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Trophic ecology and assessment of the predatory impact of the Moon jellyfish *Aurelia aurita* (Linnaeus, 1758) on zooplankton in the Black Sea

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Abstract: Experiments on the feeding of the Moon jellyfish *Aurelia aurita* have shown that digestion time of zooplankton typically varies between 2.2 and 5.1 h depending on the body weight of the predator, diet composition, amount of food, and seawater temperature. The daily ration of a Moon jellyfish with a wet body mass of 1 g reached 0.025-2.845 mg zooplankton.ind^{-1}.day^{-1} corresponding to a carbon-specific food uptake of 0.2-9.1% C day^{-1} with a mean value around 0.5% C day^{-1}. Such mesozooplankton consumption rates are consistent with the ration values (around 0.9% C day^{-1}) calculated from the feeding rate experiments of jellyfish at natural food concentrations. However, in both cases the amount of mesozooplankton was insufficient to compensate for the minimum food requirements, calculated from oxygen consumption (6.7 ± 0.6% C day^{-1}) of the jellyfish. On average, the metabolic expenses of *A. aurita* were about one order of magnitude greater than its ration supplied by mesozooplankton, indicating the important role of visually overlooked food components in the jellyfish diet.

Résumé : *Écologie trophique et estimation de l'impact lié à la prédation par la méduse commune* Aurelia aurita *(Linnaeus, 1758) sur le zooplancton de la Mer Noire.* Des expériences de nutrition menées sur la méduse *Aurelia aurita* ont montré que la durée de digestion du zooplancton varie entre 2,2 et 5,1 h, selon la masse du prédateur, la nature et la quantité de la nourriture, et la température de l'eau de mer. La ration journalière d'une méduse de masse 1 g est de 0,025-2,845 mg zooplancton.ind^{-1}.jour^{-1}, ce qui correspond à une absorption de carbone de 0,2-9,1% C jour^{-1}, avec une valeur moyenne de 0,5% C jour^{-1}. Ces taux de consommation du mésozooplancton sont en adéquation avec ceux (environ 0,9% C jour^{-1}) calculés à partir d'expériences de nutrition de méduses menées à des concentrations naturelles de nourriture. Néanmoins, dans ces deux cas, la quantité de mésozooplancton est insuffisante pour compenser les besoins nutritionnels calculés à partir de la consommation d'oxygène (6,7 ± 0,6 % C jour^{-1}) de la méduse. En moyenne, les dépenses métaboliques d'*A. aurita* sont supérieures d'environ un ordre de grandeur à la ration fournie par le mésozooplancton, ce qui suggère que d'autres sources de nourriture, négligées car moins visibles, pourraient jouer un rôle important dans le régime alimentaire de cette méduse.

Keywords: Scyphozoa ● *Aurelia aurita* ● Digestion time ● Ration ● Food requirements ● Predation pressure

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Introduction

Recent climate change and other anthropogenic factors (intensification of commercial shipping, overfishing, eutrophication, pollution of coastal waters, aquaculture, and construction activities on the shelf) have resulted in the worldwide distribution and biomass increase of gelatinous plankton in marine pelagic ecosystems (Purcell et al., 2007; Richardson et al., 2009). In the cases of huge aggregations of gelatinous organisms, these planktonic predators may stimulate a qualitative and quantitative depletion of zooplankton (top-down effect), the growth of phytoplankton biomass (bottom-up effect), and the simplification of trophic relationships in the pelagic zone towards non-diverse «low-energy» systems (Parsons & Lalli, 2002) in which fish populations are in decline.

The scyphozoan jellyfish, *Aurelia aurita* (Linnaeus, 1758), is one such species whose mass appearance is often observed in eutrophic coastal areas of temperate zones of the world ocean. However, due to the taxonomic uncertainty of some related species, previously identified as *A. aurita*, the distribution range of this species may actually be narrower than it has been considered before (Dawson & Martin, 2001). The available data indicate that *A. aurita* mainly inhabits the North Atlantic, Baltic and Black Seas, but seems not to be found in the Mediterranean Sea (Scorrano et al., 2016). In the Black Sea, this jellyfish is usually observed at shallow optical depths (down to 100 m) with seawater temperatures of 4-23°C and salinities of 16-18 (Anninsky, 2009). The biomass of medusae varies significantly in time and across regions, although in offshore areas it seems to be more constant, with interannual fluctuations typically from 30 to 600 $g.m^{-2}$ (Kideys & Romanova, 2001). Despite the strong structural changes in zooplankton communities of the Black Sea since 1988 due to the invasion and mass distribution of the ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865, *A. aurita* has still remained one of the major gelatinous predators of the Black Sea (Anninsky et al., 2013).

The ubiquitous distribution of this jellyfish is due mainly to environmental tolerance and flexibility in diet. The food spectrum of *A. aurita* can include a large number of items, from dissolved organic compounds (Shick, 1975) to microorganisms (Stoecker et al., 1987; Olesen et al., 1994; Malej et al., 2007) and various representatives of meso-zooplankton (Barz & Hirche, 2005). Despite the existence of dietary opportunism, it is usually assumed that mesozooplankton is the main food of jellyfish while microorganisms, with rare exceptions (Olesen et al., 1994; Malej et al., 2007), are a much less important food source. The potential contribution of phyto-, bacterioplankton and dissolved organic compounds to the jellyfish diet has very rarely been evaluated *in situ* and systematically ignored in practice (Purcell et al., 2007). In this respect, identification of the absolute food spectrum and trophic relations of *A. aurita* remains a topical and challenging area regarding the trophic ecology of this opportunistic predator.

Another important question is the quantification of the daily ration of *A. aurita* that is often achieved through utilization of data on digestion time (Barz & Hirsche, 2005; Hansson et al., 2005; Lo & Chen, 2008). Such an approach to determining the value of daily rations depends much on initial assumptions and generalizations (FitzGeorge-Balfour et al., 2013). In the case of *A. aurita* feeding on crustacean zooplankton, the digestion time is usually taken as around 3 h (Sullivan et al., 1994; Barz & Hirsche, 2005; Hansson et al., 2005), whilst in fact it can vary from 0.5 to 24 h depending on the type and quantity of food, ambient temperature, body mass and physiological state of the predator (Martinussen & Båmstedt, 2001; Purcell, 2009). There is insufficient data available to substantiate the situational model allowing evaluation of the predatory impact of jellyfish in natural habitats. With respect to nutritional requirements needed for survival and ultimately wellbeing of the population, rations of the Moon jellyfish have rarely undergone analysis (Uye & Shimauchi, 2005; Ishii & Tanaka, 2006).

In this study we endeavour to establish 1) to what extent the digestion time of *A. aurita* is dependent on body mass, sea water temperature, composition and amount of captured zooplankton, and 2) to what extent the daily rations of jellyfish in the Black Sea correspond with estimates obtained using the empirical relationship between food concentration and feeding rate and/or evaluations of the minimum ration required for basal metabolism.

Material and methods

The Black Sea population of *A. aurita* was studied in the south-western shelf area of Crimea near Sevastopol Bay at monthly intervals between April 2009 and May 2010. Sampling was performed for meso- and macroplankton whilst the usual hydrological and meteorological observations were conducted at 3 stations located approximately two miles offshore at 50-60 m isobaths (Finenko et al., 2006).

