Chemical composition and egg production capacity throughout bloom development of ctenophore *Mnemiopsis leidyi* in the northern Adratic Sea (#96594)

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Chemical composition and egg production capacity throughout bloom development of ctenophore *Mnemiopsis leidyi* in the northern Adratic Sea

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When occurring in high abundances gelatinous zooplankton can have large impact on ambient marine ecosystem, acting as sink and source of organic matter and nutrients. In particularly, decay of gelatinous zooplankton bloom can represent large impulse of organic matter (OM), rich in proteins and characterized by low carbon to nitrogen ration, which can disrupt quality and quantity of the ambient organic matter reservoir. Different life traits and environmental factors are reflected in the variability of the quantity and quality of gelatinous OM with potential implications for its surrounding system, in particularly, for its end-consumers, microbial communities, who are true drivers of marine biogeochemical cycles. One of the most notorious invasive ctenophores *Mnemiopsis leidyi* forms massive blooms in the northern Adriatic Sea since 2016, yet the variability of chemical composition and egg production of blooming populations and the role of environmental factors in governing the potential variability are largely unknown. Our analysis of biometry, chemical composition, and fecundity of *M. leidyi* sampled at different locations in the Gulf of Trieste in 2021 revealed rather stable carbon and nitrogen content of population throughout its bloom development, exhibiting no significant correlation with ambient seawater temperature, salinity, oxygen, and chlorophyll *a* concentration. Nevertheless, maximum percentage of carbon and nitrogen content in dry mass of individuals co-occurred with increase of phytoplankton biomass in the system, indicative of more productive system and hence higher ctenophore prey abundance. Even though our studied population was very homogenous in terms of biometry and chemical composition the number of produced eggs varied substantially, with no clear correlation with environmental variables, and was somehow lower than previously reported for our study area and other invaded systems in Mediterranean basin. We observed positive correlation between wet weight of individuals and percentage of hatched eggs. We also found significant positive correlation between percentage of hatched eggs and ambient seawater temperature. Besides, we observed that the speed of hatching decreased with lowering of ambient seawater temperature in

autumn, towards end of *M. leidyi* bloom. By examining the factors that affect the chemical composition and egg production of gelatinous zooplankton, we contribute to our understanding of the microbes-gelatinous-OM interactions, which are crucial for accurate integration of gelatinous component into oceanic biogeochemical budgets.

Manuscript Title:

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Abstract

When occurring in high abundances gelatinous zooplankton can have large impact on ambient marine ecosystem, acting as sink and source of organic matter and nutrients. In particularly, decay of gelatinous zooplankton bloom can represent large impulse of organic matter (OM), rich in proteins and characterized by low carbon to nitrogen ration, which can disrupt quality and quantity of the ambient organic matter reservoir. Different life traits and environmental factors are reflected in the variability of the quantity and quality of gelatinous OM with potential implications for its surrounding system, in particularly, for its end-consumers, microbial communities, who are true drivers of marine biogeochemical cycles. One of the most notorious invasive ctenophores *Mnemiopsis leidyi* forms massive blooms in the northern Adriatic Sea since 2016, yet the variability of chemical composition and egg production of blooming populations and the role of environmental factors in governing the potential variability are largely unknown. Our analysis of biometry, chemical composition, and fecundity of *M. leidyi* sampled at different locations in the Gulf of Trieste in 2021 revealed rather stable carbon and nitrogen content of ulation throughout its bloom development, exhibiting no significant correlation with ambient seawater temperature, salinity, oxygen, and chlorophyll *a* concentration. Nevertheless, ximum percentage of carbon and nitrogen content in dry mass of individuals co-occurred with ease of phytoplankton biomass in the system, indicative of more productive system and hence higher ctenophore prey abundance. Even though our studied population was very homogenous in terms of biometry and chemical composition, mber of produced eggs varied substantially, with no clear correlation with environmental variables, and was somehow lower than previously reported for our study area and other invaded systems in diterranean basin. We observed tive correlation between w eight of individuals and percentage of hatched eggs. We also found

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Introduction

A key to successful spread of one of the most notorious invader ctenophores *Mnemiopsis leidyi* A. Agassiz, 1865 to different ecosystems around the world (Costello et al., 2012; Jaspers et al., 2018; Jaspers, Bezio & Hinrichsen, 2021) lies in its life history traits, *e.g.*, ecological plasticity regarding environmental conditions, continuous production early after hatching, ability to self-fertilize and cannibalism (Baker & Reeve, 1974; Colin et al., 2010; Jaspers, Costello & Colin, 2015; Jaspers, Møller & Kiørboe, 2015; Shiganova et al., 2019; Javidpour et al., 2020; Edgar, Miguel Ponciano & Martindale, 2022). When occurring in high abundances this species can have a large impact on the local ecosystem, *e.g.,* acting as sink of nutrients and competing for food, and interacting with local interspecies predatory relationships (Oguz, Fach & Salihoglu, 2008; Fiori et al., 2019; Schroeder et al., 2023). On the other hand, the contribution of massive occurrence of this gelatinous invasive species as source of organic matter (OM) and nutrients for the impacted ecosystem, received less attention (Pitt, Welsh & Condon, 2009; Condon, Steinberg & Bronk, 2010; Dinasquet, Granhag & Riemann, 2012; McNamara, Lonsdale & Cerrato, 2013; Dinasquet et al., 2013). In particularly, decay of ctenophore bloom can result in large impulse of ctenophore-derived organic matter in short period of time, which can disrupt quality and quantity of the ambient organic matter reservoir in the ecosystem (Fadeev et al., 2024). It has been shown

