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Reproduction rates under variable food conditions and starvation in *Mnemiopsis leidyi*: significance for the invasion success of a ctenophore

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The ctenophore *Mnemiopsis leidyi* is characterized by high growth rates and a large reproductive capacity. However, reproductive dynamics are not yet well understood. Here, we present laboratory data on food-dependent egg production in *M. leidyi* and egg hatching time and success. Further, we report on the reproduction of laboratory-reared and field-caught animals during starvation. Our results show that the half-saturation zooplankton prey concentration for egg production is reached at food levels of 12–23 μgC L^{-1}, which is below the average summer food concentration encountered in invaded areas of northern Europe. Furthermore, starved animals continue to produce eggs for up to 12 days after cessation of feeding with high overall hatching success of 65–90%. These life history traits allow *M. leidyi* to thrive and reproduce in environments with varying food conditions and give it a competitive advantage under unfavourable conditions. This may explain why recurrent population blooms are observed and sustained in localized areas in invaded northern Europe, where water exchange is limited and zooplankton food resources are quickly depleted by *M. leidyi*. We suggest that these reproductive life history traits are key to its invasion success.

KEYWORDS: ctenophore; hatching success; egg production; self-fertilization

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INTRODUCTION

The rate of marine biological invasions is rising due to increased globalization and ship-traffic activity (Carlton and Geller, 1993; Molnar *et al.*, 2008) and combined effects of biological invasions and global climate change have been highlighted as severe stressors to marine biodiversity (Stachowicz *et al.*, 2002; Butchart *et al.*, 2010; Sorte *et al.*, 2010).

The processes determining a successful invasion are complex, but generally invasive species are characterized by tolerating a broad set of environmental and anthropogenic stressors (Crooks *et al.*, 2011; Lenz *et al.*, 2011). In addition, the success of an invader will depend on its life history traits, the recipient ecosystem and the species composition (Facon *et al.*, 2006). Intrinsic attributes such as fast growth, high reproduction rates (r-strategists) and phenotypic plasticity have been shown to be characteristics of competitive invaders, especially under circumstances where natural predators are lacking or the ecological niche of the invader is not occupied (Sax and Brown, 2000; Facon *et al.*, 2006; Sorte *et al.*, 2010). If combined with asexual reproduction or self-fertilizing hermaphroditism, an invader has an additional advantage by offsetting the Allee effect, which may otherwise limit sexually reproducing species during early colonization due to problems finding a mate (Tobin *et al.*, 2011).

The ctenophore *Mnemiopsis leidyi*, native to the east coast of the American Continent, is an example of a successful invasive species which has been present in European waters since the 1980s (Purcell *et al.*, 2001; Faasse and Bayha, 2006; Costello *et al.*, 2012). *Mnemiopsis leidyi* shares many of the above outlined characteristics of a potent invasive species with, for example, high reproduction rates of >11 000 eggs ind^{-1} day^{-1} (Baker and Reeve, 1974; Kremer, 1976; Jaspers *et al.*, 2015). Its reproduction potential along with simultaneous hermaphroditism seem to be key to understanding its invasion dynamics, however detailed knowledge about food-dependent egg production rates, hatching success and capability to withstand starvation are lacking. Laboratory investigations from native habitats have suggested that egg production is highly dependent on food concentration at high temperatures (26°C), with somatic growth being favoured over reproduction at low food densities <60 μgC L^{-1}) (Reeve *et al.*, 1989). In contradiction to this, dense ctenophore blooms of up to 800 ind m^{-3}, with active recruitment, are commonly observed and maintained in eutrophic, semi-enclosed systems of northern Europe, where the food resources are quickly depleted due to the high grazing pressure exhibited by *M. leidyi* (Riisgård *et al.*, 2007, 2010, 2012a, b; Javidpour *et al.*, 2009). Mechanisms behind this have not been examined. One hypothesis is that *M. leidyi* can switch from "income" to "capital" breeding. The ability to change energy allocation from (i) a direct utilization of concurrent food intake to reproduction to (ii) a strategy, where reserves are used to maintain egg production. A shift between those reproductive strategies, as described for Arctic copepod populations (Varpe *et al.*, 2009), might allow *M. leidyi* to maintain high reproduction rates despite fast changing food conditions. In combination with high feeding rates (Colin *et al.*, 2010), this would enable *M. leidyi* to efficiently utilize short-lived or local food patches. We test this hypothesis by examining the effect of food concentration on reproduction rates in *M. leidyi* in the laboratory, including effects of starvation on reproduction rates and size development in laboratory-reared as well as wild animals. Furthermore, for the first time, quantitative data on hatching time and hatching success are presented.

