *Artemia salina*, the specific growth will remain high and constant at prey concentrations > 6 *Artemia* l^{-1}. The aim of the present study was to verify this statement by conducting controlled feeding and growth experiments on small jellyfish in tanks. It was found that prey organisms offered in concentrations of 25, 50, and 100 *Artemia* l^{-1} resulted in specific growth rates in fair agreement with the model-predicted rates. The high prey concentrations resulted in superfluous feeding and production of pseudofeces which indicated that not all captured prey organisms were ingested but instead entangled in mucus and dropped. The high prey concentrations did not influence the filtration rate of the jellyfish.

Keywords: weight-specific growth; bioenergetic growth model; filtration rate; pseudofeces

1. Introduction

The common filter-feeding jellyfish *Aurelia aurita* occurs in many coastal ecosystems and can be very abundant and exert a considerable predatory impact on zooplankton [1–9]. *A. aurita* swims by means of umbrella pulsation and prey organisms are captured by tentacles on the bell rim during the recovery stroke [10]. *A. aurita* has a life cycle that includes a pelagic medusa and a benthic polyp stage. Medusae reproduce sexually, and females release planula larvae that settle and metamorphose into polyps that produce ephyrae that develop into medusae [11,12]. In temperate waters, an annual life cycle of *A. aurita* is typical [12,13]. Thus, in temperate Danish waters, ephyrae are released in spring resulting in a distinct cohort of medusae that reproduce sexually during summer, followed by loss of body mass ("degrowth") and disappearance of medusae in late autumn [14,15].

The population density and individual size of *Aurelia aurita* have over the years been investigated in the shallow semi-enclosed Danish cove Kertinge Nor [14–16]. In this cove, the numerous medusae are characterized by their small umbrella diameter. The population predation impact exerted by numerous small *A. aurita*, with estimated zooplankton half-lives of only about 1 to 3 d, indicates that shortage of prey controls the maximum umbrella size of typically 30 to 50 mm in Kertinge Nor [14,15], although in some years up to 60 to 70 mm [16] before subsequent degrowth.

In a recent study, [17] presented a bioenergetic model for the weight-specific growth rate of *Aurelia aurita* fed on 3-day-old brine shrimp *Artemia salina* as a reference prey organism. According to this model, the specific growth rate increases linearly with prey concentration in the range of 1 to 6 *Artemia* l^{-1} but remains high and constant at prey concentrations > 6 *Artemia* l^{-1}. The aim of the present study was to verify this last-mentioned statement by conducting controlled feeding and growth experiments in tanks with small food-limited jellyfish from Kertinge Nor exposed to various high prey concentrations resulting in superfluous feeding.

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2. Materials and Methods

2.1. Collection of Jellyfish

Small (<65 mm umbrella diameter) jellyfish, *Aurelia aurita*, were collected on 3 June 2022 in Kerting Nor, Denmark, and brought to the nearby Marine Biological Research Centre for feeding and growth experiments.

2.2. Laboratory Feeding and Growth Experiments

Jellyfish were kept in tanks and continuously fed with 3-day-old *Artemia salina* nauplii obtained from cysts. Therefore, every day a new cohort of *A. salina* was started in air-mixed 3 l flasks. *A. salina* nauplii were transferred to a magnetic stirrer mixed 10 l stock culture in glass flask. By means of a peristaltic pump, the *Artemia* prey organisms were continuously dosed from the stock flask to the jellyfish growth tank and the same water volume (6.5 ml min^{-1}) was simultaneously taken out by another channel of the dosing pump. All experiments were conducted at 13 °C in a temperature-controlled aquarium hall and 20 psu as measured at the collecting site.