that in particularly dissolved part of gelatinous zooplankton-derived OM, rich in proteins and characterized by low C:N ratio, can be subject to rapid decomposition by opportunistic microbes exhibiting high growth efficiency (Tinta et al., 2020; Fadeev et al., 2024). This implies that a major fraction of the gelatinous-OM is rapidly incorporated into bacterial biomass, which is then *e.g.,* accessible to bacterial grazers and thus not lost from the system *via* respiration (Tinta et al., 2020). This has important implications for the fate and flux of gelatinous-derived OM and for marine ecosystem functioning and its biogeochemical state (Dinasquet et al., 2013; Tinta et al., 2023; Fadeev et al., 2024). However, the composition of gelatinous-OM can vary between species and within population of the same species, because of specific properties of individual organisms, such as biometrics, fertility, age, several season-related environmental factors, prey type and its availability, and possible infestation with parasites (Condon, Steinberg & Bronk, 2010; McNamara, Lonsdale & Cerrato, 2013). This variability can have important implications for dynamics of its surrounding system, in particularly, for its end-consumers, microbial communities, who are true drivers of marine biogeochemical cycles (Azam & Malfatti, 2007). Understanding the factors determining the chemical composition and egg production of gelatinous-OM is thus important to better understand the interaction between microbes and gelatinous-OM, which will eventually allow us to accurately incorporate jelly-OM into biogeochemical budgets of a system.

Since 2016 annual blooms of *M. leidy* also observed from summer until late autumn in the northern Adriatic (Malej et al., 2017; Pestorić et al., 2021). Some aspects of potential impact of this bloom formations on the local ecosystem have been studied (Fiori et al., 2019; Ciglenečki et al., 2021; Paliaga et al., 2021; Fadeev et al., 2024), yet there is limited data available on chemical composition and egg production capacity of northern Adriatic *M. leidyi*

populations (Malej et al., 2017; Fadeev et al., 2024). Our aim was to elucidate variability of biometry, chemical composition, and fecundity of *M. leidyi* population throughout its annual bloom development and address our hypothesis that ambient seawater environmental variables affect observed potential variations. To address our objective, we sampled *M. leidyi* individuals at different locations in the Gulf of Trieste throughout their blooming season from August to October 2021 and measured biometric parameters (wet and dry mass), chemical composition (carbon and nitrogen content) and conducted egg production experiments. At the same followed a set of environmental factors and applied statistical analysis to infer correlations between variables.

Material and methods

Field sampling

We sampled *M. leidyi* twice a month, from August to October 2021 (Table 1). In this way, we covered the period when specimens of *M. leidyi* are most numerous in the northernmost part of the Adriatic Sea - the Gulf of Trieste (Fig. 1). To account for spatial heterogeneity of populations, sampling was done at different locations in our study area (Fig. 1). Ctenophores were collected directly from a boat or ~~from~~ the pier using a plastic bucket, which was priorly cleaned with ambient seawater. Afterwards collected ctenophores were transferred in buckets, directly to the laboratory, at *in situ* temperature and light conditions. During each sampling campaign collected around 15 – 20 individuals (Table S1). For each sampling campaign retrieved data on ambient seawater temperature, salinity, oxygen and chlorophyll a concentrations from 3 m depth at our reference long-term sampling station - oceanographic buoy

Vida (https://www.nib.si/mbp/en/oceanographic-data-and-measurements/buoy-2) (Fig. 1, Table S1).

Biometry and elemental composition analysis

First, we measured total body length (TBL) of each collected individual (*i.e.*, oral-aboral length including lobes) and determined the wet mass of each ctenophore using the calibrated scale Sartorius TE1502S. Afterwards, we placed each specimen in separate clean zip lock bag and stored at -20 °C, for at least 24h until further processed. For elemental composition analysis, we freeze-dried each specimen for 3 days. The dry mass for each individual was determined using the calibrated scale Sartorius CP225D (d=0.01mg (80g), d=0.1mg (220g). Dry material of each specimen was then homogenized with pre-sterilized pestle and agate mortar and stored separately in sterile 15 grainer tubes at -20° C until further analysed. From each sample weighed about 15 – 20 mg of dry homogenized matter into small capsules using a calibrated Micro scale (Mettler Toledo). Elemental composition of carbon (C) and nitrogen (N) was determined after combustion at 1150° C (Elementar, Vario Micro Cube elemental analyser) with 3 % accuracy.

Reproduction experiment

During each sampling campaign we selected a batch of 5 individuals, similar in size (on average 6.9 ± 1.1 cm) and wet weight (on average 24.1 ± 7.8 g), to determine reproduction capacity of sampled ctenophores (Table 1). Each of the 5 specimens selected was placed individually into a 1L glass Erlenmeyer flask filled with 800mL of pre-filtered seawater (GF/F Whatman filters) and covered with parafilm. Afterwards 20 hours of incubation at the *in situ* seawater temperature in the dark, we examined seawater for produced eggs and/or other developmental stage using Olympus stereo microscope SZH. For this we first reduced volume of analysed seawater using

mesh filter with pore size of 200 µm and then analysed sample water using a small container with grid pattern bottom. We counted all the eggs and other developmental phase in each sample after 24h and 48h of the experiment. Once we terminated the experiment, we sacrificed ctenophores for further analysis of dry mass and elemental composition analysis, as described above (see *Biometrics and elemental composition analysis*).

Statistics

All the statistics and visualization were performed using specific packages in R (https:// www.r-proje ct. org/). Pearson correlation coefficient and Holm-Bonferroni p-value adjustment method was determined using R correlation package. For visualization we used ggplot2 package in R. Figures we combined in Bio render.

Results

Environmental parameters

Ambient seawater temperature fluctuated slightly around 22°C throughout our sampling campaign, with maximum of 25 °C in August and minimum of 17°C recorded at the end of October in our study (Fig. 2A). Salinity of ambient seawater temperature varied around 36-37, with minimum of 35 recorded in August and maximum of 38 measured in October during our sampling campaign (Fig. 2A). Chlorophyll concentration was increasing from 0.39 µg mL^{-1} in August to 1.19 µg mL^{-1} in first half of the October during our study (Fig. 2B). A slight drop of Chl *a* concentration down to 1 µg mL^{-1} was recorded in the second half of October. Concentration of oxygen in ambient seawater was the lowest in August (4.48 mg mL^{-1}) and the highest in October (5.06 mg mL^{-1}) during our sampling campaign (Fig. 2B).