METHOD

Food-dependent egg production

Food-dependent egg production in laboratory-cultured *M. leidyi* was measured in a new laboratory cohort, spawned in early August 2010 at the Sven Lovén Centre for Marine Sciences, Kristineberg, Sweden. Animals were raised on *ad libitum* food consisting of the copepod *Acartia tonsa* and kept at 19 ± 0.5°C and a salinity of 33. *Acartia tonsa* carbon content was estimated from measurements of their lengths, based on specimens preserved with 2% acidified Lugol and length-carbon relations (Berggreen *et al.*, 1988) accounting for shrinkage (Jaspers and Carstensen, 2009). Egg production and clearance rates of individually kept *M. leidyi* ($n = 4-5$ per food concentration) were measured in 20-L containers in the dark over 24 h. Incubations were made with two size classes of *M. leidyi* (16.4 ± 2.7 and 21.4 ± 2.7 mm) to differing prey concentrations (μgC L^{-1}) of 100 ($n = 5$), 84 ($n = 4$), 60 ($n = 4$), 30 ($n = 5$) and 0 ($n = 6$) μgC L^{-1} for small and 78 ($n = 5$), 30 ($n = 4$) and 0 ($n = 5$) μgC L^{-1} for large animals, respectively. To ensure that animals had the same feeding history and to allow sufficient time to acclimatize to the respective food treatment, all animals were starved for 12–16 h and then acclimatized to the desired food concentration for 24 h. To check whether a 1-day acclimatization period was sufficient volume-specific daily egg production was compared for animals kept 2 and 3 days at the respective food condition during a pilot study. Egg production rates at Days 2 and 3 did not differ (paired *t*-test, $t = -0.7$, df $= 3$, $P = 0.5$), which indicates that steady state was reached at Day 2. Ctenophore oral aboral lengths remained similar during these 3 days. Therefore, all egg production rates presented here are based on a 1-day acclimatization period and egg production rates measured for the consecutive 24 h, hence on Day 2 of the experiment. Experiments always started in the morning (10–12 am) on Day 1. After 24 h and again after 48 h, the animals were transferred to new incubation containers with the same initial prey concentration as before. Eggs and prey were concentrated by reverse filtration at each transfer and at the end of the experiment were preserved with acidified Lugol's solution and enumerated within 3 days. Adult *M. leidyi*, submersed in a water-containing bowl, were photographed using a Nikon D60 with a macro lens and sizes were assessed from image analyses using the freeware ImageJ (Rasband, W. S., ImageJ). Clearance was measured from prey disappearance over time (see Jaspers *et al.*, 2011). Food control experiments without predators were performed simultaneously. Container volume and animal sizes were set to target a clearance rate of 30% of the container volume. Mean prey concentrations during the incubations were estimated assuming exponential decay over time (Frost, 1972). We described the dependency of egg production on prey concentration by Michaelis–Menten kinetics: $\mathrm{EPR} = \mathrm{EPR}_{\mathrm{max}} C (K_{\mathrm{m}} + C)^{-1}$, where EPR = egg production rate in eggs $(\mathrm{mL}\ M.\ leidyi)^{-1}\ \mathrm{day}^{-1}$, $\mathrm{EPR}_{\mathrm{max}}$ = maximal egg production rate, C = average prey concentration and K_{m} = half-saturation constant. Similarly, specific growth rates versus prey concentrations have been modelled for ciliates using Michaelis–Menten kinetics (Hansen, 1995).

To develop a length–body volume relation for *M. leidyi*, displacement volume was measured for differently sized *M. leidyi* ($n = 28$, oa length: 8–26 mm). Animals were blotted, to remove attached water, and transferred into 25–250 mL water-containing graduated cylinders to measure their body volume. The resulting relationship was ($R^2 = 0.89$, $F_{1,27} = 237.4$, $P < 0.0001$):

$$M.\ leidyi\ (\mathrm{mL}) = 0.0009 \times \mathrm{length}\ (\mathrm{mm})^{2.84} \qquad (1)$$

We used this relationship to convert egg production rates to volume-specific rates to facilitate comparisons between experiments.