Digestion time of Aurelia aurita

Digestion time of *A. aurita* feeding on copepod prey was studied experimentally from April to June 2009 and from March to June 2010, when the seawater temperature at the Black Sea surface changed between 8 and 24°C. Experimental specimens were obtained either by scooping from the near surface or by the Bogorov-Rass (BR) plankton net (mouth diameter 80 cm, mesh size 500 μm) equipped with a 1-liter collecting bucket to minimize their damage (vertical hauls from about 60 m depth). Immediately after capture, the medusae were placed into 10-liter tanks filled with freshly filtered (through 112 μm nylon mesh) seawater, at ambient temperature and starved for approximately one day. Only small-sized (umbrella diameter 3.4-52 mm, wet mass 0.002-6.948 g) and immature individuals with no morphological defects were used for digestion time estimation. Specimens were individually transferred into glass jars (150 ml) with filtered seawater at ambient temperature (or at near ambient temperature in rare cases). Live zooplankton (in general 1 individual of any species, see table 2) was simultaneously added to the jars close to the manubrium. In cases of multiple individuals, individuals consumed together at the same time were sometimes of different sex and/or developmental stage. If capture of the prey did not happen immediately, this was achieved manually with care taken to avoid disturbance of the jellyfish. In each separate case, specimens could swim and feed naturally with preferred spatial orientation and full bell pulsation. The moment of prey entry into the gastric cavity was determined with a one minute degree of accuracy and taken as the starting point of digestion. All stages of the feeding process, from capture of a prey organism by *A. aurita* to entrance into the gastric cavity and subsequent digestion, were visualized under a microscope at low magnification (16-32). Both the degree of digestion and the seawater temperature (being maintained approximately constant, ± 1°C) were monitored at intervals of 10-30 min (more frequently in the final stages of the experiment). Digestion times were assumed to be completed when the prey could no longer be visually identified as an extraneous solid substance. The presence of separate undigested particles, such as wax droplets and minute fragments of the carapace in the gastric cavities of jellyfish were disregarded.

Size and wet mass parameters of medusae were determined following each experiment. Umbrella diameters of *A. aurita* were measured to the nearest 1 mm - as the distance between statocysts during maximum muscle relaxation of the body on a graduated glass plate. The wet body mass (*WW*, g) was calculated using these data and the power equation obtained earlier (Anninsky, 2009):

$$WW = 0.053 \times 10^{-3} \times D^{2.98} \qquad (1)$$

where D = umbrella diameter (mm).

Eight taxa of mesozooplanktonic organisms (2-59 replicates for each prey type) were proposed as food items to *A. aurita* in our experiments: four species (*Acartia clausi* Giesbrecht, 1889; *Calanus euxinus* Hulsemann, 1991; *Centropages ponticus* Karavaev, 1895; *Paracalanus parvus* (Claus, 1863)) are mass representatives of mesozooplankton in the Black Sea, two taxa (*Harpacticus* sp. and Cirripedia nauplii) are predominantly coastal organisms with limited distribution, whilst the last two species (*Brachionus plicatilis* Müller, 1786, *Calanipeda aquae dulcis* Kriczagin, 1873) are cultivated specifically for the feeding of larval fish (Table 1). The taxonomic position, developmental stage and size of prey items captured by jellyfish were microscopically monitored during the passage of food through oral lobes. The initial wet body mass for the majority of these organisms was calculated according to Arashkevich et al. (2014). In the case of *C. aquae dulcis*, relevant data were provided by LS Svetlichny (pers. comm.). The wet body mass of *B. plicatilis* was estimated volumetrically as an average volume of 10 rotifers, taking their density to be equal to 1.

A one-way ANOVA was used to test whether the differences for digestion time were temperature-dependent in the experiments. Appropriate regression equations were calculated using the standard Grapher 3.00 software for Windows. Additional statistics presented in figures are the coefficients of determination (R^2) and values of significance level (p). Temperature dependences of prey digestion by jellyfish (Q_{10}) were estimated according to the Van’t Hoff equation:

$$Q_{10} = (DR_1/DR_2)^{[10/(t1-t2)]} \qquad (2)$$

where DR_1 and DR_2 are the rates at the higher (t_1) and lower (t_2) temperatures respectively.

Diet composition of A. aurita *in the Black Sea*

The availability and composition of mesozooplankton in the gastric cavity of the jellyfish was studied during a full annual cycle, running a series of observations (14) from April 2009 to May 2010. Usually medusae were caught using the plankton net, as indicated above. Immediately after capture, all individuals were measured (with an accuracy of 1 mm for diameter) and fixed separately in 4% formalin. Subsequent analysis of the jellyfish diet composition was conducted within a few hours in the laboratory: gastric

Table 1. *Aurelia aurita*. Representatives of fodder zooplankton used in experiments for determination of digestion time in the gastric cavity (*N* ind. is the number of organisms eaten by jellyfish; *n* is the number of determinations. (1): n.d. = no data. (2): According to Arashkevich et al. (2014)

Taxa (Stages: *N* ind.)	**Body length mm**	**Body mass mg WW**	**Organic carbon, % *WW* (2)**	***n***
Copepoda: Calanoida:				
Acartia clausi (♂:24, ♀: 25, Cop.V: 25)	1.0 - 1.4	(20 - 48) × 10^{-3}	8.0	59
Calanipeda aquae dulcis (♂: n.d., ♀: n.d.)(1)	1.2 - 1.3	(24 - 47) × 10^{-3}	8.0	27
Calanus euxinus (Cop.III: 1,V: 9)	1.6 - 2.8	(130 - 770) × 10^{-3}	8.0	10
Centropages ponticus (♀: 3, Cop.V: 2)	1.1 - 1.6	(33 - 50) × 10^{-3}	8.0	5
Paracalanus parvus (Cop.IV-V: 2, ♂: 9, ♀: 1)	0.5 - 0.8	(5 - 14) × 10^{-3}	8.0	12
Copepoda: Harpacticoida:				
Harpacticus sp (Cop.: 4)	0.3 - 0.6	(6 - 18) × 10^{-3}	6.6	4
Cirripedia: Sessillia: Balanidae:				
Balanidae nauplii	0.4	~6 × 10^{-3}	8.0	2
Rotifera: Ploima: Brachionidae:				
Brachionus plicatilis (♂: n.d., ♀: n.d.)	0.3 - 0.4	(3.1 ± 0.4) × 10^{-3}	6.8	32

pouches were microscopically viewed inside the body, prey items were identified as accurately as possible up to species and developmental stage. In total, about 200 jellyfish specimens with umbrella diameters of between 8 to 210 mm have been analyzed regarding diet composition and food quantity.

Sampling and biomass estimation of jellyfish and mesoplankton

The quantitative collection of macro- and mesoplankton was conducted in the first half of the day. In general, medusae were collected using the Bogorov-Rass net while mesoplankton samples were obtained with the Juday net (mouth diameter 36 cm, mesh size 112 µm). Only vertical net hauls from the bottom (depth ~60 m) to the sea surface were performed in both cases. Post collection and prior to fixation all medusae were measured to the nearest millimeter. The jellyfish biomass was calculated from appropriate wet body mass parameters with data on the number of specimens. Mesoplankton samples retrieved from the Juday net were fixed in 4% formalin

Table 2. *Aurelia aurita*. Experimental estimates of digestion time (*DT* ± SD, h) for some zooplankton species in the gastric cavity (Month/Year is the period of experimentation; SST, °C is the sea surface temperature; *WW* g is the body mass of jellyfish; *N* ind. is the number of organisms eaten by jellyfish; *t exp.*, °C is the experimental temperature; *n* is the number of determinations).