Biometric parameters and elemental composition of ctenophore populations

We collected between 15 to 20 individuals during each sampling event, altogether resulting in 89 individuals collected in total, representing ctenophore population blooming between August and October 2021. Total body length (*i.e.*, oral-aboral length including lobes) and width of individuals were on average 6.6 ±1.1 cm and 4.2 ± 0.6 cm, respectively (Table S2). The average wet weight (WW) was 30.8±13.6 g (Fig. 3A). Dry weight (DW) was on average 1.3 ± 0.6 g (Fig. S1) and on average represented 4.1 ± 0.2 % of wet weight (Fig. 3B). Both minimum and maximum wet and dry weights (*i.e.*, min WW = 4.96 g and max WW = 70.2 g; min DW = 0.2 g and max DW = 2.93 g) were detected within the population collected in the first half of September, which was overall most size heterogenous population (Table S1). To test our first hypothesis that changes in environmental variables affect biometric properties of ctenophore populations we calculated Pearson correlation coefficient for the entire set of selected environmental variables (temperature, salinity, oxygen, and chlorophyll a concentration) and all biometric characteristics of ctenophores (wet weight, dry weight, and percentage of dry weight) using R correlation package. We found significant correlation between salinity and percentage of dry weight ($r=0.40$, $p < 0.001$**, p-value adjustment method: Holm-Bonferroni) (Fig. 3C). Else, no other environmental variable correlated with biometric characteristics of ctenophore populations (Table S3).

The average percentage of carbon and nitrogen in the dry mass of all the individuals of the total studied ctenophore population was 1.59±0.29% and 0.42±0.08 %, respectively (Table S1). The minimum percentage of carbon and nitrogen in the dry mass was measured for the population collected in the second half of September and was 1.03% and 0.28%, respectively (Table S1). The maximum percentage of carbon and nitrogen in the dry mass was measured for the population in the second half of October and was 2.73% and 0.71%, respectively (Table S1).

The carbon and nitrogen content did not show any significant trend throughout the study period nor any significant correlation with ronmental variable in our dataset (Fig. 4A, Table S3). The carbon to nitrogen (C:N) molar ratio remained relatively constant throughout the study period, and was on average 4.46±0.19:1, with minimum measured in first half of August (3.81:1) and maximum in the first half of September (4.95:1) (Table S1, Fig. 4). We found no significant correlation between C to N ratio and environmental variables in our dataset (Table S3).

Egg production

For our egg production experiment, we selected Individuals similar in size, with a body length of 6.6 ±1.1 cm on average and body width of 4.2 ± 0.6 cm on average (Table S2). Their average wet mass (24.1 ± 7.8 g), dry mass percentage of WW (4-1 ± 0.3%), carbon (1.57 ± 0.33%) and nitrogen (0.42 ± 0.09%) content and C:N ratio (4.4 ± 0.2:1) was in the range of values measured for total collected population in our study (Table 1, Table S1, S2). Slightly over half (57 %) of individuals produced eggs in our study, the average being 165 eggs per individual (Table 1). Percentage of individuals, which did not produce any eggs was the highest within the population collected in the second half of September and in the first half of October (Table 1). There was great variability in terms of total number of eggs produced by individuals, over the entire dataset and within specific experiment (Table 1, Fig. 5A). The largest number of eggs produced (638) was recorded in the second half of October, and the lowest (3) in the first half of September. We found no significant correlation between total number of eggs produced and/or chemical characteristics of individuals or environmental variables (Table S4).

After first 24h of our 48h fecundity experiment most eggs were already at the cydippid larva stage. We thus calculated the percentage of hatched eggs by dividing the number of hatched eggs after 24h by the number of total eggs produced by each in 24h. We calculated

196 average percentage of hatched eggs per each experiment by considering only those individuals
197 which produced eggs. The average percentage of hatched eggs over the entire dataset was
198 67±32%, with minimum of 13% in the second half of October and maximum of 100% in first
199 half of August and first half of September (Fig. 5B). We found significant correlation between
200 percentage of hatched eggs and ambient seawater temperature ($r=0.36$, $p < 0.05$*), which is even
201 more significant if we only consider those individuals, which produced eggs ($r=0.72$, $p <0.01$**)
202 (Fig. 5C, Table S4). There was also significant positive correlation between percentage of
203 hatched eggs and wet weight of ctenophores ($r=0.38$, $p < 0.05$*) (Fig. 5D, Table S4). Note that
204 these correlations were significant but were not confirmed with Holm-Bonferroni method. We
205 found no significant correlation between percentage of hatched eggs and chemical characteristics
206 of individuals or environmental variables (Table S4).

207 **Discussion**

208 ***Variations in ambient seawater environmental parameters are not reflected in the chemical***
209 ***composition of blooming ctenophore population.***

210 The abundance of *M. leydi* populations in our study area begins to increase only from late July
211 on, reaching the peak between September and October, with intermediate massive blooms, while
212 individuals are rarely observed in the study area during colder part of the year (Malej et al.,
213 2017; Budiša et al., 2021). Hence, we sampled *M. leydi* from the second half of August until the
214 end of October, which captured the bloom of the population in the study area in 2021. In the
215 same period, from August to October, we observed change of ambient seawater variables;
216 ambient seawater temperature decreased from 25 to 17 °C, salinity increased from 35 to 38,
217 chlorophyll *a* increased from app. 0.4 to 1.2 µg mL^{-1} and oxygen concentration increased from

