

# Experimental feeding rates of gelatinous predators *Aurelia aurita* and *Mnemiopsis leidyi* at low northern Baltic Sea salinity

Aino Hosia<sup>1)</sup>, Lena Granhag<sup>2)</sup>, Tarja Katajisto<sup>3)</sup> and Maiju Lehtiniemi<sup>3)</sup>

<sup>1)</sup> Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway (corresponding author's e-mail: [aino.hosia@imr.no](mailto:aino.hosia@imr.no))

<sup>2)</sup> Department of Marine Ecology-Kristineberg, University of Gothenburg, Kristineberg 566, SE-45078 Fiskebäckskil, Sweden

<sup>3)</sup> Finnish Environment Institute, Marine Research Centre, P.O. Box 140, FI-00251 Helsinki, Finland; and Tvärminne Zoological Station, J.A. Palménin tie 260, FI-10900 Hanko, Finland

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The effect of the northern Baltic Sea's low salinity on feeding rates of a native scyphozoan *Aurelia aurita* and a recent invader to southern Baltic Sea, ctenophore *Mnemiopsis leidyi*, was investigated experimentally. Incubations with *Acartia* spp. prey (4.19–25.16 indiv. l<sup>-1</sup>) were used to estimate clearance rates for both predators. *Mnemiopsis leidyi* digestion times were measured for several natural prey items. Wet weight (ww):length/diameter relationships as well as clearance rates ( $0.49 \pm 0.15 \text{ l g}_{\text{ww}}^{-1} \text{ h}^{-1}$  [mean  $\pm$  SE] for *M. leidyi* [mean oral–aboral length  $\pm$  SD =  $9.6 \pm 1.5$  mm]; and  $0.18 \pm 0.07 \text{ l g}_{\text{ww}}^{-1} \text{ h}^{-1}$  [mean  $\pm$  SE] for *A. aurita* [mean bell diameter  $\pm$  SD =  $37.3 \pm 6.9$  mm]) and digestion times at salinity 5.7 were within the ranges reported from higher salinities. These preliminary results suggest that the low salinity does not significantly depress the feeding rates or potential predatory impact of these gelatinous predators.

## Introduction

The Baltic Sea is a semi-enclosed, brackish, estuarine system defined by a strong surface salinity gradient from up to 25 in the Danish straits to almost 0 in the northernmost reaches of the Gulf of Bothnia (Leppäranta and Myrberg 2009). The surface salinity of the northern Baltic Sea (i.e. northern Baltic Proper and north thereof) is generally below 8, and thus falls within the brackish-water salinity range with minimum diversity (Remane 1934). In addition to low salinity, winters are cold, with frequent ice cover (Leppäranta and Myrberg 2009).

The only native macroplanktonic gelatinous predator occurring in this relatively hostile environment is the scyphozoan *Aurelia aurita*, which is observed all the way to the Gulf of Bothnia (Finnish Environment Institute unpubl. data). *Aurelia aurita* polyps and ephyrae are found in the southwestern Finnish archipelago (Wikström 1932, Palmén 1953). Late summer and autumn occurrences of *A. aurita* are a known northern Baltic phenomenon (Wikström 1932, Segerstråle 1951, 1952), but to what extent these autumnal congregations result from local reproduction or advection from further south is not documented, and may alter with changes in salinity

(Segerstråle 1951, 1952). The recently reidentified population of small *Mertensia ovum* ctenophores (Gorokhova et al. 2009, Gorokhova and Lehtiniemi 2010) apparently represents the only other gelatinous predator permanently established in the northern Baltic Sea. Further south in the Baltic Sea, both salinity and gelatinous zooplankton diversity are higher (Kramp 1937, Barz et al. 2006, Hansson 2006), and the fauna also includes a notorious recent invader, ctenophore *Mnemiopsis leidyi* (Hansson 2006, Javidpour et al. 2006, Haslob et al. 2007, Schaber et al. 2011).

*Aurelia aurita* and *M. leidyi* are both common, widely spread and extensively studied neritic gelatinous predators that show a wide tolerance of environmental conditions and plasticity in their life history traits (Lucas 2001, Purcell et al. 2001a). Both species can, when abundant, exert top-down control on mesozooplankton (Olesen 1995, Shiganova and Bulgakova 2000, Purcell et al. 2001a) and induce trophic cascades (Schneider and Behrends 1998, Roohi et al. 2010). While for example prey type and temperature are known to have a significant effect on the observed clearance rates of gelatinous zooplankton (e.g. Møller and Riisgård 2007), little is known on the potential effects of salinity (but see Båmstedt et al. 1999). We present the first experimental results on the clearance rates of *A. aurita* and *M. leidyi* feeding on *Acartia* spp. copepods at low (< 6) northern Baltic Sea salinity. Digestion times for *M. leidyi* feeding on a mix of local prey were also measured. The feeding rates observed at low salinity were compared with rates published in literature.