Month/Year	**SST (°C)**	***WW* (g)**	**Taxa**	***N (ind.)***	***t exp.* (°C)**	***n***	***DT* (h)**
June 2010	25.4	0.03-1.63	*Acartia clausi*	1	25.4 ± 0.5	6	2.6 ± 0.7
Apr.-May 2010	18.5	0.03-6.95	*Acartia clausi*	1-3	19.4 ± 0.9	20	2.3 ± 0.5
Apr. 2010	15.6	0.03- 6.18	*Acartia clausi*	1-3	14.4 ± 1.1	18	2.7 ± 0.5
Mar. 2010	10.4	0.03-5.82	*Acartia clausi*	1	10.5 ± 0.4	15	5.1 ± 0.8
Apr.-May 2009	17.6	0.01-6.95	*Calanipeda aquae dulcis*	1-3	20.1 ± 1.3	27	3.8 ± 0.6
June 2009	24.5	0.05-7.78	*Calanus euxinus*	1	19.7 ± 1.4	10	5.1 ± 0.4
Apr.-May 2010	18.5	0.03-1.78	*Centropages ponticus*	1	17.5 ± 3.3	5	3.5 ± 1.3
June 2009	24.5	0.01-7.78	*Paracalanus parvus*	1	21.0 ± 0.4	12	2.3 ± 0.9
May 2010	21.6	0.03-0.04	Balanidae nauplii	1	21.4	2	2.2
May 2010	21.6	0.004-0.14	*Harpacticus* sp.	1	19.3 ± 0.5	4	2.6 ± 0.9
Apr.-May 2009	17.6	0.002-0.46	*Brachionus plicatilis*	1-10	19.3 ± 0.4	32	2.9 ± 0.9

and later microscopically examined in the laboratory to estimate the composition and biomass of organisms.

Daily ration and predation of jellyfish

Three methods were employed to estimate the daily ration of *A. aurita* in the Black sea: 1) the composition and biomass of prey items and digestion times, 2) the empirical relationship between feeding rates of jellyfish and food concentration, and 3) following the assumption that food intake occurs at the level of minimal sustenance requirements of the jellyfish.

In the first method, the ration (F, mg C.day^{-1}) was calculated using the following equation:

$$F = Bp \times DT^{-1} \times 24 \qquad (3)$$

where Bp, mg C.ind^{-1}, is prey biomass in the gastric cavity of *Aurelia* and DT, h is the expected digestion time of zooplankton. In the calculations, we took into account that $Bp = f(WW)$, and $DT = f(WW, t, Bp)$, where WW is the individual body mass of jellyfish (g) and t is seawater temperature (°C). Empirical coefficients for a given functional dependency were determined on the results of these experiments (see results) and other measurements performed by taking into account the known recommendations for use of this method (Purcell et al., 2014). Digestion time was thus calculated to be about 3.4 h on average in the case of total predominance of crustacean zooplankton in the jellyfish diet. Concurrently, if veligers were observed in the jellyfish diet, their digestion time was additionally adjusted by a factor ×2.67 (Hansson, 2005).

In the second method, the daily ration of *A. aurita* (F, mg C.day^{-1}) was calculated as previously described (Anninsky, 2009), using the dependence between feeding rate and zooplankton concentration at 7.8 °C:

$$F = 0.126 \times K^{1.11} \times WW^{0.86} \times k_t \times 24 \qquad (4)$$

where K (mg C.l^{-1}) is the concentration of zooplankton in the sea, WW (g.ind^{-1}) represents jellyfish body mass and k_t is a temperature correction factor for ambient conditions.

In the third method, the daily ration of *A. aurita* (F, mg C.day^{-1}) was estimated in terms of minimal energy requirements estimated by oxygen consumption (ml O_2.h^{-1}) at 19.7°C (Anninsky, 2009):

$$F = 0.00936 \times WW^{0.84} \times 0.97 \times 12 \times 24^{-0.1} \times AE^{-1} \times k_t \times 24 \qquad (5)$$

where WW is the body mass (g), 0.97 is the respiratory quotient, $12 \times 24^{-0.1}$ is the weight of carbon in 1 mole of carbon dioxide; AE is the assimilation efficiency (assumed to be 0.8 for the typical predator).

Carbon-specific daily rations were calculated assuming that jellyfish of 1 g WW typically contains approximately 2.92 mg of organic matter (OM) where organic carbon is around 52.6% OM (Anninsky, 2009).

Results

Digestion time of A. aurita

The feeding experiments have shown that about 3-7 min is needed for each jellyfish to deliver prey items to the gastric cavity. Further digestion of the fodder organisms was accompanied by gradual body discoloration, deformation and fragmentation into smaller amorphous particles. Average digestion times for different zooplankton species ranged from 2.2 to 5.1 h (Table 2).

Among food organisms, Balanidae nauplii and the small copepods *P. parvus* and *A. clausi* at the temperature range of 19.4-21.0°C were digested more rapidly than most other prey items. The digestion times of *A. clausi* at 10.5°C and a large copepod, *C. euxinus*, at 19.7°C were the longest. Equal quantities of consumed organisms were digested at different rates mainly dependent on body mass of jellyfish and seawater temperature. A one-way ANOVA showed a strong temperature effect ($p < 0.001$), which is responsible for 77% of variance of digestion time. Larger medusae digested the same number of copepods and rotifers more rapidly and the rate of this process increased as seawater temperatures rose to around 20°C after which dependence was reversed, namely, digestion slowed down at higher ambient temperatures.

The relationship between digestion time of the copepod *A. clausi* by jellyfish and their body mass is fairly well expressed by a power equation ($R^2 = 0.60$-0.82; $P < 0.01$), where the exponent has similar values (-0.087, -0.098, -0.123) at different temperatures (Fig. 1A).

It follows that medusae of different body masses displayed no differences regarding their tolerance to ambient temperature. At the same time, along with the rise in seawater temperature, the gradual weakening of its influence on digestion time was observed. Evidence of this is the sequential decrease of the Van't Hoff (Q_{10}) coefficient when approaching the upper boundary of the temperature tolerance range for *A. aurita*. In the temperature ranges of 10.5-14.4, 14.4-19.4 and 19.4-25.4°C, the values of Q_{10} reached 4.84, 1.41 and 0.79, respectively (Fig. 1B). Similar digestion rates at 14.4-25.4°C clearly indicate a wide range of thermal tolerance of the jellyfish under these conditions.