4.5 to 5 mg mL^{-1}. Yet, we did not observe any significant temporal trend of wet weight, dry weight, percentage of carbon and nitrogen content or carbon to nitrogen molar ratio in the sampled population (Fig. 3, Fig. 4). Carbon to nitrogen ratio remained relatively constant with an average at 4.5:1, in accordance with previous reports (Pitt, Welsh & Condon, 2009; Lucas et al., 2011) and exhibit no correlation with environmental variables (Table S3, Fig. 4). In this way, we can say that we rejected our hypothesis that changes of environmental variables in the ambient seawater would be reflected in the carbon to nitrogen ratio of ctenophore biomass. However, we found significant correlation between salinity and percentage of dry weight ($r=0.40$, $p < 0.001$**, p-value adjustment method: Holm-Bonferroni) (Fig. 3C, Table S3). The percentage of dry mass was getting progressively higher during our sampling campaign, most likely as due to an increase of ambient seawater salinity, resulting in increase of salt content in jellyfish due to osmoregulation process (Hirst & Lucas, 1998). Also, maximum percentage of carbon and nitrogen in the dry mass was measured for the population collected in the second half of October (Table S1), co-occurring with recorded peak of chlorophyll *a* concentration. Higher concentration of chlorophyll a in ambient seawater implies more productive system and could be indicative of higher zooplankton prey abundance. Besides, the annual pattern of zooplankton biomass in our study area typically shows bimodal distribution with maximum in spring and secondary peak in autumn (October – November) (Mozetič et al., 2012).

Egg production is highly variable within population.

We found that the number of eggs produced varied greatly between the individuals selected for each of the conducted fecundity experiments and over the entire dataset, with about half of individuals not producing any eggs at all, even though in terms of biometric properties selected population was very homogenous. Percentage of individuals which did not produce any eggs

was higher in autumn month as compared to summer month (Table 1), yet we did not find any correlation with environmental variables (Table S4). Overall, average number of eggs produced was 165 ± 179, which is lower than previously reported for northern Adriatic Sea (4320 ± 3980 eggs, (Malej et al., 2017) or other areas in Mediterranean Sea, within studies where reproductive output of freshly collected animals from the natural environment was assessed (Table 2). Indeed, Baker and Reeve (Baker & Reeve, 1974) pointed out that the daily egg production of laboratory-reared animals never reached the maximum values recorded for the animals collected from their natural environment. Also, egg production was found to be highly variable in different invaded and native areas. In the northern Europe (e.g., 3000 eggs ind^{-1} day^{-1}; (Javidpour et al., 2009); maximum rates of 11 232 eggs ind^{-1} day^{-1}, (Jaspers, Costello & Colin, 2015) or southern Europe (e.g., 12 000 eggs ind-1 day-1, Zaika and Reeve, 1974) or in its native areas (e.g., 9390 and 14 233 eggs ind^{-1} day^{-1} (Kremer, 1976; Graham et al., 2009) and 9910 eggs ind^{-1} day^{-1} (Baker & Reeve, 1974). To some extent the observed discrepancy between reports can be due to different size of selected individuals, as the number of eggs produced generally increases with the size of individuals (Sasson & Ryan, 2016). In our study we deliberately chose individuals with a body length of 6.6 ±1.1 cm and body width of 4.2 ± 0.6 cm, to minimize the effect of body size, as our aim was to find out how the changing environmental conditions affect the reproductive potential of ctenophores. Yet, we found no significant correlation between total number of eggs produced, biometric and/or chemical characteristics of individuals or environmental variables (Table S4). Some of the more recent studies also hypothesize that change towards oligotrophy (Mozetič et al., 2012) in the northern Adriatic might have a negative effect on fecundity of ctenophores (Ciglenečki et al., 2021). On the other hand, the lower reproductive performance of our *Mnemiopsis* population compared to the measurements in the initial year of colonisation (Malej

et al., 2017) could be related to the decline in invasive opportunistic traits since the invasion. Jaspers and her colleagues (Jaspers et al., 2018) observed no such effect and explained the persistent invasive traits in *Mnemiopsis* with multiple reinvasions and a large variation in reproductive traits in the (native) source population.

We found significant correlation between percentage of hatched eggs and ambient seawater temperature ($r=0.36$, $p < 0.05$*) and wet weight of ctenophores ($r=0.38$, $p < 0.05$*) (Figure 5C, D). Else, we found no significant correlation between percentage of hatched eggs and chemical characteristics of individuals or environmental variables. Hence, our hypothesis that reproduction capacity of ctenophores is affected by changing environmental variables and biometric and chemical characteristic of ctenophores is partly true. The positive correlation between wet weight and percentage of hatched eggs per individual is in line with the observation that number of eggs produced generally increases with the size of individuals (Sasson & Ryan, 2016). We observed that the percentage of hatched eggs reached upwards of 80 % when the temperature was around 25 °C, but was much lower in the second half of October, when the seawater temperature decreased to 17 °C. When the seawater temperature dropped to 17 °C, only around 20 % of eggs had reached a cydippid larva stage after the first day of incubation, while this percentage was much higher (between 56 and 91 %) at temperatures higher than 20 °C. Thus, we can see that the lower temperatures decreased the speed of embryo development, comparable to some other studies (Sullivan & Gifford, 2004; Gambill, Møller & Peck, 2015), where they showed that embryo development speed increases with temperature, up to an optimum of around 25 °C.