The wanted steady-state prey concentrations of 25, 50, and 100 *Artemia* l^{-1} in 3 parallel growth experiments (Exp #1, #2 and #3) were ensured by adjusting the number of *Artemia* added to the 12 l jellyfish tank to match the steadily increasing clearance rate of the growing jellyfish during the experimental period. Every day all jellyfish were carefully taken out and placed with the aboral side on a millimeter paper to measure their umbrella diameter. The concentration of prey organisms in each of the jellyfish growth tanks was measured every day by taking out samples for counting under a stereo microscope to adjust the number of prey organisms that had to be added to maintain the wanted mean concentration. The experiments were started on 7 June 2022 with 6 small jellyfish in each of the 3 tanks (50 cm diameter Breeding Air Kreisel, Schuran Seawater Equipment, www.schuran.com, accessed on 18 September 2022) with slowly air-driven circulating seawater to keep the jellyfish freely and undisturbed swimming. The feeding experiments ran for 17 d.

2.3. Equations

In a recent study, Ref. [17] set up the following bioenergetic model for weight-specific growth rate of *Aurelia aurita* fed on 3-day-old *Artemia salina*: $\mu = (n \times 0.07 - 0.08)W^{-0.2}$, where W (mg) is the jellyfish dry weight and n is the number of *Artemia* l^{-1} in the range of 1 to 6 *Artemia* l^{-1}. At prey concentrations > 6 *Artemia* l^{-1} the model conforms to:

$$\mu_{model} = (6 \times 0.07 - 0.08)W^{-0.2} = 0.34W^{-0.2}. \quad (1)$$

The aim of the present study was to verify if this simple growth model applies to superfluous feeding jellyfish.

The filtration rate (=clearance rate, F_{exp}) of jellyfish in the tanks was experimentally measured by the steady-state method which is based on the principle: [prey organisms removed by jellyfish ($F_{est} \times C_c$)] = [number of prey organisms dosed from stock-culture flask ($Fl \times C_p$) − prey washed out with outflowing seawater ($Fl \times C_c$)], so that:

$$F_{exp} = (Fl \times C_p - Fl \times C_c)/C_c, \quad (2)$$

where Fl = dosing pump rate, C_p = concentration of *Artemia* in stock-culture flask, C_c = concentration of *Artemia* in jellyfish tank.

The average size of *Aurelia aurita* during the growth period was estimated as:

$$W_{avg} = (W_0 \times W_t)^{1/2}, \quad (3)$$

where W_0 and W_t express the mean individual body dry weight of jellyfish at time t_0 and time t_t, respectively.

The following allometric equation was used to estimate dry weight (W, mg) from umbrella diameter (d, mm) of *Aurelia aurita* medusae ($\geq$10 mm), [14]:

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

The following equation for filtration rate (F_{model}, l d^{-1}) of *Aurelia aurita* fed on 3-day *Artemia* as a function of dry weight W (mg) was used in the bioenergetic model [17] and adapted from [7]:

$$F_{model} = 3.9W^{0.78}. \tag{5}$$

3. Results

The increase in the size of *Aurelia aurita* fed 25, 50, and 100 *Artemia* l^{-1} are shown in Figures 1–3 along with inserted exponential regression lines and their equations. The exponents of the regression equations that express the mean weight-specific growth rates (μ_{exp}) are shown in Table 1 along with the model-predicted growth rate (μ_{model}).

Table 1. *Aurelia aurita.* Experimental data and calculated parameters for feeding and growth experiments (Exp #1, #2, #3). C_c = mean $\pm$ s.d. concentration of *Artemia* prey organisms in the tank. Umbrella diameter on Day 0 = d_0, and on Day 17 = d_{17}. Estimated dry weight on Day 0 = W_0 and on Day 17 = W_{17} using Equation (4). W_{avg} = average size during the 17-day time interval estimated as $W_{avg} = (W_0 \times W_{17})^{1/2}$, cf. Equation (3). The predicted mean weight-specific growth rate (μ_{model}) was estimated using Equation (1). The experimentally determined specific growth (μ_{exp}) was determined as the b-exponent in the exponential regression equation for lines shown in Figures 1–3. Values for μ_{exp} leaving out the first 3 days are shown in brackets. F_{exp} = experimentally measured individual filtration rate using Equation (2). F_{model} = filtration rate estimated using Equation (5).