Starvation

Three sets of starvation experiments were performed where size and egg production were monitored for laboratory-reared animals with known food history, as well as for field-collected animals (Table I). In the first experiment, laboratory animals ($n = 4$) were starved for 11 days after a 3-day food treatment with a mean *A. tonsa* prey concentration of 80 μgC L^{-1} with single individuals kept in 20-L containers each. During starvation, water was changed daily, though eggs were only enumerated for a 24-h period on Day 1–4 and on Day 11. Animal sizes were assessed from pictures as outlined above. The second experiment consisted of 50 *M. leidyi* larvae raised for 20 days post hatch on a copepod diet of *A. tonsa* at 100 μgC L^{-1}. Ten larvae were pooled in 0.7-L squared tissue culture flasks (Flacon®) containing GFF-filtered seawater and placed on a plankton wheel rotating at 0.9 revolutions min^{-1}. Their starvation was followed for 21 days. Sizes were assessed by measuring the first five larvae encountered in each flask under a dissecting microscope every second day. There was no significant difference between average sizes based on measuring the first five larvae encountered, compared with measuring all larvae ($t = 0.95$, df = 73, $P = 0.35$). The whole water volume was scanned for eggs. Eggs always consisted of early cleavage stages and average rates are presented as eggs ind^{-1} for 2 day^{-1}. Eggs were produced up to Day 4 without food. The third experiment used field-collected animals from two sampling events (August/September 2010) and followed individual egg production 24 h^{-1} in 7.5-L GFF-filtered seawater beakers in the laboratory, at different time intervals, for up to 12 days. Water was changed every day and egg counts (24 h^{-1}) and sizes were assessed (Fig. 3). Egg counts were always performed after reverse filtration and Lugol preservation. Handling controls showed a negligible egg loss of 0.56%. At the end of all three starvation experiments (Table I), mortality was calculated from the difference between initial and final number of *M. leidyi* present in the starvation treatments. Size and egg production during starvation were analysed using single and multiple linear regression models after log-transformation of the dependent variable using GraphPad Prism 4.0. Slopes and intercepts between regressions were analysed using co-variance analyses.

Hatching time and success

Mnemiopsis leidyi originated from Gullmar Fjord, Skagerrak (position: Latitude 58.250N, Longitude 11.447E) during August and early September 2010. Animals were collected in the evening (ca. 6 pm) and individually transferred to 4- or 7.5-L GFF-filtered seawater containers (salinity of 22.5, 16.5°C). Incubations were performed in a temperature-controlled room following natural temperature and light conditions, which simulated 9 h dark (10 pm–7 am) and 15 h light (7 am–10 pm). Experiments started at 7 pm and egg production of individually kept *M. leidyi* was followed over two consecutive 12-h periods. *Mnemiopsis leidyi* were transferred to new GFF-filtered seawater containers

Table I: Starvation experiments of northern European M. leidyi *populations from laboratory cultures (no. 1 and 2, reared with* Acartia tonsa*) and field-collected animals (no. 3)*

Experiment (no.)	Origin	Food history	*n*	Temperature (°C)	Age	Vol. (L)	Starv. (days)	Start (oa and tl, mm)	End (oa and tl, mm)	Egg prod. 4-day starv.
1: Laboratory	Skagerrak, Kristineberg, SE	80 μgC L^{-1} for 3 days	4	19 ± 0.5	ca. 5–7 weeks	20	1–11	22.7 ± 0.6 and 32.6 ± 2.7	15.3 ± 1.8 and 23.5 ± 2.5	7.5 ± 3%
2: Laboratory	Kattegat, Charlottenlund, Dk	100 μgC L^{-1} since hatch	50	19.5 ± 0.5	20 days	0.7	21	5.6 ± 1.3 and 8.6 ± 2.4	3.6 ± 0.8 and 5 ± 1.6	Av. 0.6 ± 0.7 eggs ind^{-1} 2 $days^{-1}$
3: Field	Skagerrak, Kristineberg, SE	Unknown	8	16.5	–	7.5	1–12	26.2 ± 5.5 and 40.1 ± 9.8	20.1 ± 4.8 and 29.6 ± 6.6	9.3 ± 9.4%

n, number of individuals; age, age of animals at start of incubation; volume, volume of incubation container; starv., duration of starvation period; start and end sizes [oral aboral (oa) and total (tl)]; mm ± SD); egg prod. 4-day starv., egg production rates as % of initial rate after 4 days of starvation.