Conclusions and future perspectives

Our analysis of chemical composition of northern Adriatic *M. leidyi* population revealed rather stable carbon and nitrogen content of population throughout its bloom development, exhibiting no significant correlation with ambient seawater temperature, salinity, oxygen, and chlorophyll *a* concentration. Nevertheless, maximum carbon and nitrogen content in individuals co-occurred with shift towards more productive system, hence we can speculate that it is related to higher abundance of ctenophore prey. However, please note that our study focused on the part of the year, when *M. leidyi* population is blooming in the northern Adriatic, while individuals present from winter to spring in our system were not considered. Overall, the number of eggs produced per individual was somehow lower than previously reported for the same area and for other invaded Mediterranean Sea basins, and was highly variable, despite biometric and chemical homogeneity of studied population. This implies that one should include larger set of environmental factors that play potential role in fecundity of ctenophores. We did observe positive correlation between percentage of hatched eggs with ambient seawater temperature. By examining the factors that affect the chemical composition and egg production of gelatinous zooplankton, we contribute to our understanding of the microbes-gelatinous-OM interactions, which are crucial for accurate integration of gelatinous component into oceanic biogeochemical budgets. Nevertheless, effort should be made in examining biochemical composition of ctenophores at individual molecular compound level, which are eventually fuelling ambient dissolved organic matter pool that is determining the structure and function of ambient microbial communities, propelling biogeochemical cycles at the base of marine food web.

Acknowledgment

We would like to thank to the staff of Marine Biology Station Piran and crew of RV Carolina for their help with sampling.

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Figure Legends:

Figure 1: **Study area.** The Gulf of Trieste, located in the northernmost basin of the Adriatic Sea. Ctenophore sampling areas are highlighted in light red. Oceanographic buoy Vida is marked with red star.

Figure 2: **Dynamics of environmental parameters**. Dynamics of environmental parameters at 3 m depth at the reference station Oceanographic buoy Vida, located in the middle of the Gulf of Trieste, throughout our sampling campaign. **A** – ambient seawater temperature (°C, in red) and salinity (in blue); **B** – Chlorophyll *a* (μg mL^{-1}, in green) and oxygen (mg L^{-1}, in grey) concentration.

Figure 3: **Dynamics of wet and dry weight of studied ctenophore population**. Dynamics of **A** - Wet weight (WW in g), **B** - percentage of Dry Weight (%DW) and **C** - relationship between percentage of Dry Weight (%DW) and Salinity in the ctenophore population collected between August and October 2021 in the Gulf of Trieste, northern Adriatic Sea.

Figure 4: **Dynamic of carbon and nitrogen content of studied ctenophore population**. The percentage of carbon and nitrogen (**A**) and the carbon to nitrogen molar ratio (**B**) in the ctenophore population collected between August and October 2021 in the Gulf of Trieste, northern Adriatic Sea.

Figure 5: **Dynamic of produced and hatched eggs of studied ctenophore population** Total number of eggs produced (**A**) and percentage of hatched eggs (**B**) by ctenophores collected from August until October 2021 in the northern Adriatic Sea. Correlation between percentage of hatched eggs and (**C**) ambient seawater temperature and (**D**) wet weight of individuals. All individuals, also those that did not produce any eggs are considered.

459

460 **Table Legends:**

461 **Table 1**: **Biological and chemical characteristics of studied ctenophore population**. Biological
462 and chemical characteristics of the subset of ctenophore samples selected for egg production
463 experiments with total number of eggs produced and percentage of hatched eggs after 24h per
464 individual and average for each experiment.

465 **Table 2**: **Egg production of field-collected *Mnemiopsis leidyi* from native areas and the**
466 **Mediterranean Sea.**

467

Figure 1

Study area.

Study area, the Gulf of Trieste, located in the northernmost basin of the Adriatic Sea. Ctenophore sampling areas are highlighted in light red. Oceanographic buoy Vida is marked with red star.

Figure 2

Dynamics of environmental parameters

Dynamics of environmental parameters at 3 m depth at the reference station Oceanographic buoy Vida, located in the middle of the Gulf of Trieste, throughout our sampling campaign. **A** – ambient seawater temperature (°C, in red) and salinity (in blue); **B** – Chlorophyll *a* (µg mL^{-1}, in green) and oxygen (mg L^{-1}, in grey) concentration.

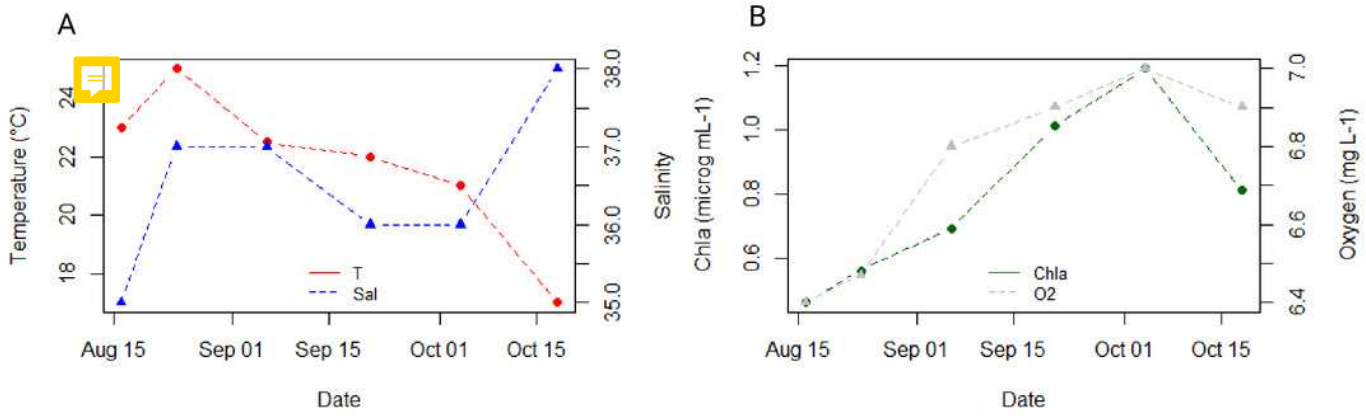

Figure 3

Dynamics of wet and dry weight of studied ctenophore population.

Dynamics of **A** - Wet weight (WW in g), **B** - percentage of Dry Weight (%DW) and **C** - relationship between percentage of Dry Weight (%DW) and Salinity in the ctenophore population collected between August and October 2021 in the Gulf of Trieste, northern Adriatic Sea.