Exp	C_c (ind. l^{-1})	d_0 (mm)	d_{17} (mm)	W_0 (mg)	W_{17} (mg)	W_{avg} (mg)	μ_{model} (% d^{-1})	μ_{exp} (% d^{-1})	F_{exp} (l d^{-1})	F_{model} (l d^{-1})
#1	25 $\pm$ 10	48 $\pm$ 4	82 $\pm$ 8	95 $\pm$ 21	444 $\pm$ 137	170	12.1	10.1 (10.3)	343 $\pm$ 130	214
#2	49 $\pm$ 11	65 $\pm$ 4	101 $\pm$ 3	226 $\pm$ 41	778 $\pm$ 68	419	10.2	8.9 (10.6)	306 $\pm$ 100	433
#3	105 $\pm$ 70	61 $\pm$ 5	86 $\pm$ 11	191 $\pm$ 39	507 $\pm$ 191	331	10.7	5.4 (5.8)	362 $\pm$ 153	360

Because relatively low specific growth rates may be expected in the beginning of the feeding period due to mobilization of digestion processes in the previously starving jellyfish, and further, because possible initial growth in body thickness may take place before subsequent increase in umbrella diameter takes place, the weight-specific growth rates (μ_{exp}) have also been calculated leaving out the first 3 days and shown in brackets in Table 1. It is seen that these values are somewhat higher and in fair agreement with the model-predicted values (μ_{model}). Thus, it may be concluded that the simple bioenergetic model Equation (1) applies for small superfluous feeding *Aurelia aurita*.

The experimentally measured average filtration rates (=clearance rate of 3-day-old *Artemia*, F_{exp}) are in fair agreement with the estimated (F_{model}) using Equation (5) although pseudofeces (mucus entangled with prey organisms) accumulated at the bottom of the tanks (Figure 4). Superfluous feeding took place in all experiments and the amount of pseudofeces accumulated increased with increasing prey concentration, most pronounced in Exp #3. Therefore, the tanks had to be cleaned every 3 to 4 days.

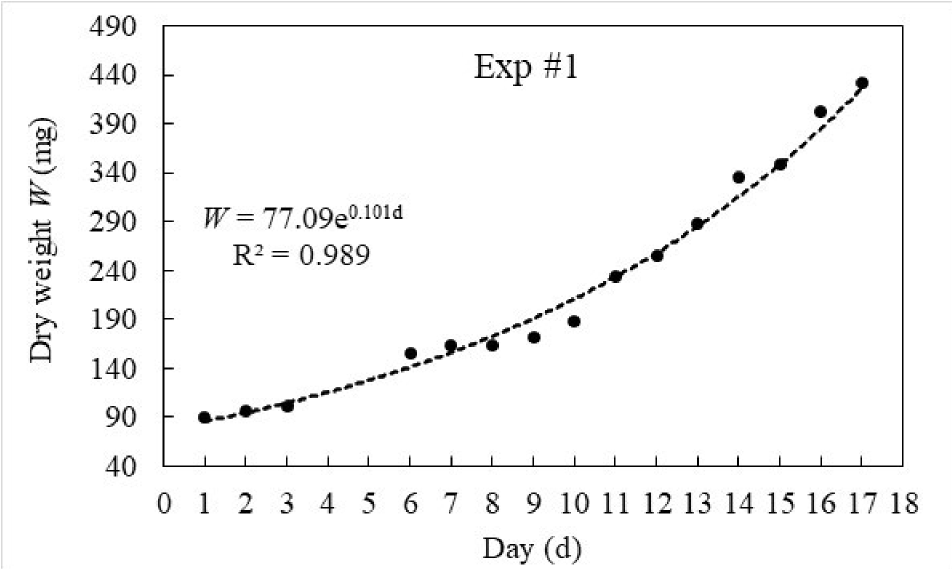

Figure 1. *Aurelia aurita*. Increase in dry weight of jellyfish fed 25 *Artemia* l^{-1}. The *b*-exponent of the exponential regression equations shows that the mean weight-specific growth rate is 10.1% d^{-1}.

