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SHORT COMMUNICATION

Carbon content of *Mnemiopsis leidyi* eggs and specific egg production rates in northern Europe

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The comb jelly *Mnemiopsis leidyi* is considered to be a successful invasive species, partly due to its high reproduction potential. However, due to the absence of direct carbon measurements of eggs, specific reproduction rates remain uncertain. We show that egg carbon is $0.22 \pm 0.02 \mu\text{g C}$ and up to 21 times higher than previously extrapolated. With maximum rates of $11\,232 \text{ eggs ind}^{-1} \text{ day}^{-1}$, largest animals in northern Europe invest $\sim 10\% \text{ day}^{-1}$ of their body carbon into reproduction.

The comb jelly *M. leidyi* has received wide public and scientific attention during the last decades due to its commonly observed formation of bloom abundances in native and invaded areas (e.g. Costello *et al.*, 2012;

Rüsgård *et al.*, 2012). One of the traits suggested to be responsible for *M. leidyi*'s invasion success is its high fecundity. At the northern end of its distribution range in native areas, *M. leidyi* has been shown to produce up to 9380 and 14 233 eggs $\text{ind}^{-1} \text{ day}^{-1}$ (Kremer, 1976a; Graham *et al.*, 2009), with similar rates of 9910 eggs $\text{ind}^{-1} \text{ day}^{-1}$ for the native southern population in Biscayne Bay, FL, USA (Baker and Reeve, 1974). Within invaded European waters, rates of up to 3000 and 12 000 eggs $\text{ind}^{-1} \text{ day}^{-1}$ have been recorded for northern and southern populations, respectively (Zaika and Revkov, 1994; Javidpour *et al.*, 2009). Since *M. leidyi* is a simultaneous hermaphrodite and fertilized eggs are produced on a daily basis

during favorable conditions (Jaspers, 2012), *M. leidyi* can circumvent the Allee effect and efficiently seed new populations even from few founding individuals. Although the documented reproduction potential is large, carbon investment into reproduction remains speculative due to the lack of direct carbon measurements of eggs. Literature values of carbon content of eggs vary by a factor of 21, from $0.012 \mu\text{g C egg}^{-1}$ (Reeve *et al.*, 1978) to $0.25 \mu\text{g C egg}^{-1}$ (Anninsky *et al.*, 2007) but so far there have been no direct measurements. This leads to the discrepancy between high feeding rates (Colin *et al.*, 2010) and negligible investment into reproduction with 0.03 to <2% of *M. leidyi*'s body carbon per day, which is several fold less than its respiratory carbon demand (Reeve *et al.*, 1989). The aim of this study is to present direct carbon and nitrogen measurements of *M. leidyi* eggs to clarify carbon specific reproduction rates along with its maximum reproduction capacity within invaded, northern European waters. This information is crucial for understanding population dynamics and assessing carbon budgets of *M. leidyi* throughout its distribution range.

Carbon and nitrogen content of freshly spawned eggs ($n = 2800$) were measured from wild caught *M. leidyi* ($n = 5$) originating from Woods Hole, MA, USA (position: Latitude 41.525N, Longitude -70.674°E). Animals were incubated overnight in GFF-filtered seawater. Eggs were individually picked using a micropipette and washed three times in GFF-filtered seawater before being placed, with as little water as possible, onto pre-combusted, pre-weighed GFF filters. To assure sufficient carbon and nitrogen content for the analyses, eggs were pooled into batches of 200, 300, 400 and 500 eggs per GFF filter. Filters with eggs were dried at 60°C for 3 days, stored in a desiccator and analyzed within 3 days at the Marine Biological Laboratory, USA, using a

FLASH 2000 NC Analyzer (ThermoFisher Scientific, Cambridge, UK). Blank filters to correct for contribution of filter and seawater were prepared at the same time using equivalent amount of water from the final washing step which was used as background correction. The measurements were repeated on 2 days with independently caught animals ($n = 5$) with replicates for each egg batch of 200–500 eggs, respectively.