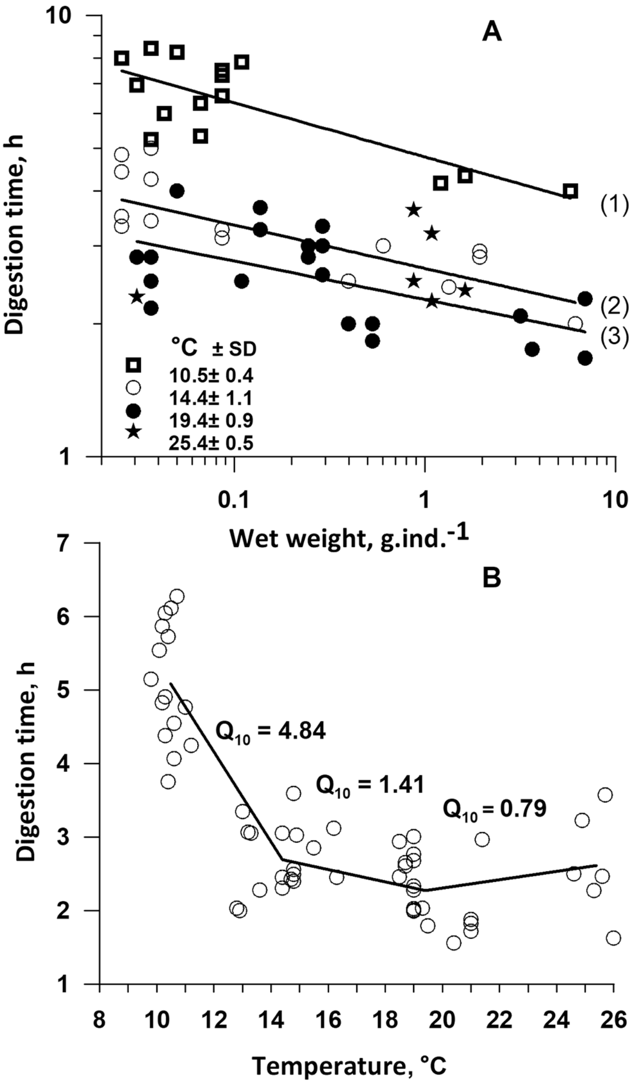

Figure 1. *Aurelia aurita.* **A.** Differences in digestion times of the copepod, *Acartia clausi*, dependent on wet body mass of jellyfish (g.ind.$^{-1}$) and seawater temperature (°C). Dependencies: (1) $Y = 4.78\ X^{-0.123}$ ($R^2 = 0.62$); (2) $Y = 2.67\ X^{-0.098}$ ($R^2 = 0.54$); (3) $Y = 2.26\ X^{-0.087}$ ($R^2 = 0.36$). **B.** Impact of seawater temperature on digestion time of the copepod, *Acartia clausi*, with the appropriate Van't-Hoff coefficients (Q_{10}) for the rate of the process at 10.5-25.4°C.

Taking into consideration such temperature influence, all estimates of digestion time for *A. aurita* consuming *A. clausi* were recalculated to one temperature, namely 19.4°C. As a result of these conversions, the dependence of digestion time (*DT*, h) on the body mass of *A. aurita* (*WW*, g) at 19.4°C can be expressed as:

$DT = 2.27 \times WW^{-0.097}$ ($R^2 = 0.46$; $n = 59$; $p < 0.001$) (6)

According to the equation above, in the case of digestion of *A. clausi* by *A. aurita,* the body mass exponent is close to -0.1. This exponent showed similar values when the jellyfish were fed on copepods *C. aquae dulcis* (-0.099) and *C. euxinus* (-0.119). At the same time, slightly different values for this constant were obtained for the digestion of copepods *P. parvus* (-0.176) and rotifers *B. plicatilis* (statistically significant level was not attained, $p > 0.05$) (Fig. 2).

If in the equation $DT = DT_1\ WW^k$ for prey items the coefficient k is insignificantly different from -0.1, then the digestion time of organisms by jellyfish of 1 gram (DT_1) can be calculated as:

$DT_1 = DT\ /\ WW^{-0.1}$ (7)

As follows from calculated DT_1 for prey items, it typically takes longer to digest larger organisms that could be a special case of a more general dependence linking the duration of this process with amount of food in the gut (Fig. 3). Such dependence was perceived as a result of the general summing of all available data, regardless of the species composition of food organisms. According to our estimates for a jellyfish of 1 g wet weight at 19.4°C, the digestion time of zooplankton doubles with every 100-fold increase in food quantity. The variability of the data may indicate that other factors (such as food quality, availability, and exoskeleton characteristics) also affect the digestion process, though such circumstances are unlikely to be taken into account in practice.

Based on above equations, the digestion time of typical (mostly crustacean) zooplankton by jellyfish at 19.4°C can be measured as:

$DT = 6.20 \times Bp_1^{0.14} \times WW^{-0.1}$ (8)

where Bp_1 is prey biomass (mg C) in gut of 1 g *WW* jellyfish.

Taking into account that the prey biomass depends allometrically on predator body mass:

$Bp_1 = Bp/WW^{0.76}$ (see below for details), the above equation can be rewritten as:

$DT = 6.20 \times (Bp/WW^{0.76})^{0.14} \times WW^{-0.1}$ (9)

Thus, after simplifying the expression the algorithm for determining digestion time of zooplankton by *A. aurita* (*DT*, h) can be formulated as follows:

$DT = 6.20 \times Bp^{0.14} \times WW^{-0.21}\ k_t\ k_{sp}$ (10)

where *Bp* is prey biomass in the gastric cavity of jellyfish (mg C); *WW* is the body mass of jellyfish (g); k_t is a temperature coefficient describing changes in digestion time with a deviation of seawater temperature from 19.4°C; k_{sp} is a correction factor to account for slower digestion of some peculiar species of zooplankton (such as veliger larvae of mollusks) relative to the majority of planktonic crustaceans, having $k_{sp} = 1$. It follows from the above equation that at a temperature of about 20°C, 10 g *WW A. aurita*

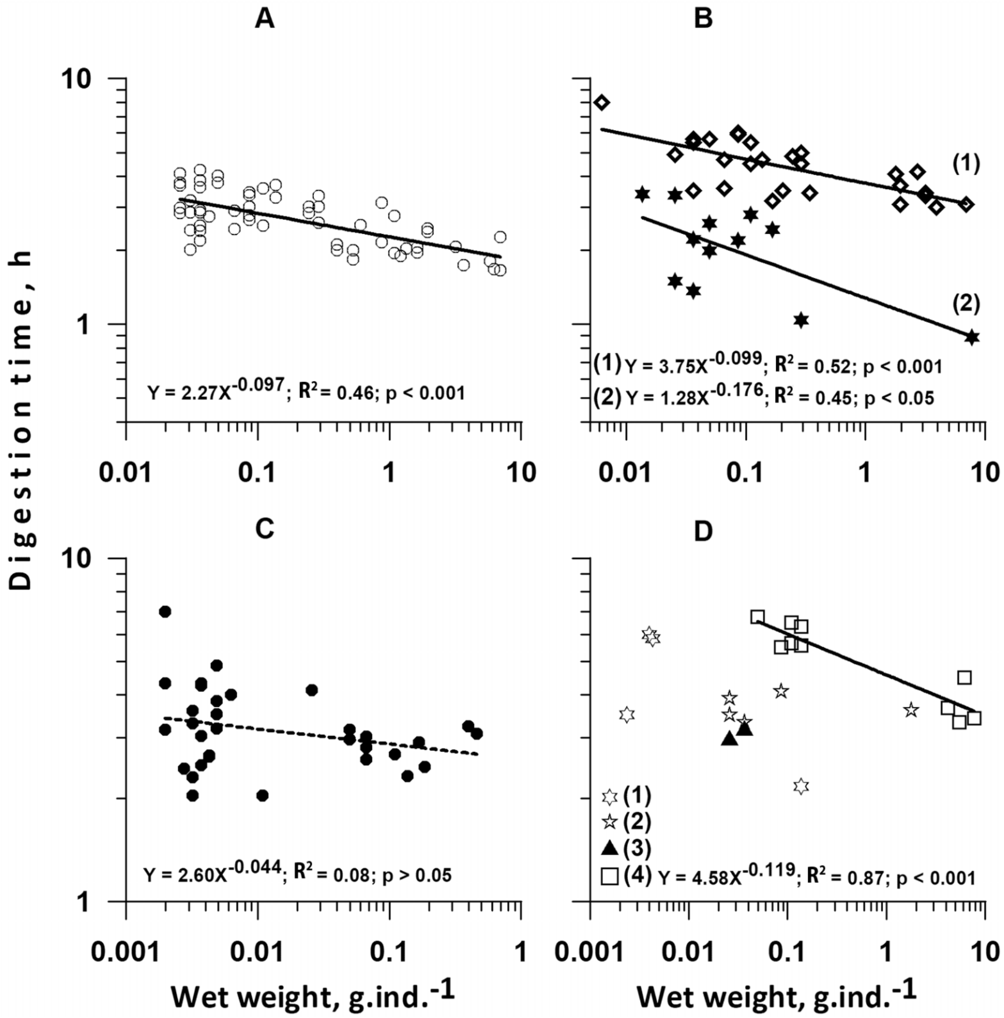

Figure 2. *Aurelia aurita*. Digestion time of various zooplankton species at the temperature ~20°C depending on wet body mass of jellyfish. Feed organisms: **A.** *Acartia clausi*. **B.** (1) *Calanipeda aquae dulcis*, and (2) *Paracalanus parvus*. **C.** *Brachionus plicatilis*. **D.** (1) *Harpacticus* sp., (2) *Centropages ponticus*, (3) Balanidae nauplii, and (4) *Calanus euxinus*.

can digest prey equivalent to *A. clausi* wet body mass (~0.0024 mg $C.ind^{-1}$) for approx. 1.7 h while digestion of the larger food amount that is comparable to *C. euxinus* wet body mass (~0.0616 mg $C.ind^{-1}$) occurs in this case during approx. 2.7 h.