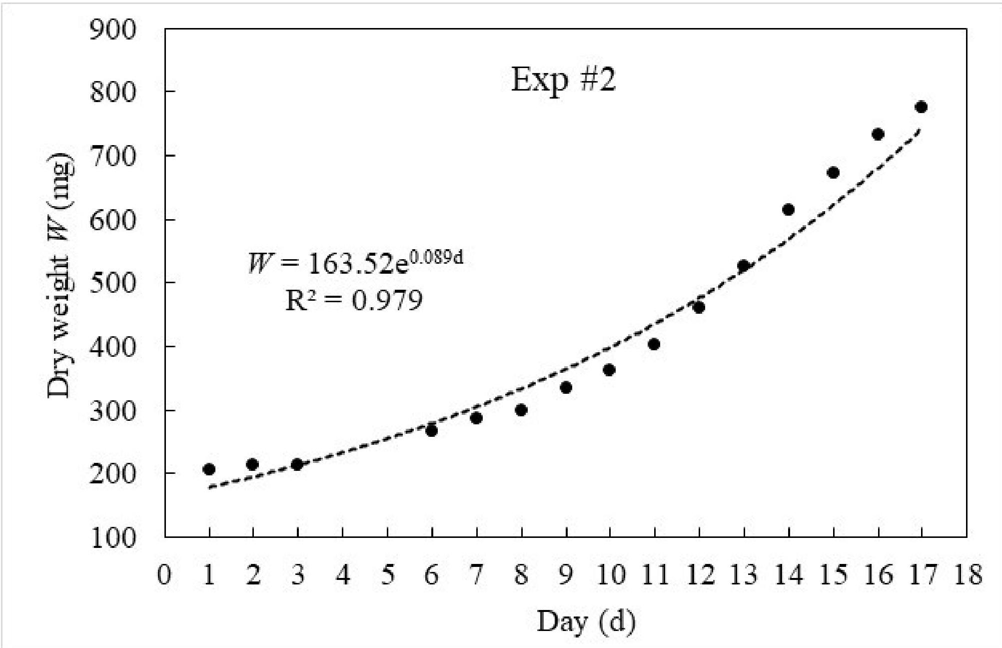

Figure 2. *Aurelia aurita*. Increase in dry weight of jellyfish fed 50 *Artemia* l^{-1}. The *b*-exponent of the exponential regression equations shows that the mean weight-specific growth rate is 8.9% d^{-1}.