Egg production rates of *M. leidyi* were measured during late August and early September 2010 in intermediate saline waters of northern Europe (position: Latitude 58.250°N , Longitude 11.447°E —Skagerrak, Gullmar Fjord, Sweden), representing high saline waters of the Baltic Sea region. Freshly caught, >50 mm sized animals (oral–aboral length, $n = 5$) were individually incubated in 7.5-L GFF-filtered seawater at ambient salinity (22.5) and temperature (16.5°C) following natural light conditions. After 24 h of incubation, *M. leidyi* were removed, total and oral–aboral lengths measured and eggs concentrated via reverse filtration. Eggs were preserved in acidified Lugol solution at a final concentration of 2% for later enumeration under a dissecting microscope. To calculate specific egg production (SEP), the regression from total length (TL) to dry weight (DW) from Baker (Baker, 1973), as cited in Kremer *et al.* (Kremer *et al.*, 1986) was used (i) and the DW to carbon regression based on analyses of Table I in Kremer *et al.* (Kremer *et al.*, 1986) leading to regression (ii) with the following regression parameters ($F_{1,7} = 1698$, $P < 0.0001$, $R^2 = 0.997$, $n = 8$).

$$\text{Dry weight (mg)} = 0.038 \times \text{total length (mm)}^{2.42} \quad (1)$$

$$\begin{aligned} \text{Mnemiopsis carbon (mg)} \\ = 0.0018 \times \text{DW (mg)}^{1.318} \end{aligned} \quad (2)$$

Table I: Mnemiopsis leidyi (n = 5) reproduction rates in northern Europe (August/September 2010 during two sampling events) at in situ salinity (22.5) and temperature (16.5°C), with highest egg production ($11\,232 \text{ eggs day}^{-1}$, 78 mm total length) recorded in northern Europe so far

	Maximum	Minimum	Average	SD
Total length (mm)	78	70	73.8	3.5
Oral–aboral length (mm)	57	51	54.3	2.5
Eggs ($\text{ind}^{-1} \text{ day}^{-1}$)	11 232	6432	8432	1884
SEP	10.4	7	8.4%	1.4%

Carbon specific egg production (SEP) is presented based on given length to carbon conversions (see text) and egg carbon of $0.22 \mu\text{g C egg}^{-1}$.

Direct measurement of early egg cleavage stages shows that the carbon and nitrogen content is $0.22 \pm 0.02 \mu\text{g C egg}^{-1}$ and $0.07 \pm 0.01 \mu\text{g N egg}^{-1}$, respectively (Fig. 1). The average *M. leidyi* egg size is $503 \pm 58 \mu\text{m}$ ($n = 25$), similar to egg sizes observed in invaded northern Europe of $565 \pm 66 \mu\text{m}$ (Jaspers *et al.*, 2013). Early cleavage stages are shown in Fig. 2. Largest sized animals found during August/September 2010 were 70–78 mm in TL, with an average reproduction rate of $8432 \pm 1884 \text{ eggs ind}^{-1} \text{ day}^{-1}$. The highest egg production rate of $11\,232 \text{ eggs day}^{-1}$ was attained by the largest sized animal (Table I).

Calculation of carbon SEP shows that ca. 8.5% day^{-1} of the *M. leidyi* body carbon is channeled into reproduction (Table I).

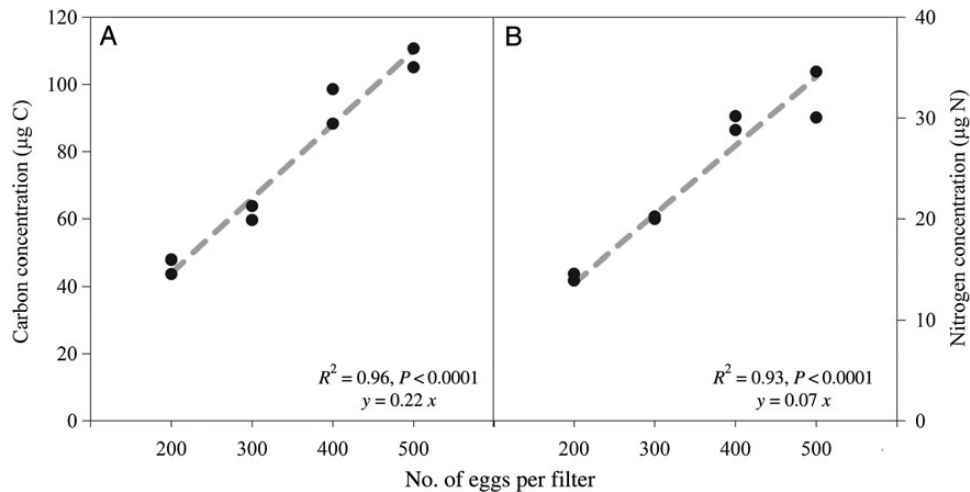


Fig. 1. Carbon and nitrogen content of *Mnemiopsis leidyi* eggs. The average is $0.22 \pm 0.016 \mu\text{g C egg}^{-1}$ and $0.07 \pm 0.005 \mu\text{g N egg}^{-1}$, respectively.