Diet composition of A. aurita

Almost all the major groups and species of Black Sea mesozooplankton were detected in the diet of *A. aurita*

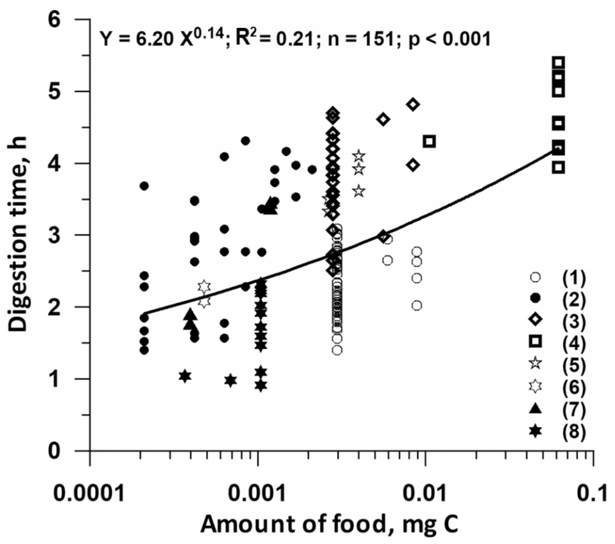

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Figure 3. *Aurelia aurita*. Variability in digestion time of prey for 1 g *WW* jellyfish dependent on amount of food in gastric cavity (mg C). Feed organisms: (1) *Acartia clausi*, (2) *Brachionus plicatilis*, (3) *Calanipeda aquae dulcis*, (4) *Calanus euxinus*, (5) *Centropages ponticus*, (6) Balanidae (nauplii), (7) *Harpacticus* sp. and (8) *Paracalanus parvus*.

during the period from April 2009 to May 2010. Overall, the dominant prey of jellyfish (in terms of biomass) consisted mostly of veliger larvae of mollusks (39.9%), copepods (21.4%), appendicularians (10.9%), cladocerans (8.8%) and chaetognaths (7.1%) (Table 3). Among the Copepoda, the dominant species were the adults and copepodites of *P. parvus* (8.6%), *C. euxinus* (4.3%), *A. clausi* and *A. tonsa* Dana, 1849 (4.1%), and *Eucalanus elongatus* (Dana, 1848) (2.2%). Despite being rather frequent, the copepodites of *Oithona similis* Claus, 1866 and *Oithona davisae* Ferrari F.D. & Orsi, 1984 (0.9%) and Copepoda nauplii (0.8%) were only secondary components in the jellyfish diet in terms of biomass. Another important food source of jellyfish were Cladocera, represented mainly by *Pleopis polyphemoides* (Leuckart, 1859) (7.7%) and *Penilia avirostris* Dana, 1849 (1.0%).

Being an opportunistic feeder, *A. aurita* can easily switch to alternative prey depending on the season. Veliger larvae, copepods and the appendicularian *Oikopleura dioica* Fol, 1872 were dominant in the jellyfish diet throughout most of the year, but during June - September, when copepods were rare in the plankton, *A. aurita* preyed mainly on cladocerans and chaetognaths. The contribution of different taxonomic zooplankton groups to the daily jellyfish ration was close to expected, provided the contacts with organisms were equiprobable. This pattern in prey selectivity ($E \approx 0.50$) was observed when feeding *A. aurita* on appendicularians, chaetognaths and most species of copepods (*P. parvus*, *C. euxinus*, *Acartia* spp., *E. elongatus*). However, some representatives of mesoplankton were found in the diet of jellyfish in clearly excessive quantities ($E > 0.50$) (decapod larvae, veliger larvae of mollusks, *P. polyphemoides*, rotifers), or conversely, in sparse quantities ($E < 0.50$) (e.g. *Noctiluca scintillans* (Macartney) Kofoid & Swezy, 1921, *Pseudevadne tergestina* (Claus, 1877), *P. avirostris*).

Food requirements and predatory impact of A. aurita *on the zooplankton community*

In the equation ($Bp = Bp_1 \, WW^b$) where the total biomass of prey in the jellyfish gut (Bp, mg C.ind^{-1}) is

Table 3. *Aurelia aurita*. Dominant zooplankton species (% biomass) in pelagial waters of the Black Sea (M_1), the prey composition of jellyfish (M_2) and estimates of selective consumption of zooplankton (E) in the region of the outer shelf off the Crimea near Sevastopol Bay (April 2009 - May 2010).

Spp.	**M_1 ± SE (%) (n = 13)**	**M_2 ± SE (%) (n = 13)**	**$E = M_2 / (M_1 + M_2)$ (n = 13)**
Copepoda	21.4 ± 4.0	21.4 ± 3.2	0.50
Acartia spp.	3.8 ± 0.7	4.1 ± 1.2	0.52
Calanus euxinus Hulsemann, 1991	4.5 ± 1.2	4.3 ± 1.8	0.49
Centropages ponticus Karavaev, 1895	0.3 ± 0.1	0.6 ± 0.3	0.68
Oithona spp.	1.8 ± 0.9	0.9 ± 0.4	0.32
Paracalanus parvus(Claus, 1863)	8.6 ± 1.9	8.6 ± 1.5	0.50
Pseudocalanus elongatus (Boeck, 1865)	1.9 ± 0.4	2.2 ± 0.4	0.54
Nauplii	0.4 ± 0.8	0.8 ± 0.2	0.64
Cladocera	3.6 ± 2.1	8.8 ± 3.8	0.71
Penilia avirostris Dana, 1849	2.7 ± 2.1	1.0 ± 3.0	0.27
Pleopis polyphemoides (Leuckart, 1859)	0.6 ± 0.3	7.7 ± 2.8	0.92
Pseudevadne tergestina (Claus, 1877)	0.3 ± 0.1	0.1 ± 0.0	0.19
Decapoda: larvae	0.1 ± 0.0	1.3 ± 0.6	0.96
Cirripedia: Balanidae nauplii	0.3 ± 0.1	0.2 ± 0.5	0.36
Appendicularia: *Oikopleura dioica* Fol, 1872	11.3 ± 2.2	10.9 ± 2.6	0.49
Mollusca: veligers	2.0 ± 0.5	39.9 ± 4.3	0.95
Chaetognatha: *Parasagitta setosa* J. Müller, 1847	7.3 ± 2.7	7.1 ± 4.4	0.49
Rotifera	0.3 ± 0.2	1.8 ± 0.6	0.85
Dinophyceae: *Noctiluca scintillans* (Macartney) Kofoid & Swezy, 1921	53.9 ± 7.7	8.7 ± 1.6	0.14

represented as a function of wet body mass (*WW*, g), the parameters Bp_1 and *b* during the annual cycle were obtained within the range of (0.4-16.6) × 10^{-3} and 0.52-1.03, respectively. With an average value of *b* (± SE) 0.76 ± 0.06, the values of the intercept (Bp_1) varied in the range between 0.4 × 10^{-3} and 22.8 × 10^{-3}. Therefore, the biomass of prey items in the gastric cavity of 1 g *A. aurita* ($Bp/WW^{0.76}$) ranged from (0.4-2.0) × 10^{-3} mg C.ind^{-1} in April-June 2009 to (22.8-22.9) × 10^{-3} mg C.ind^{-1} in September 2009, and further to (0.9-2.5) × 10^{-3} mg C.ind^{-1} in the period from October 2009 to May 2010 (Fig. 4A). The daily ration, calculated with seasonally adjusted seawater temperature and the digestion time in these conditions, was within 0.002-0.109 mg C.ind^{-1}, and displayed similar fluctuations throughout the year. Moreover, daily ration values for *A. aurita* in the sea varied in parallel with changes in zooplankton biomass (Fig. 4B).