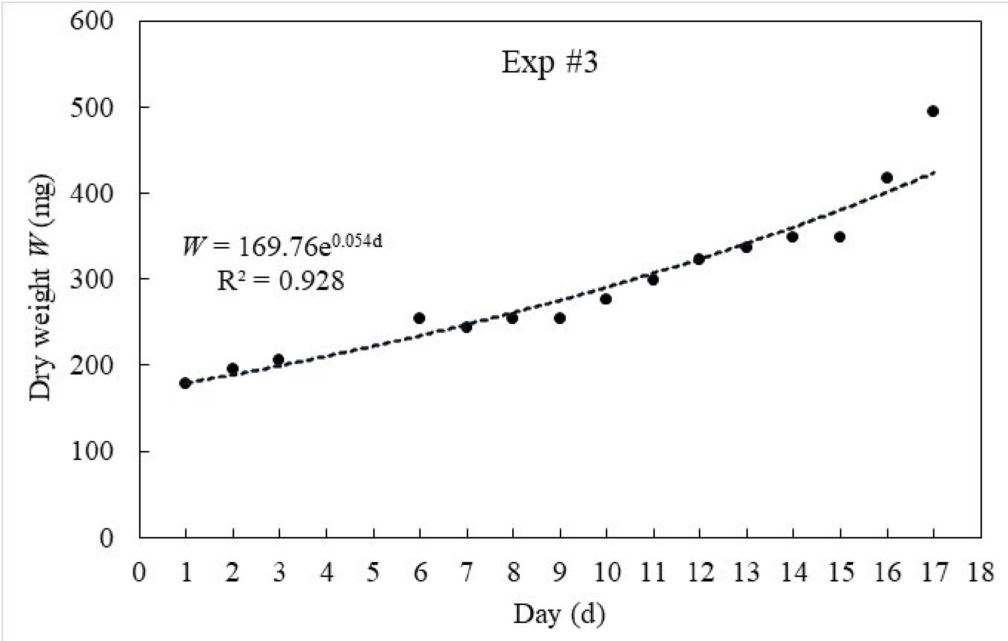

Figure 3. *Aurelia aurita*. Increase in dry weight of jellyfish fed 100 *Artemia* l^{-1}. The *b*-exponent of the exponential regression equations shows that the mean weight-specific growth rate is 5.4% d^{-1}.

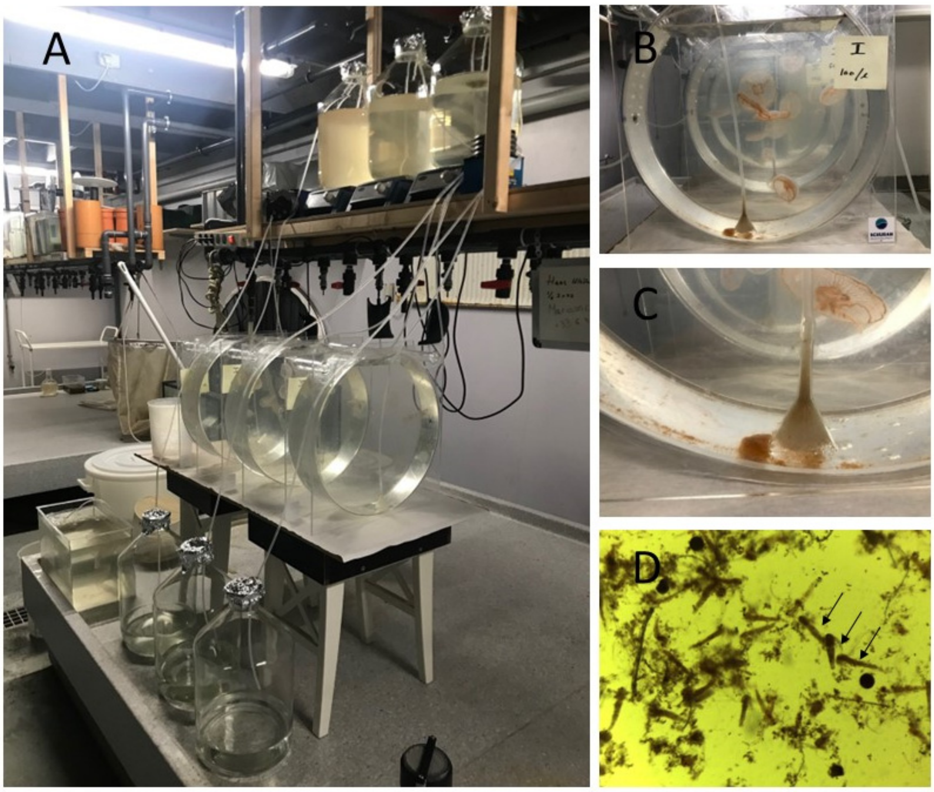

Figure 4. (**A**) Experimental set-up with 3 Kreisler tanks on a bench and above that a shelf with peristaltic pumps dosing 3-day *Artemia* from well-mixed 10 l stock glass flasks placed on magnetic stirrers. The outflow water is collected in glass flasks below the tanks. (**B**) Tank with 6 small *Aurelia aurita*. (**C**) Accumulated pseudofeces on the bottom near a small glass funnel packed with cotton and connected to the opening of the outflow tube to prevent jellyfish from being sucked up. (**D**) Jellyfish pseudofeces consists of both living and dead 3-day *Artemia* (arrows) as well as black sphere-shaped unhatched cysts entangled in mucus.