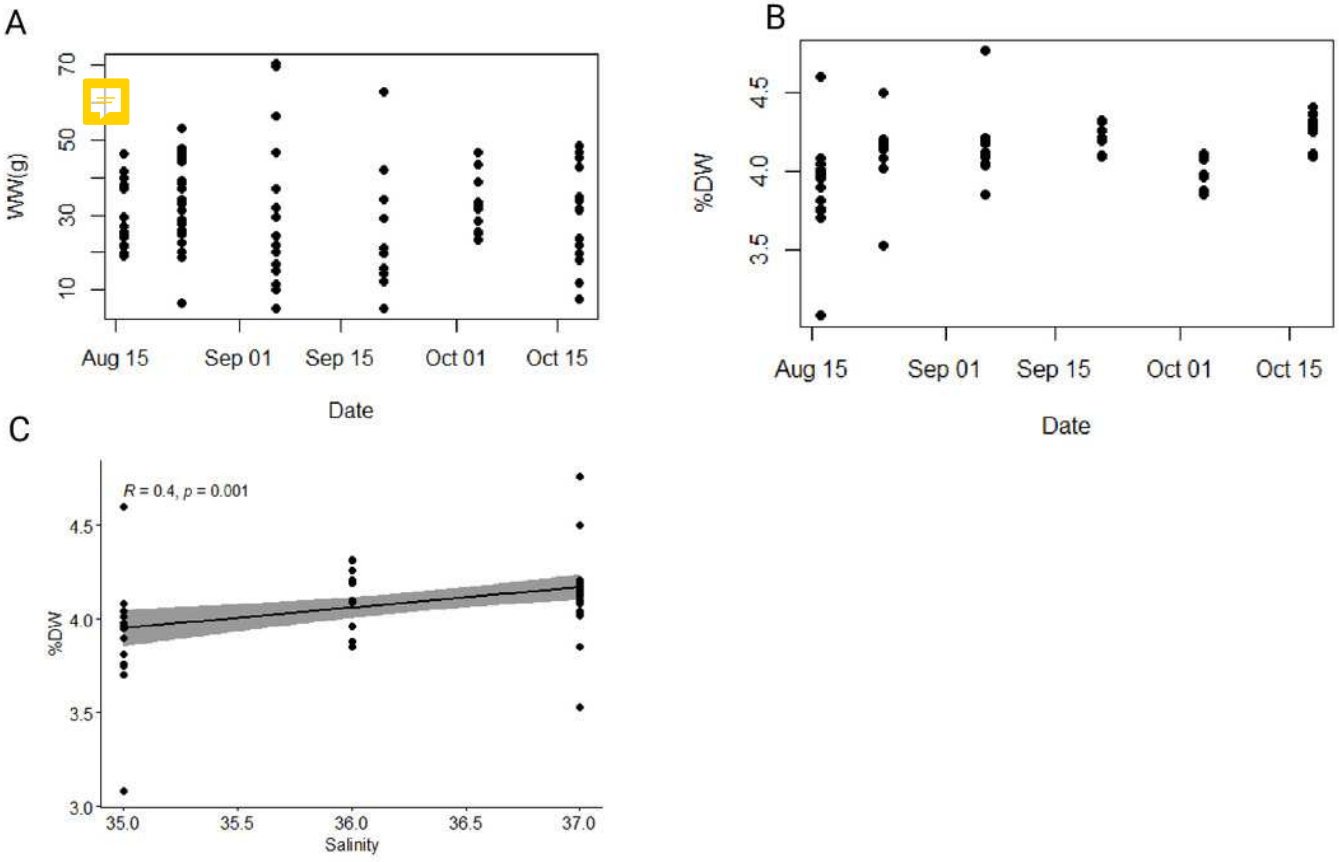

Figure 4

Dynamic of carbon and nitrogen content of studied ctenophore population

The percentage of carbon and nitrogen (**A**) and the carbon to nitrogen molar ratio (**B**) in the ctenophore population collected between August and October 2021 in the Gulf of Trieste, northern Adriatic Sea.

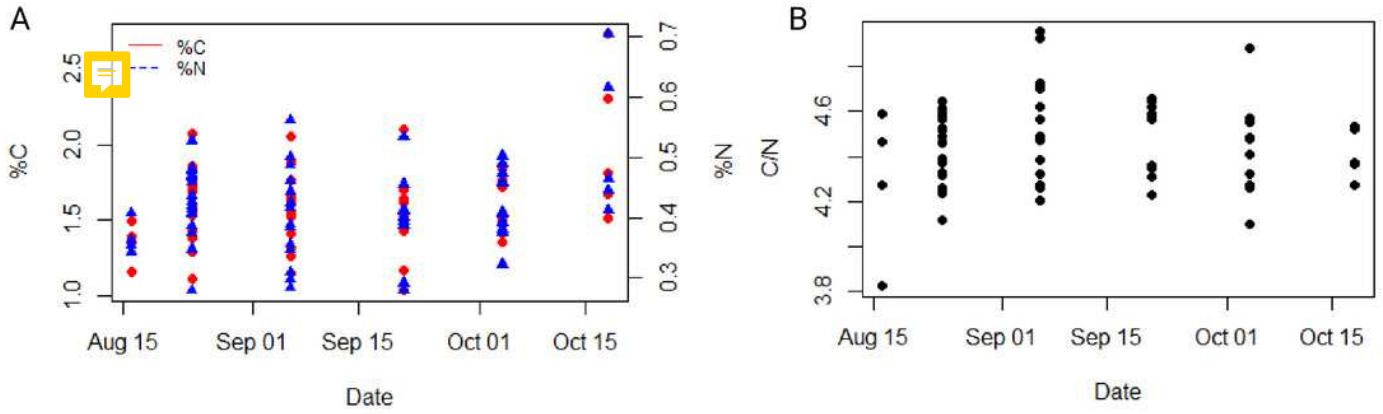

Figure 5

Dynamic of produced and hatched eggs of studied ctenophore population

Total number of eggs produced (**A**) and percentage of hatched eggs (**B**) by ctenophores collected from August until October 2021 in the northern Adriatic Sea. Correlation between percentage of hatched eggs and (**C**) ambient seawater temperature and (**D**) wet weight of individuals. All individuals, also those that did not produce any eggs are considered.