On the whole, predation by jellyfish on mesozooplankton was unstable with low values for the daily ration during most of the year. An outburst of predatory activity by *A. aurita* in September 2009 was caused by a sharp increase in the diet of cladocerans and chaetognaths due to the seasonal decrease in seawater temperature and the penetration of jellyfish into near-surface horizons of epipelagial waters where aggregations of these organisms were observed. According to our calculations, the mean daily ration for a jellyfish of wet body mass 1 g (27 mm in umbrella diameter) was (19.1 ± 9.1) × 10^{-3} mg C.ind^{-1}, or about 7.2 × 10^{-3} mg C.ind^{-1} if calculated as a geometric mean. Thus, the most probable daily ration value was much less than the mean ration level. Such a ration is equivalent to the consumption of approximately three mean-sized specimens of Copepod stage V of species such as *A. clausi* or ten smaller Copepods stage V of *P. parvus*.

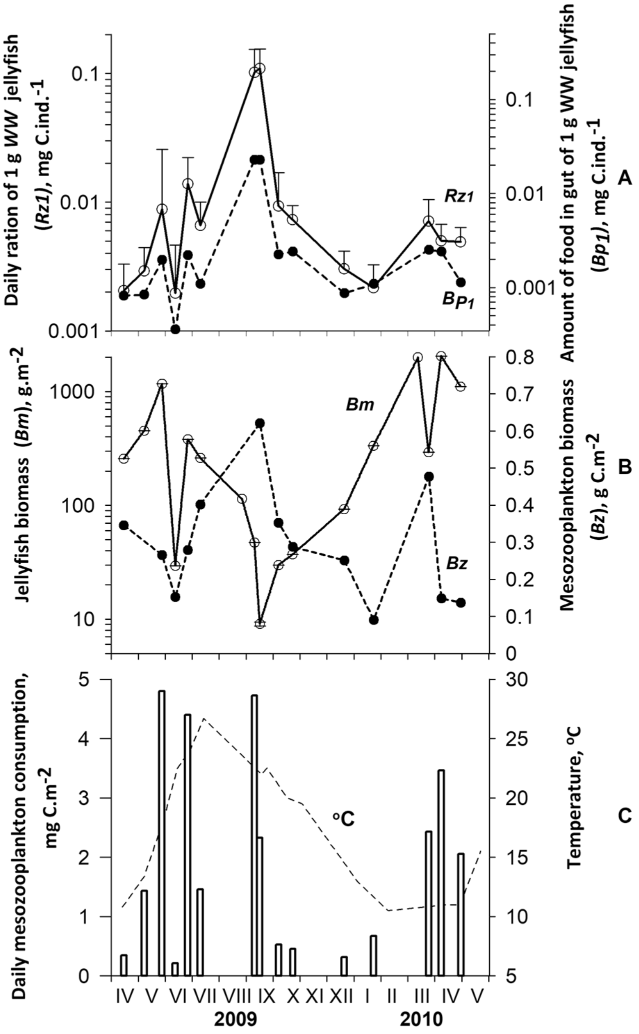

Figure 4. *Aurelia aurita*. **A.** Amount of food in gastric cavity of 1 g WW jellyfish (Bp_1, mg C.ind^{-1}), daily ration of 1 g WW jellyfish (Rz_1, mg C.ind^{-1}). **B.** Jellyfish biomass (*Bm*, g.m^{-2}), zooplankton biomass (*Bz*, g C.m^{-2}). **C.** Seawater temperature (°C) and consumption of zooplankton by jellyfish (mg C.m^{-2}.day^{-1}). Crimean shelf of the Black Sea, April 2009-May 2010.

The predatory impact of *A. aurita* on zooplankton tended to increase in the periods of population growth (usually during spring and the first half of summer) and gradually reduced with the elimination of the preceding generation (from the second half of summer until February). Data for September 2009 showing the most significant predation on zooplankton to be exerted by jellyfish with a lower biomass, apparently, should be considered an exception to the general rule. In total the daily ration of *A. aurita* for the period from April 2009 to May 2010 ranged between 0.2-4.8 mg C zoopl.m^{-2} with a mean value (± SE) of 2.0 ± 0.4 mg C zoopl.m^{-2} (Fig. 4C). Taking into account the monthly variations in mesozooplankton biomass (excluding *N. scintillans*) in the range of 90.5-621.4 mg C zoopl.m^{-2}, the average reduction in these organisms due to jellyfish predation can be estimated as (± SE) 0.76 ± 0.21 % day^{-1}. Alternatively, in relation to the daily production of mesozooplankton (~10% of total biomass), the predatory impact of jellyfish could be hypothetically evaluated as 7.6 ± 2.1%. Thus, despite the increase in biomass of *A. aurita* on the Crimean shelf of the Black Sea, the predatory impact of this jellyfish on the composition, abundance and population dynamics of mass species of mesozooplankton in 2009-2010 was extremely insignificant.

Discussion

The digestion time of *A. aurita* from the Black Sea was approximately the same as that obtained (typically between 2-4 h) for similar species of jellyfish from other regions where analogous investigations were previously conducted (Martinussen & Bamstedt, 2001; FitzGeorge-Balfour et al., 2013). The variability in data indicates that some methodological nuances such as experimental conditions, disparities in start and end point criteria and observation resolution are among the most important factors for such evaluations. Even when only one species (e.g. the copepod *Acartia tonsa*) is considered as food for *A. aurita*, variations in experimental approaches may result in differences of digestion time estimates by approximately four-fold (FitzGeorge-Balfour et al., 2013). However, if the feeding and swimming behaviour of medusae is natural with full contraction of the bell, digestion time varies insignificantly. This is confirmed by our data which are in good agreement with these estimates of digestion time for similar prey items (about two hours for *Acartia tonsa* and *A. clausi*) in natural feeding experiments.

Apart from different experimental approaches influencing digestion time, estimated values can be dependent on a number of natural factors: body mass and physiological state of the jellyfish, amount and composition of food, as well as some abiotic factors amongst which temperature conditions are especially important (Hansson et al., 2005; Purcell, 2009). In general, the less zooplankton eaten per unit of wet body mass of jellyfish under the same conditions, the faster its digestion will occur.

Contrary to some opinions (Martinussen & Bamstedt, 2001) that the effect of temperature on the digestion time in *A. aurita* is difficult to predict in each specific case due to weakness of dependency and a need for the permanent adaptation of organisms to environmental temperature, we found no evidence for this. In particular, temperature dependence of digestion of the copepod *A. clausi* by *A. aurita* showed essentially the same characteristics as for food ingestion, or respiration (Fig. 5). Although Q_{10} values were slightly higher than expected using previously obtained data on digestion of this copepod in the temperature range of 10.5-14.4°C, the maximum rate of this process (Q_{10} = 1) was also detected at ~20°C. Similar data were obtained for *A. aurita* from the North Sea (Martinussen & Bamstedt, 2001) although in this case the geometric mean digestion rate likely reached its peak already at 17-18°C. The cause of such a divergence for peak temperatures is unclear: possibly the methods used (in the latter case, ephyrae were raised in laboratory from cultivated polyps) or minor differences in heat tolerance between these populations. It is also important to recognize that being physiologically inefficient at > 20°C, both populations are practically adapted within the same temperature range. Exceeding this thermal threshold leads to a general decrease in the metabolic activity of jellyfish with a reduction in feeding and digestion rates.