4. Discussion

The growth potential of jellyfish in nature is generally not utilized due to a shortage of food. Thus, the increase in umbrella diameter of *Aurelia aurita* in the field was compared with "well-fed" jellyfish kept in tanks by [18]. The two groups showed near identical initial values at the start of May but began to diverge in June to become about 80 mm in the field and about 130 mm in the well-fed experiment. A re-plot of the well-fed *A. aurita* based on the estimated dry weight from umbrella diameter showed a systematic deviation between the data and regression curve because the weight-specific growth rate was not constant but decreased with a size that could be described by a power-function curve with $b = -0.24$ [17], which is close to the model-predicted b-value of -0.2 in Equation (1).

The present work shows that prey organisms offered in concentrations 4, 8, and 17 times above the lowest of six *Artemia* l^{-1}, which give rise to maximum growth of *Aurelia aurita* [17], results in superfluous feeding where a substantial number of the captured prey organisms are not being ingested but become entangled in mucus and dropped as pseudofeces. When the digestive system is filled up with prey the pseudofeces production ensures that the jellyfish may still utilize its growth potential while likewise, the filtration rate remains undisturbed up to at least 100 *Artemia* l^{-1} (Table 1). However, it should be stressed that *Artemia* used here as a reference prey organism is not among the natural zooplankton in the sea, but it is easily available food for cultured predatory organisms such as jellyfish. The 3-day-old *Artemia* have no escape behavior and are captured by jellyfish with higher efficiency than other prey. Thus, 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 [19].

The present study emphasizes that jellyfish are continuously filtering the ambient water at high rates and therefore in controlled feeding and growth experiments need to be fed continuously at relatively low prey concentrations. Thus, a mean individual filtration rate of 340 l d^{-1} or 236 mL min^{-1} as measured here in a 12 L tank with six jellyfish implies that the half-life of *Artemia* is: $t_{1/2} = 12{,}000/(236 \times 6) \times \ln 2 = 5.9$ min. If all the prey organisms were offered one daily meal the prey organisms would have a mean residence time of only 5.9 min and would therefore rapidly be captured and most of them subsequently dropped to the bottom as pseudofeces resulting in suboptimal growth. As [14] noticed, when the guts of medusae were filled up with prey organisms at high prey concentrations, that part of the captured prey was killed and "apparently rejected instead of being digested". Obviously, a better understanding of the rejection and protection processes involved in superfluous feeding is needed, not least because knowledge of the actual prey ingestion rate and assimilation efficiency is important in bioenergetic studies on jellyfish.

5. Conclusions

When *Aurelia aurita* is offered prey concentrations 4, 8, and 17 times above the lowest needed for maximal growth this gives rise to superfluous feeding by which a substantial number of the captured prey organisms are not being ingested but become entangled in mucus and dropped as pseudofeces. Nevertheless, this does not influence the filtration rate of the jellyfish, which remains high and constant. Likewise, the weight-specific growth rate of *A. aurita* remains in fair agreement with the model-predicted growth. However, a better understanding of the processes involved in superfluous feeding in jellyfish is needed because knowledge of the actual prey ingestion rate is important in bioenergetic studies.