after the initial 12 h at 7 am, when the light was turned on. This procedure was repeated at 7 pm. Eggs produced during the night (first 12-h interval) were compared with day time (second 12-h interval) production for 27 individuals from 4 different sampling events. At the same time, water from the bottom of the night egg production buckets (ca. 30 mL) from 19 animals on 3 sampling days (Table II) was transferred into two 50-mL Kautex bottles before the remaining water was concentrated and preserved. To estimate egg hatching time and success, the eggs in the Kautex bottles were preserved after 24 and 48 h using Lugol solution. Hatching success and time was assessed by the ratio of larvae to total number of eggs and larvae after 24 and 48 h.

RESULTS

Volume-specific egg production rates increased with food concentration in both small (16.4 ± 2.7 mm; $P = 0.0002$) and larger (21.4 ± 2.7 mm; $P = 0.006$) sized *M. leidyi* (Fig. 1). Estimated maximum rates for egg production were 25 and 51 eggs (mL *M. leidyi*)$^{-1}$ day^{-1} for small and larger sized animals, respectively, and half-saturation prey concentrations were 12 and 23 μgC L^{-1}, respectively.

Egg production following starvation remained unaffected during the initial 24 h and declined thereafter (Fig. 2). Generally, animals kept reproducing during the first 4 days, while reducing their body size. After 2 and 4 days of starvation, egg production rates were ca. 40 and 10% of the reproduction rates observed under fed conditions, respectively (Figs 2 and 3). However, no eggs were recorded after 11 days without food in laboratory animals of known food history. Oral aboral lengths were reduced by 33 ± 6% following 11 days without food, corresponding to a volume reduction of 67 ± 9% (Fig. 2). All animals were in good shape at the end of the experiment and no mortality was observed.

Similarly, a reduction in size, while maintaining reproduction, was observed for 20-day-old *M. leidyi* during a 21-day starvation period (Table I). Although *M. leidyi*

Table II: Hatching success after 24 and 48 h of Mnemiopsis leidyi *eggs from field-caught animals (*n *= 19, 16.5°C) in Skagerrak, Gullmar Fjord, Sweden*

Individuals, *n*	Date	Total eggs	Hatched 24 h (%)	Hatched 48 h (%)
5	10 September 2010	2049	26 ± 11.3	88 ± 5.0
9	8 September 2010	2873	20 ± 9.5	64 ± 18.1
5	6 September 2010	2051	29 ± 15.2	82 ± 6.0