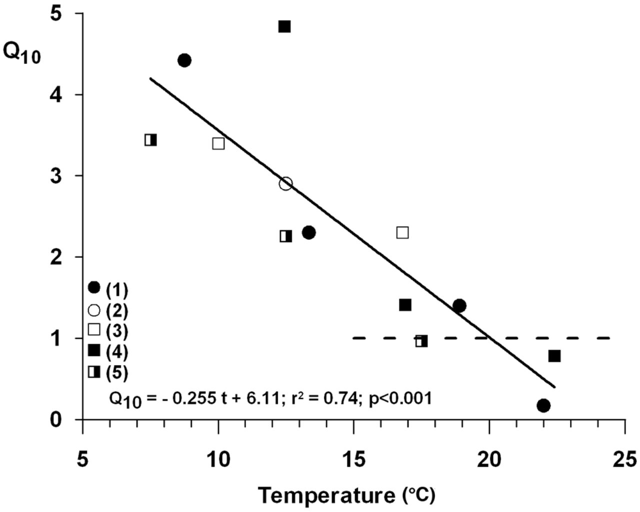

Figure 5. *Aurelia aurita*. Heat acceleration in physiological activity of jellyfish (Q_{10}) dependent on seawater temperature (°C). Q_{10} values: 1. respiration (our data); 2. respiration (Larson, 1987); 3. feeding (our data); 4. digestion (our data); 5. digestion (Martinussen & Bamstedt, 2001). Dotted line corresponds to maximum rate of metabolism (Q_{10} = 1).

This would obviously be incorrect concerning jellyfish from low latitudes (Dawson & Martin, 2001). These species of *Aurelia* are able to successfully survive and function under such temperature conditions (~30°C) which could be fatal for the jellyfish from the Black Sea. Although the Black sea jellyfish sometimes also penetrate into the upper epipelagic zone with temperatures of 22-24°C (generally weak, dying specimens), the bulk of the population is constantly within the thermocline zone or below it. Such environmental physiological features of *A. aurita* are important in reference to the common practice of summarizing all available data (in the range 0-30°) for related species (Hansson et al., 2005; Purcell, 2009) or even the entire Phylum Cnidaria (Martinussen & Bamstedt, 2001) when assessing the effects of ambient temperature on physiological activity of these animals. Within the genus *Aurelia* there may be 9-13 cryptic species with differences in tolerance to temperature (Dawson & Martin, 2001; Scorrano et al., 2016). Such dependencies characterize rather interspecific temperature effects but not the adaptations for separate populations. Hence, any temperature coefficients calculated at the highest level of generalization can hardly have a practical value, in particular for determining exact digestion time of zooplankton by jellyfish in natural conditions.

Given the body mass of jellyfish, amount of food consumed and seasonal fluctuations in ambient temperature, the mean digestion time of crustacean zooplankton by *A. aurita* in the Black Sea in 2009-2010 can be estimated as (± SE) 3.40 ± 0.94 h. However, in reality the digestion time of the natural zooplankton, most likely, was 5.30 ± 1.42 h, because of high biomass of mollusk veligers (about 33%) in the diet and their slower digestion compared with the crustaceans. Almost the same digestion time estimates (≥ 3 h) were given for *A. aurita* in most similar studies (Sullivan et al., 1994; Barz & Hirche, 2005; Hansson et al., 2005). However, some studies found shorter digestion time that can be due to measurement approaches (FitzGeorge-Balfour et al., 2013) or using dyes (provoking premature egestion) for prey items (Uye & Shimauchi, 2005).

Because of the small amount of food coupled with its slow digestion, the carbon-specific daily ration of 1 g *WW* jellyfish ranged from 0.2 to 9.1% with a geometric mean value around 0.5%. This ration was only 24% less than the calculated alternative based on the potential feeding rate of this species at a given concentration of zooplankton in the sea (Fig. 6). Since, in both cases, many variables and factors were included into the calculations, such a difference between the ration values could not be considered significant. In particular, an obvious source of possible underestimation of the ration calculated using digestion time could be the loss of prey items (from mucus traps, oral lobes or with the tentacular fragments) whilst catching jellyfish in the sea, as well as interspecies differences in digestion time of zooplankton prey (*B. plicatilis* and *C. aquae dulcis* were digested by *A aurita* more slowly than most similar prey organisms). On the other hand, the rations calculated *via* experimental feeding rates and a prey concentration in the sea might not always be achieved in reality because of uneven distribution of zooplankton. It is also unclear to what extent the trophic activity of jellyfish in the sea can be disoriented through contact with their microzooplankton prey (Malej et al., 2007). Given the above discrepancies and random factors, we should recognize that alternative evaluations of the daily ration of jellyfish on the Crimean shelf were approximately equal, i.e. in 2009-2010 *A. aurita* had consumed zooplankton as expected from the mean feeding rate (or slightly lower than the mean) food concentration in the Black Sea.

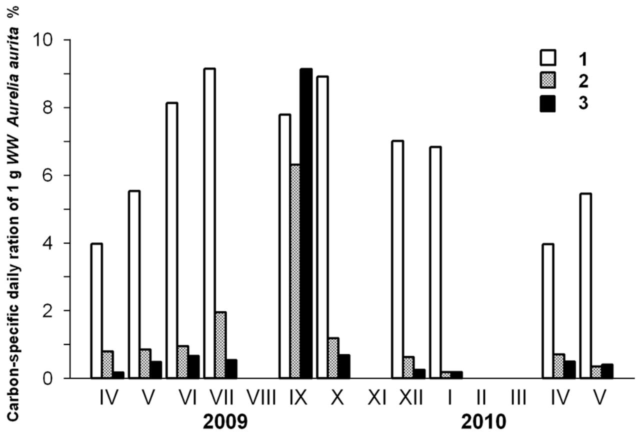

Figure 6. *Aurelia aurita*. Alternative estimates of carbon-specific daily ration (daily prey carbon vs. jellyfish carbon content, %) of 1 g *WW* (~1.54 mg C.ind.$^{-1}$) jellyfish on Crimean shelf of the Black Sea during the period April 2009-May 2010. Calculations based on 1) oxygen consumption, 2) jellyfish feeding rate at the mean natural zooplankton concentration, and 3) prey biomass and digestion time of prey in natural conditions.

Regardless of the method used for estimating the ration, the amount of mesozooplankton consumed by jellyfish was much less than minimum (sustenance) food requirements which were calculated for this species by the oxygen consumption rate adjusted for the assimilation efficiency of food (*AE* = 80%). These respiratory requirements for 1 g *WW* jellyfish ranged from 4.0 to 9.1% C day^{-1} with a mean value (± SE) 6.7 ± 0.6% C day^{-1}. Thus, the average annual metabolic needs of *A. aurita* were approximately one order of magnitude more than an actual ration (~0.5% C day^{-1}) based on mesozooplankton biomass and the digestion time of prey in the sea. The only exception is October 2009 when alternative rations were about the same magnitude (6.3-9.1% C day^{-1}).