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References

1. Möller, H. Population dynamics of *Aurelia aurita* medusae in Kiel Bight, Germany (FRG). *Mar. Biol.* **1980**, *60*, 123–128. [CrossRef]
2. Båmstedt, U. Trophodynamics of scyphomedusae *Aurelia aurita*. Predation rate in relation to abundance, size and type of prey organism. *J. Plankton Res.* **1990**, *12*, 215–229. [CrossRef]
3. Behrends, G.; Schneider, G. Impact of *Aurelia aurita* medusae (Cnidaria, Scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea). *Mar. Ecol. Prog. Ser.* **1995**, *127*, 39–45. [CrossRef]
4. Lucas, C.H. Population dynamics of *Aurelia aurita* (Scyphozoa) from an isolated brackish lake, with particular reference to sexual reproduction. *J. Plankton Res.* **1996**, *18*, 987–1007. [CrossRef]
5. Uye, S.-I.; Fujii, N.; Takeoka, H. Unusual aggregations of the scyphomedusa *Aurelia aurita* in coastal waters along western Shikoku, Japan. *Plankton Biol. Ecol.* **2003**, *50*, 17–21.
6. Hansson, L.A.; Moeslund, O.; Kiørboe, T.; Riisgård, H.U. Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). *Mar. Ecol. Prog. Ser.* **2005**, *304*, 117–131. [CrossRef]
7. Møller, L.F.; Riisgård, H.U. Feeding, bioenergetics and growth in the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina*. *Mar. Ecol. Prog. Ser.* **2007**, *346*, 167–177. [CrossRef]
8. Møller, L.F.; Riisgård, H.U. Population dynamics, growth and predation impact of the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina* in Limfjorden (Denmark). *Mar. Ecol. Prog. Ser.* **2007**, *346*, 153–165. [CrossRef]
9. Matsakis, S.; Conover, R.J. Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. *Can. J. Fish. Aqua. Sci.* **2011**, *48*, 1419–1430. [CrossRef]
10. Costello, J.H.; Colin, S.P. Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. *Mar. Biol.* **1994**, *121*, 327–334. [CrossRef]
11. Hernroth, L.; Gröndahl, F. On the biology of *Aurelia aurita* (L.): 2. Major factors regulating the occurrence of ephyrae and young medusae in the Gullmar Fjord, western Sweden. *Bull. Mar. Sci.* **1985**, *37*, 567–576.
12. Lucas, C.H. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia* **2001**, *451*, 229–246. [CrossRef]
13. Hamner, W.M.; Jenssen, R.M. Growth, degrowth, and irreversible cell differentiation in *Aurelia aurita*. *Am. Zool.* **1974**, *14*, 833–849. [CrossRef]
14. Olesen, N.J.; Frandsen, K.; Riisgård, H.U. Population dynamics, growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. *Mar. Ecol. Prog. Ser.* **1994**, *105*, 9–18. [CrossRef]
15. Goldstein, J.; Riisgård, H.U. Population dynamics and factors controlling degrowth of the common jellyfish, *Aurelia aurita*, in a temperate semi-enclosed cove (Kertinge Nor, Denmark). *Mar. Biol.* **2016**, *163*, 33–44. [CrossRef]
16. Lüskow, F.; Riisgård, H.U. Population predation impact of jellyfish (*Aurelia aurita*) controls the maximum umbrella size and somatic degrowth in temperate Danish waters (Kertinge Nor and Mariager Fjord). *Vie Milieu-Life Environ.* **2016**, *66*, 233–243.
17. Riisgård, H.U.; Larsen, P.S. Bioenergetic model and specific growth rates of jellyfish *Aurelia aurita*. *Mar. Ecol. Prog. Ser.* **2022**, *688*, 49–56. [CrossRef]
18. Ishii, H.; Båmstedt, U. Food regulation of growth and maturation in a natural population of *Aurelia aurita* (L.). *J. Plankton Res.* **1998**, *20*, 805–816. [CrossRef]
19. Riisgård, H.U.; Madsen, C.V. Clearance rates of ephyrae and small medusae of the common jellyfish *Aurelia aurita* offered different types of prey. *J. Sea Res.* **2011**, *65*, 51–57. [CrossRef]