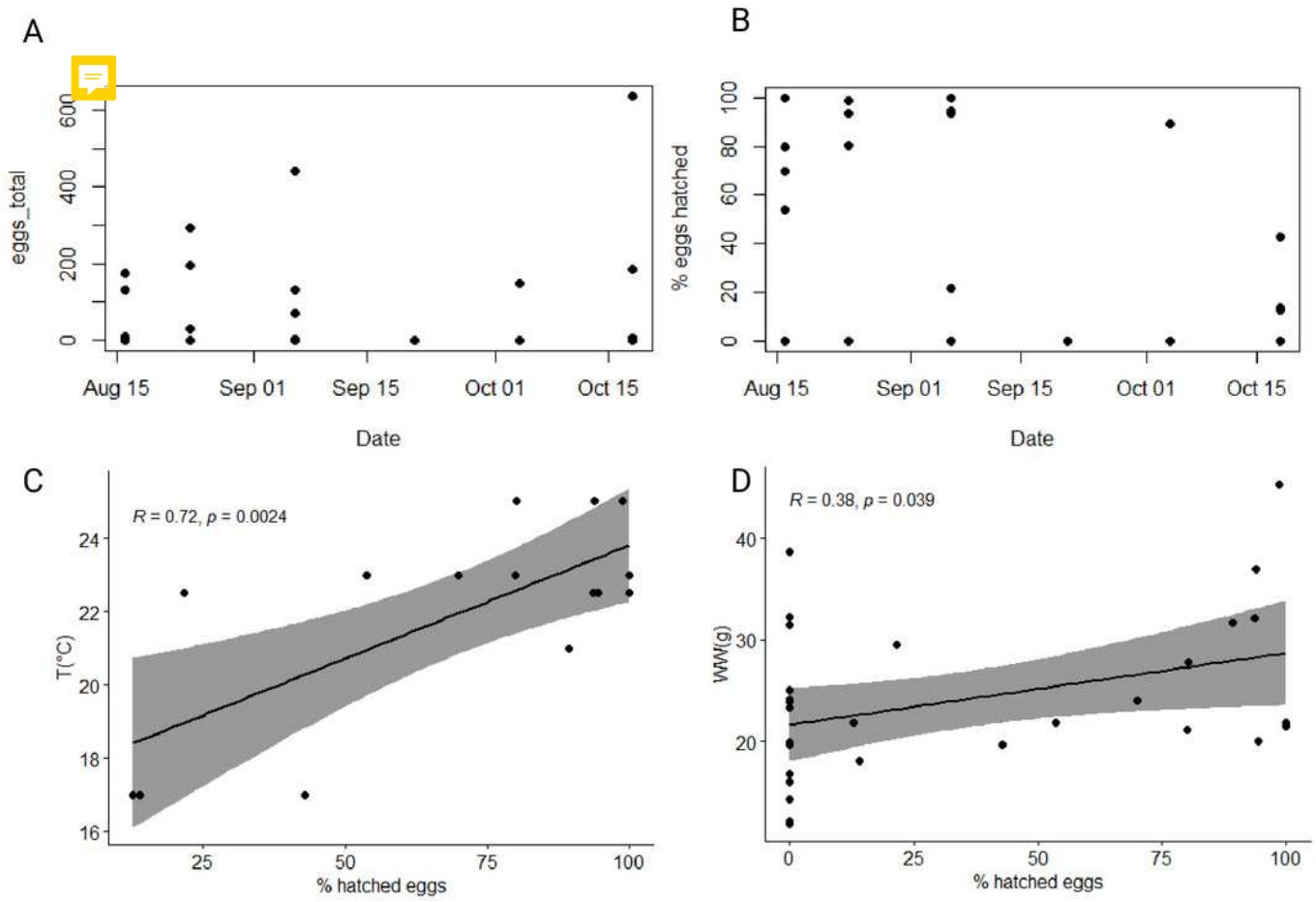

Table 1(on next page)

Biological and chemical characteristics of studied ctenophore population

Biological and chemical characteristics of the subset of ctenophore samples selected for egg production experiments with total number of eggs produced and percentage of hatched eggs after 24h per individual and average for each experiment.

1 **Table 1**: Biological and chemical characteristics of the subset of ctenophore samples selected for egg production experiments with total
2 number of eggs produced and percentage of hatched eggs after 24h per individual and average for each experiment.