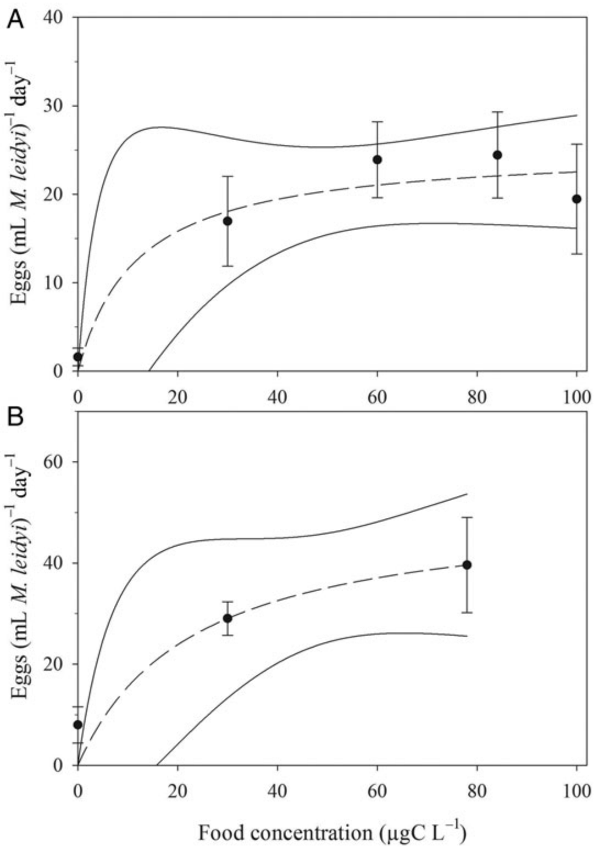

Fig. 1. *Mnemiopsis leidyi* volume-specific egg production rates as a function of prey concentration was described using Michaelis–Menten kinetics. Average reproduction rates at different food concentrations (±SE) are shown with 95% confidence bands for (**A**) small (16.4 ± 2.7 mm) and (**B**) large (21.4 ± 2.7 mm) sized *M. leidyi*. Half-saturation food density for egg production was reached at low food levels of 12 ($F_{1,23} = 19.44$, $P = 0.0002$) and 23 ($F_{1,13} = 10.8$, $P = 0.006$) μgC L^{-1} for small and large sized animals, respectively.

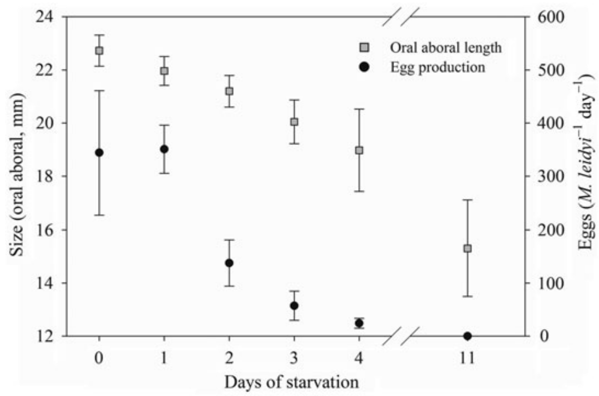

Fig. 2. *Mnemiopsis leidyi* size development (oral aboral, oa, mm) and egg production (EP, average ± SD) as a function of starvation time. Volume-specific egg production rates of un-starved and after 1 day of starvation do not show a significant difference ($t = 0.51$, df = 6, $P = 0.6283$). No egg production was observed after 11 days of starvation. Linear regression models on log-transformed size and egg production data show a significant decrease during starvation, leading to the following regressions: log (size) $= -0.016x + 1.353$ ($R^2 = 0.84$, $F_{1,22} = 116$, $P < 0.0001$) and log (EP) $= -0.39x + 2.92$ ($R^2 = 0.92$, $F_{1,14} = 170$, $P < 0.0001$) considering egg production data of Days 1–4 only.

were very small at the start of the experiment (8.6 ± 2.4 total length, mm), on average 0.6 eggs ind^{-1} 2 days^{-1} were produced after 2 and 4 days without food (Table I). Following 21 days of starvation, animals showed a significant reduction in total and oral aboral lengths of 42 and 35%, respectively (Table I, Fig. 3A). At the onset of starvation experiments, animals had just metamorphosed but they kept the adult morphology while shrinking to very small sizes. After 21 days, *M. leidyi* were exceptionally small with an oral aboral length of only 3.6 ± 0.8 mm and a total length of 5 ± 1.6 mm. Mortality rates were low, 10.5 ± 7% during the entire 21-day period.

Field-collected animals followed in the laboratory for 12 days in the absence of food showed similar responses as the cultured animals. First, reproduction rates after 2 and 4 days without food were similar to laboratory-reared animals with average reproduction rates of 43 and 9% of rates observed during the first 24 h (Fig. 3B). But after 11 and 12 days without food, 7 of 8 animals still reproduced, though at very low rates with up to 20 eggs ind^{-1} day^{-1} (av. 0.4%). Sizes in field-collected animals were reduced by 23 and 26% in oral aboral and total lengths after 12 days, respectively (Fig. 3A). No mortality was observed. The rates of decline in size, as well as egg production, during starvation were not significantly different between laboratory-reared and field-collected animals and could therefore be expressed by a single slope of −0.01 and −0.21 for reduction in size and egg production, respectively (Figs 2 and 3). This corresponds to a reduction in size of 15, 28 and 38% after 1, 2 and 3 weeks of starvation and a reduction in egg production rates of 62 and 86% after 2 and 4 days of starvation, respectively.

The investigation of spawning and hatching success based on field-caught *M. leidyi* revealed that >98% of the eggs were produced during the dark period (range: 97.8 ± 6–99.9 ± 0.2% for 33 942 eggs with significant difference between day and night production, $t = 5.38$, df = 52, $P < 0.0001$). Although we do not know exactly when spawning occurred, eggs primarily consisted of un-cleaved or first/second cleavage stages when investigated at the end of the dark period (at 7 am), suggesting that eggs were newly spawned and presumably not older than ca. 4 h.