We can see no significant omissions in the calculations which might potentially be a reason for such strong differences between these evaluations. According to our calculations, oxygen consumption rates of *A. aurita* calculated for minimum energetic requirements (Anninsky, 2009), though perhaps closer to the upper limit, were not significantly different from other available data (Table 4). Moreover, even on the assumption that metabolic requirements of jellyfish had been overestimated two-fold (albeit highly unlikely), and inversely, estimations of the ration had been underestimated two-fold, predation by *A. aurita* on mesozooplankton alone could not compensate for the minimum nutritional

Table 4. *Aurelia aurita.* Respiration rate parameters ($RR = q\ WW^k$) from different sources. Values *RR* and *WW* are expressed as µl O_2 ind.$^{-1}$.h^{-1} and g, respectively. ^{1}: Calculated assuming DW = 3.74% of WW at seawater salinity 34. ^{2}: Calculated assuming DW = 2.33% of WW at seawater salinity 20. ^{3}: Calculated assuming DW = 1.81% of WW at seawater salinity 15. ^{4}: Calculated assuming k = 0.84

Temperature (°C)	*WW* (g)	*q*	*k*	q^4	Source
7.6-23	0.02-96.9	3.21-9.92	0.81-0.89	3.28-9.36	Anninsky, 2009
10-15	~0.27-173.8^1	5.60-10.53^1	0.91-0.92	~6.53-12.05	Larson, 1987
15	~0.02-93.7^3	5.48^3	0.86	~5.51	Frandsen & Riisgard, 1997
15-20	53.48-454.5^1	0.40-6.20^1	1.00-1.40	~6.78-14.05	Ishii & Tanaka, 2006
15	~1.12-320.0^2	4.81^2	1.01	~7.93	Möller & Riisgard, 2007
20	5.3–220.8	5.42	0.93	~7.45	Han et al., 2012

needs of this species. The same conclusion follows from the results of similar studies in the open Black Sea in autumn 2010 when daily zooplankton consumption by jellyfish was estimated at a level of about 2% of total organic carbon content of the body (Anninsky et al., 2013). Consequently, such a low feeding rate of *A. aurita*, when mesozooplankton is consumed in insufficient quantity to compensate for the metabolic expenses, is the norm rather than exception of the general rule.

Thus the estimation of daily ration *via* oxygen consumption often exaggerates the true predatory impact of *A. aurita* on mesozooplankton, while similar calculations based on food composition and digestion time can seriously understate the actual ecological role of jellyfish in marine ecosystems. This usually occurs when the trophic significance of visually unidentified or ignored food components has been underestimated. In particular, such a method for the determination of food rations in the sea can not be sufficiently accurate for those species which consume large amounts of microplankton (Purcell et al., 2007).

Moreover, we should note that the trophic role of *A. aurita* in natural ecosystems in detail remains uncertain and is the cause of some controversy (Costello & Colin, 1994). The literature indicates that microzooplankton, being an important food source for this species, is systematically underestimated as a component of the diet (Stoecker et al., 1987; Olesen et al., 1994; Malej et al., 2007). Since the average biomass of ciliates, rotifers and small juvenile stages of planktonic organisms in the upper 10 m layer on the Crimean shelf can reach 0.5 g.m^{-2} (Finenko et al., 2006), their daily production (P/B = 0.2-1) only at this depth is well comparable with the total mesozooplankton production. Accordingly, these prey items may also contribute significantly to the jellyfish diet and, because of their rapid digestion, their role may be more significant than it would appear from their presence in the gut. It is not excluded that micro- as opposed to mesozooplankton are in fact a predominant food for this species.

The possibility of the use of phyto- and bacterioplankton as additional food sources for this jellyfish also cannot be entirely excluded. Although jellyfish predation usually promotes the increase in populations of microalgae (bottom-up effect) (Malej et al., 2007; Purcell et al., 2007; Richardson et al., 2009), some species of diatoms (*Coscinodiscus janischii* A.Schmidt, 1878, *Proboscia alata* (Brightwell) Sundström, 1986) can be found in the gastric cavity of *A. aurita* in quantities exceeding the total crustacean biomass (Anninsky et al., 2013). The appearance of clarified cells, empty cell walls and chloroplast fragments in the gut indicates that the digestion of phytoplankton by jellyfish can be quite successful although apparently occurs even slower than that of mollusk veligers.

Finally, another potential food source for the Moon jellyfish is dissolved organic matter which *A. aurita* apparently is also able to absorb (Shick, 1975); however the nutritional contribution to the daily ration is difficult to assess in practice. The idea of the possible use of dissolved organic matter as a main food source for this species has a long history beginning from the polemic between A. Pütter and A. Krogh (Anninsky et al., 2009).

The data available does not allow us to conclude how much these food components could compensate the difference between values of actual and required daily rations of jellyfish in the sea. We can only state that there are significant gaps in understanding of the trophic biology of this species or perhaps in methods of its assessment. In similar calculations for *A. aurita* from Tokyo Bay (the species is now identified as *Aurelia coerulea* von Lendenfeld, 1884; Scorrano et al., 2016), the carbon specific daily ration of jellyfish (0.6-5.6% of total organic carbon content) was also lower than that expected according to the minimum food requirements (2.7-9.5% of total organic carbon content), which the authors believe is due to low oxygen concentration of the sea water (Ishii & Tanaka, 2006). At the same time, in a separate study from the Inland Sea (Uye & Shimauchi, 2005), the imbalance between food uptake (4.7-23.4% of total organic carbon content per day) and energy requirement for metabolic maintenance (2.5-7.1% of total organic carbon content per day) was not detected.

Since all data on the content and composition of prey items in the gastric cavity of *A. aurita* was obtained during the second quarter of the day, the approximate 10-fold discrepancy between the actual and necessary state of the ration of jellyfish could also be a consequence of the circadian feeding rhythm. It is well known that both the medusae and their prey undertake regular diurnal migrations in the water column (Malej et al., 2007) which explains why the concentration of mesozooplankton in the upper epipelagic zone of the Black Sea at night may increase several times. This allows the suggestion that *A. aurita* may capture prey more successfully at night or during shorter time intervals when intensive vertical migration of zooplankton occurs. As seen for respiration rate, the increased activity of jellyfish is usually observed in the morning and evening hours especially during sunrise and sunset (Anninsky, 2009). And although in other studies the diurnal variations in *A. aurita* feeding activity were not detected (Barz & Hirche, 2005; Uye & Shimauchi, 2005), according to our unpublished data, in the open sea in autumn 2010, *Aurelia* consumed 20-30% more zooplankton at night than during the day. This may be the case for this study also, however, the available data is insufficient to estimate variations in jellyfish feeding rates throughout the whole day.

The successful existence of the *A. aurita* populations in the Black Sea in 2009-2010 is difficult to explain if we assume that the mesozooplankton representatives are the major or only food source for this jellyfish. In this case, daily food requirements obtained for this species given respiration rates (assuming 80% assimilation efficiency) will be equivalent to approximately 12% of biomass of organisms in the sea which is already greater than the daily production (10% of biomass). It is unclear what amount of zooplankton consumed is shared among ctenophores (*M. leidyi* and *Pleurobrachia pileus* (O.F. Müller, 1776)), chaetognaths, small pelagic fish, and other planktonic predators, which are competing with jellyfish. Or what fraction of zooplankton production, in addition to the above expenses, is lost due to considerable natural mortality of organisms (dead crustaceans may account for up to 50% of the total biomass of zooplankton). Also why no appreciable damage for mesozooplankton was observed despite such exorbitant losses - and why the dependence between the biomasses of jellyfish and mesozooplankton is typically missing when compared on interannual time scales. All of the above statements lead us to conclude that in reality *A. aurita* consumes much less mesozooplankton than required to compensate for its metabolic needs (and therefore growth), and by its nature this species relates to the more opportunistic predators than usually assumed when evaluating its position in the food web and ecological role in marine ecosystems.

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