Date	T (°C)	Sal	chl *a* (ug mL^{-1})	O_2 (mg L^{-1})	WW (g)	DW (g)	%DW	%N	mg N ind^{-1}	%C	mg C ind^{-1}	C:N	eggs_total	% hatched eggs in 24h
16.08.2023	23	35	0.46	6.4	21.86	0.81	3.7	0.36	2.92	1.39	11.26	4.5	177	54
					21.57	0.81	3.75	0.34	2.75	1.35	10.94	4.6	9	100
					24.00	0.74	3.08	0.35	2.59	1.16	8.58	3.8	133	70
					19.76	1.53	4.6	0.42	6.43	1.58	24.17	4.4	0	n.a.
					21.16	1.02	3.76	0.41	4.18	1.50	15.30	4.3	5	80
avg±sd					**21.7±1.53**	**1.0±0.32**	**3.8±0.54**	**0.4±0.04**	**3.7±1.6**	**1.4±0.16**	**14.1±6.1**	**4.3±0.31**	**64.8±83.9**	**75.9±19.4**
24.08.2023	25	37	0.56	6.47	27.75	1.25	4.50	0.41	5.13	1.57	19.63	4.5	197	80
					36.89	1.53	4.15	0.44	6.73	1.69	25.86	4.5	32	94
					24.16	1.03	4.17	0.38	3.91	1.43	14.73	4.5	0	n.a.
					45.26	1.88	4.15	0.53	9.96	2.07	38.92	4.6	295	99
					31.44	1.11	3.53	0.41	4.55	1.43	15.87	4.1	0	n.a.
avg±sd					**33.1±8.27**	**1.4±0.35**	**4.1±0.35**	**0.4±0.06**	**6.1±2.4**	**1.6±0.26**	**23.0±9.9**	**4.4±0.19**	**104.8±134.1**	**90.9±9.6**
06.09.2021	22.5	37	0.69	6.8	16.85	0.71	4.21	0.39	2.77	1.52	10.79	4.6	0	n.a.
					21.84	1.04	4.76	0.28	2.91	1.15	11.96	4.7	3	100
					32.17	1.24	3.85	0.46	5.70	1.77	21.95	4.5	443	94
					29.56	1.21	4.09	0.43	5.20	1.53	18.51	4.2	130	22
					20.09	0.84	4.18	0.36	3.02	1.32	11.09	4.3	72	94
avg±sd					**24.1±6.49**	**1.0±0.23**	**4.2±0.33**	**0.4±0.07**	**3.9±1.4**	**1.5±0.23**	**14.9±5.1**	**4.5±0.21**	**129.6±183.3**	**77.4±37.4**
21.09.2021	22	36	1.01	6.9	16.00	0.69	4.31	0.39	2.69	1.54	10.63	4.6	1	0
					19.97	0.85	4.26	0.39	3.32	1.55	13.18	4.7	0	n.a.
					12.20	0.52	4.26	0.28	1.46	1.03	5.36	4.3	1	0
					19.72	0.84	4.26	0.41	3.44	1.61	13.52	4.6	0	n.a.
					14.38	0.62	4.31	0.46	2.85	1.7	10.54	4.4	0	n.a.
avg±sd					**16.5±3.38**	**0.7±0.14**	**4.3±0.03**	**0.4±0.07**	**2.8±0.8**	**1.5±0.26**	**10.6±3.3**	**4.5±0.16**	**0.4±0.5**	**0.0±0.0**
04.10.2021	21	36	1.19	7	32.28	1.28	3.96	0.41	5.25	1.51	19.33	4.3	0	n.a
					38.66	1.54	3.98	0.39	6.01	1.48	22.79	4.4	0	n.a
					31.66	1.3	4.11	0.38	4.94	1.41	18.33	4.3	149	89.26
					25.01	0.99	3.96	0.5	4.95	1.34	13.27	4.3	0	n.a
					23.4	0.93	3.97	0.41	3.81	1.5	13.95	4.3	0	n.a
avg±sd					**30.2±6.15**	**1.2±0.25**	**4.0±0.06**	**0.4±0.05**	**4.9±0.8**	**1.4±0.07**	**17.5±3.9**	**4.3±0.04**	**29.8±66.6**	**89.3**
18.10.2021	17	38	0.81	6.9	23.93	1.03	4.3	0.41	4.22	1.51	15.55	4.3	0	0
					11.92	0.52	4.36	0.71	3.69	2.73	14.20	4.5	0	0
					21.81	0.96	4.4	0.44	4.22	1.67	16.03	4.4	638	12.7

					18.09	0.79	4.37	0.62	4.90	2.31	18.25	4.4	187	13.9
					19.69	0.85	4.37	0.46	3.91	1.81	15.39	4.5	7	42.86
avg±sd					**19.1±4.57**	**0.8±0.20**	**4.4±0.04**	**0.5±0.13**	**4.2±0.5**	**2.0±0.50**	**15.9±1.5**	**4.4±0.08**	**166.4±275.5**	**23.2±17.1**

Note that average percentage of hatched eggs is calculated by considering only those individuals that produced eggs. T- temperature (°C); Chl a – chlorophyll a concentration; O_2 – oxygen concentration; WW – wet weight; DW – dry weight; mg N ind^{-1} – mg of nitrogen per individual specimen; mg C ind^{-1} – mg of carbon per individual specimen; C:N – carbon to nitrogen molar ratio.

Table 2(on next page)

Egg production of field-collected *Mnemiopsis leidyi* from native areas and the Mediterranean Sea.

1 **Table 2**: Egg production of field-collected *Mnemiopsis leidyi* from native areas and the Mediterranean Sea.

Native areas	T (^{0}C)	TBL (cm)	No. eggs	% ind. eggs	% hatching
Narragansett Bay (Costello et al., 2006)	6 – 25		0 – 3300	59	n.d.
Narragansett Bay (Kremer, 1976)	11 – 29		0 – 14 000		
Biscayne Bay (Baker & Reeve, 1974)	21 – 31	3.8 – 8.5	0 – 9990	90	n.d.
Biscayne Bay (Stanlaw et al., 1981)	21		up to 10 000	most individuals	most eggs
Mediterranean Sea					
Aegean Sea (Shiganova et al., 2004)	21 – 25	1.7 – 3.4	0 – 448	75	82
Northern Adriatic (Malej et al., 2017)	20 – 22	5.4 – 11.5	136 – 13,512	100	n.d.
Northern Adriatic (Kogovšek et al., 2018)	20	4.1 – 9.8	0 – 1400	65	n.d.
Northern Adriatic (Kogovšek et al., 2019)	6 – 28	5.1 – 8.5	1 – 2506	10 – 86	n.d
This study	17 - 25	5 – 7	0 – 638	57	12 – 100

2 T = temperature, TLB = total body length, No. eggs = number of eggs produced by individual in 24 hours, % ind. eggs = percentage of

3 individuals that produced eggs, % hatching = percentage of hatched eggs after 24 hours

4