Most of the eggs hatched within 24 (20–29%) or 48 h (64–88%) (Table II). Because the animals were incubated individually in 0.2-μm filtered seawater, this demonstrates successful self-fertilization in *M. leidyi*.

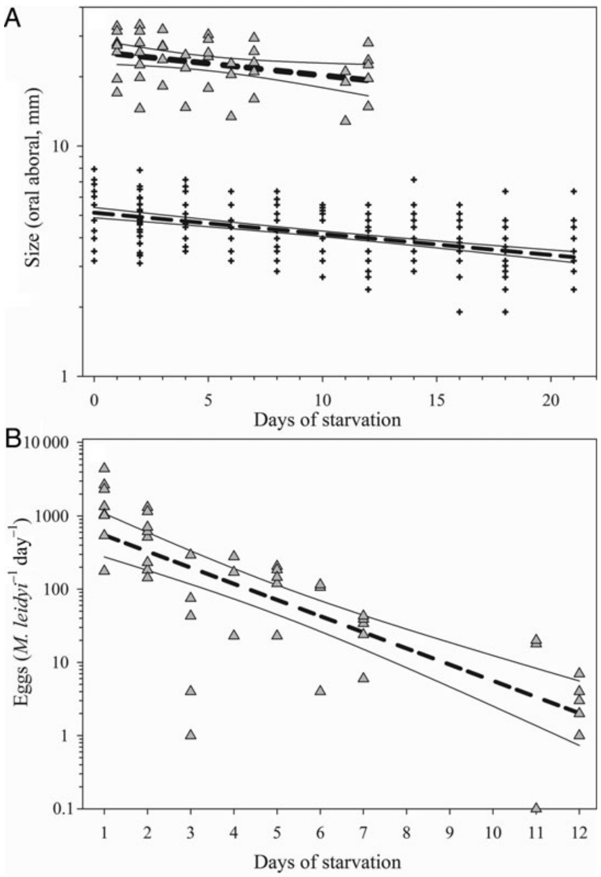

Fig. 3. *Mnemiopsis leidyi* (**A**) size development (size) and (**B**) change in egg production (EP) during starvation of field-caught (grey triangle, Exp. no. 3) and laboratory-reared (cross, Exp. no. 2) animals. Linear regression of log-transformed data lead to the regressions (dashed line; 95% confidence intervals, solid line) A: grey triangle, log (size) $= -0.01x + 1.41$ ($R^2 = 0.12$, $F_{1,43} = 5.93$, $P = 0.019$); cross, log (size) $= -0.009x + 0.71$ ($R^2 = 0.26$, $F_{1,273} = 93.66$, $P < 0.0001$). The slope of all three size regressions (Figs 2 and 3A) are not significantly different (co-variance analyses $F_{2,338} = 0.7$, $P = 0.48$) and can be given by one common slope of -0.01 but with differing intercepts ($F_{2,340} = 110.2$, $P < 0.001$). B: log (EP) $= -0.22x + 2.96$ ($R^2 = 0.60$, $F_{1,43} = 64.84$, $P < 0.0001$). The slopes of the two egg regressions (Figs. 2 and 3B) are not significantly different (co-variance analyses $F_{1,56} = 2.28$, $P = 0.14$) and can be summarized by one overall slope of -0.21. The intercepts are significantly different ($F_{1,57} = 7.81$, $P = 0.007$).

DISCUSSION

We present for the first time the numerical response of egg production rates in *M. leidyi* to prey concentration in laboratory-controlled experiments. Previous work suggests that egg production in *M. leidyi* is highly sensitive to food conditions and somatic growth has been shown to be favoured over reproduction at low food densities (<60 µgC L^{-1}) (Reeve *et al.*, 1989). From model predictions, food concentrations of 24 µgC L^{-1} were estimated to be sufficient to sustain an actively reproducing ctenophore population (Kremer and Reeve, 1989). This compares well to the half-saturation food concentrations for egg production found in the present study. Similar to our findings, Graham *et al.* (2009) suggested that high egg production rates were maintained in field-collected animals even though mesozooplankton biomass was low. They concluded that egg production is not as sensitive to contemporary food availability as previously thought (Graham *et al.*, 2009).