We present the first direct carbon and nitrogen measurements of *M. leidyi* eggs. Previous studies have estimated carbon from extrapolation of larval carbon measurements or DW to carbon conversions of larvae (e.g. Reeve *et al.*, 1978, 1989; Anninsky *et al.*, 2007). Since no direct measurements of eggs are available, estimates of carbon contents used for carbon and energy budgets of *M. leidyi* vary by a factor of 21. The only direct carbon measurement of ctenophore eggs available is $0.56 \mu\text{g C egg}^{-1}$ for 200 μm larger *Bolinopsis mikado* eggs (Kasuya *et al.*, 2008). *Mnemiopsis leidyi* eggs have 37% of the volume of *B. mikado* eggs; however, the volume-specific carbon and nitrogen concentrations are similar with 1 and 1.2 times of the *B. mikado* carbon and nitrogen content, respectively. The commonly used carbon value for *M. leidyi* of $0.1 \mu\text{g C egg}^{-1}$ (Reeve *et al.*, 1989) is thus a factor 2.2 less than expected if compared with the measured carbon content of *B. mikado* eggs (Kasuya *et al.*, 2008). Reeve *et al.* (Reeve *et al.*, 1989) estimated the carbon content from the assumption that the DW of eggs is $0.5 \mu\text{g}$ and used extrapolations of carbon measurements of $>1.1\text{-mm}$ -sized larvae to estimate egg carbon using a carbon ratio to DW of 20%. The lowest carbon content used for *M. leidyi* eggs is based on *Pleurobrachia* carbon and nitrogen measurements of 3.28 ± 0.35 and $0.87 \pm 0.09\%$ (\pm SD) of DW, assuming a *M. leidyi* DW of $0.35 \mu\text{g egg}^{-1}$ (Reeve *et al.*, 1978), thus, leading to an estimated carbon and nitrogen content per *M. leidyi* egg of $0.012 \mu\text{g C egg}^{-1}$ and $0.003 \mu\text{g N egg}^{-1}$. This is $\sim 5\%$ of the C and N content measured directly in this study. Our measured carbon content of eggs is similar to direct carbon measurements of $0.26 \mu\text{g C}$ for 500 μm *M. leidyi* larvae from NE USA (Sullivan and Gifford, 2004). In an

ecological perspective, *M. leidyi* eggs have the same nutritional value and comparable size range as, e.g. copepod nauplii, echinoderm larvae, gastropod veligers and bivalve larvae (Martinussen and Båmstedt, 1995) and might therefore be an important food source for, e.g. pelagic filter feeders. Therefore, predation could contribute to high mortality rates of *M. leidyi* eggs observed in intermediate saline waters of northern Europe (Jaspers *et al.*, 2013). However, predator prey investigations are necessary to enlighten direct interactions.

The carbon : nitrogen ratio for eggs measured in this study is 3.1, while the ratio for a large range of *M. leidyi* size classes is consistently ~ 4 (Kremer, 1976a). This indicates that although the carbon per unit weight of *M. leidyi* changes with size, hence throughout its life (Reeve *et al.*, 1989), the carbon-to-nitrogen ratio remains constant apart from the egg phase, where the C : N ratio is lower.

Due to the previously underestimated egg carbon concentrations of *M. leidyi*, egg production has so far been suggested to be a small and negligible fraction of the daily carbon demand (Kremer, 1976b, 1982; Reeve *et al.*, 1989). Even though several thousand eggs may be produced over a few days, they have been estimated to represent $<2\%$ of the carbon biomass of the ctenophores per day (Kremer, 1976b; Reeve *et al.*, 1989), which is less than one-third of the respiratory carbon demand (Kremer, 1982). We show that large sized animals produce up to $11\,232 \text{ eggs ind}^{-1} \text{ day}^{-1}$ in invaded northern European waters, which is nearly four times more than previously shown for northern Europe (Javidpour *et al.*, 2009) and in the same range as for the Black Sea and other native habitats (Baker and Reeve, 1974; Kremer, 1976a; Graham *et al.*, 2009). Therefore, SEP in



Fig. 2. Pictures of *Mnemiopsis leidyi* eggs ($503 \pm 58 \mu\text{m}$) of different, early cleavage stages including one late developmental stage (the top image in the sequence) with a fully developed larvae ($300 \mu\text{m}$) inside the egg shell. Egg sizes have a similar size range in native and invaded, northern European populations ranging between 440 and 625 and 480 and 630 μm diameter, respectively.

northern Europe for largest sized animals is around $7\text{--}10\%$ day^{-1} of the body carbon. This is four times higher than previously documented, due to the underestimation of

carbon concentrations of *M. leidyi* eggs. This demonstrates that egg production should be taken into account in energy and carbon budgets of *M. leidyi* in native and invaded habitats.

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