In the extended Baltic Sea area, including higher saline regions, average summer zooplankton concentrations are ca. 40–70 and 75–200 µgC L^{-1} in offshore and coastal regions, respectively, and are generally >10–20 µgC L^{-1} when covering the period from April to November (Zervoudaki *et al.*, 2009). This shows that zooplankton biomass is generally above the half-saturation food concentrations for *M. leidyi* egg production, suggesting that *M. leidyi* can actively recruit throughout the period when they occur in high saline areas of the Baltic Sea (Haraldsson *et al.*, 2013), such as the Kattegat and western Baltic Sea with salinities >18.

Similarly, based on *M. leidyi* growth rate response to increased food concentrations published by Reeve *et al.* (1978), we calculated the half-saturation concentration in their study to be 25.5 µgC L^{-1} (Reeve *et al.*, 1978). In line with this, re-analyses of growth rates of newly hatched *M. leidyi* larvae fed on different concentrations of *A. tonsa* (up to 200 µgC L^{-1}) showed a half-saturation concentration of 29.8 µgC L^{-1} (Ditlefsen, 2009, L. F. Møller, personal communication). Therefore, low half-saturation concentrations, found in this study, are widespread in *M. leidyi* for different size classes and environmental systems. This shows that *M. leidyi* is well adapted to sustain populations in environments with low food availability and can maintain active reproduction, although not reproducing at maximum rates. The half-saturation concentrations found in this study are one order of magnitude lower compared with the average half-saturation concentration of laboratory-controlled zooplankton, ranging from heterotrophic nanoflagellates to crustaceans (Hansen *et al.*, 1997), which additionally suggests that *M. leidyi* has a competitive advantage under low food conditions.

Reeve *et al.* (Reeve *et al.*, 1989) observed that no eggs were produced after 2–4 days without food at 26°C. In the present study, at 7°C lower temperatures, we found that short-term starvation for up to 24 h has no effect on reproduction rates compared with fed conditions and egg production was still 40% of un-starved conditions after 2 days of starvation. Furthermore, we found that animals shrink while reproducing under short-term starvation, which suggests that *M. leidyi* may temporarily switch from an income to a capital breeding strategy when food becomes unavailable. This means that adult tissue and reserves are used to overcome short-term food shortage to maintain high egg production rates, which has similarly been described for other marine species e.g. Arctic copepods (Varpe *et al.*, 2009). Sacrificing adult tissue for sustaining a new generation can be regarded as a life history trait to thrive under variable food conditions (Lilley *et al.*, 2014) and to efficiently channel energy to an offspring population with a different prey size spectrum (Sullivan and Gifford, 2004).

While animals shrank under starvation, the overall body morphology remained constant, even though 21 days of starvation of small *M. leidyi* led to exceptionally small lobate animals. The observed sizes are much smaller than normally observed in nature (Haraldsson *et al.*, 2013) and suggest that animals cannot reverse metamorphosis to go back to the cydippid larvae stage. During 11–21 days of starvation mortality rates of *M. leidyi* were low, suggesting a significant capability to withstand starvation, where reduction in size is used to overcome periods of food shortage.

Hatching success in single parent incubations was high with 65–90% of the eggs being hatched within 48 h. Such a high hatching success confirms that *M. leidyi* is a self-fertilizing simultaneous hermaphrodite.

Applying these data to field observations, we can substantiate that *M. leidyi* has the potential to actively recruit in areas where food resources get quickly depleted such as observed in Limfjorden, Denmark (Riisgård *et al.*, 2007, 2012a, b). The change in *M. leidyi* size distribution indicates that animals continue active reproduction in Limfjorden even though the grazing pressure exhibited by the adult population is so high that zooplankton standing stocks are severely depleted (Riisgård *et al.*, 2012a).

CONCLUSIONS

High growth and reproductive rates make *M. leidyi* a successful invasive species. We have in addition demonstrated its ability to reproduce through self-fertilization and the capability to continue egg production even during periods of low food availability. These additional life history characteristics further explain its high invasion success. They also explain the occurrence of large population blooms that are maintained in localized areas where water exchange is limited and food resources get quickly depleted by the high grazing pressure exhibited by *M. leidyi*.

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