## Material and methods

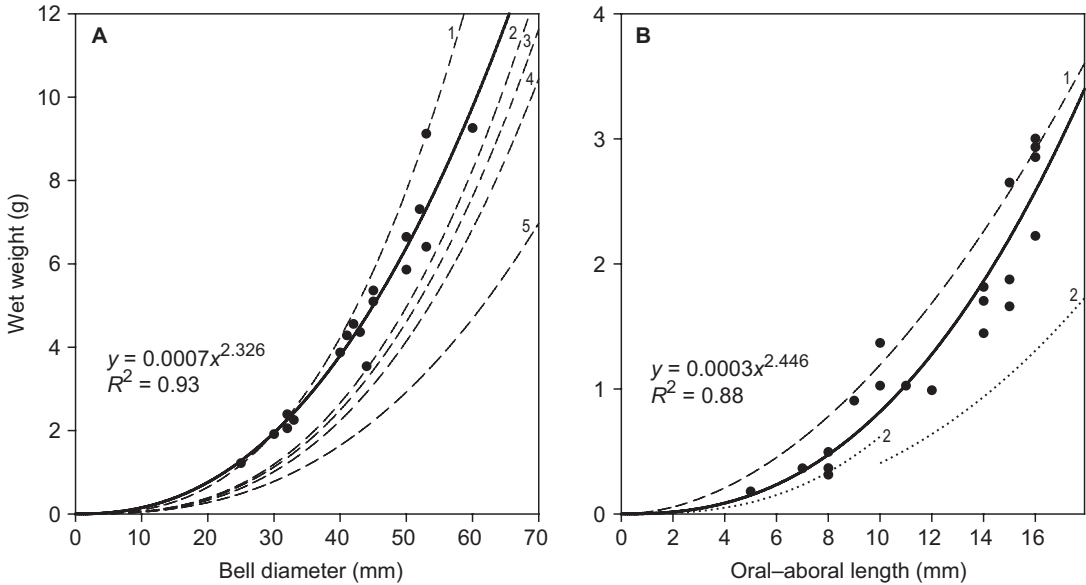
Experiments were conducted in September 2010 at the Tvärminne Zoological Station (University of Helsinki), southwestern Finland, in conjunction with a mesocosm workshop on the cascading effects of gelatinous predators on the pelagic community of the northern Baltic Sea (O. Setälä unpubl. data). Experimental water with a salinity of 5.7 was collected from Tvärminne Storfjärd and inversely filtered through a 90  $\mu\text{m}$  net. The same water was also used in the holding contain-

ers. All experiments were conducted at salinity 5.7 and 17 °C.

*Acartia* spp. (*A. biflosa* and *A. tonsa*) copepods, the dominant mesozooplankton species at the time, were collected from the upper 20 m at Tvärminne Storfjärd with a 200  $\mu\text{m}$  net and subsequently kept in a holding container with gentle bubbling. Healthy adults and large copepodites for the experiments were individually pipetted out under a stereomicroscope. *Aurelia aurita* were individually collected with buckets from the surface near the Granbusken island (Tvärminne archipelago). Many individuals with planula larvae were observed. *Mnemiopsis leidyi* were from a culture kept at the Sven Lovén Centre for Marine Sciences, Kristineberg, Sweden (courtesy of L. F. Møller). Over a period of ca. two weeks, ctenophores were gradually acclimated from salinity 32 to salinity 6 with high survival (L. F. Møller pers. comm.). Prior to the experiments, animals in the holding containers were sparsely fed with natural zooplankton. New individuals were used for all experiments.

The relationships between wet weight (ww) and size [oral–aboral length ( $L_{\text{OA}}$ ) for *M. leidyi*, and bell diameter (BD) for *A. aurita*] were calculated for both predator species and the resulting regressions (Fig. 1) were used to estimate the wet weight of the predators used in the incubations. Wet weight was used since it, unlike various measures of dry weight, is not strongly affected by the ambient salinity (Hirst and Lucas 1998).

For clearance rate incubations, single *A. aurita* ( $37.3 \pm 6.9$  mm bell diameter, mean  $\pm$  SD) or *M. leidyi* (mean  $\pm$  SD:  $L_{\text{OA}} = 9.6 \pm 1.5$  mm) were placed in 2.385 l Nalgene incubation bottles containing GF/F filtered experimental water  $\sim$ 1 h prior to the start of incubation, to acclimate them and empty their guts. Incubations were started by adding a known number of *Acartia* spp. into the bottles. The bottles were then immediately topped up and sealed to minimize air bubbles. Incubations took place in the dark, on a plankton wheel with a speed of 0.5 rpm. Incubations were stopped by removing the predator, after which remaining prey were fixed with acid lugol for later counting. Incubation times (mean  $\pm$  SD) were  $0.88 \pm 0.11$  h for *A. aurita* and  $1.76 \pm 0.42$  h for *M. leidyi*. The individual clearance rate  $F$  ( $\text{l indiv.}^{-1} \text{h}^{-1}$ ) was calculated as



**Fig. 1.** (A) Wet weight (ww) versus bell diameter (BD) of *Aurelia aurita* ( $n = 18$ ). Dots, solid lines and the equation from our data; dashed lines are relationships from: (1) Hirst and Lucas (1998), Southampton Water, salinity 32.4; (2) Olesen (1994), Kertinge Nor, salinity 18 according to Hirst and Lucas (1998); (3) Hirst and Lucas (1998), Horsea Lake, salinity ~21; (4) Schneider (1988), Kiel Bay; (5) Mutlu (2001), Black Sea. (B) Wet weight (ww) versus oral-aboral length ( $L_{OA}$ ) of *Mnemiopsis leidyi* ( $n = 20$ ). Dots, solid lines and the equation from our data; dashed and dotted lines are relationships from: (1) L. F. Møller and P. Tiselius (unpubl. data), Gullmarsfjord, salinity ~31; and (2) Finenko *et al.* (2003), Sevastopol Bay and adjacent waters salinity ~18; respectively.

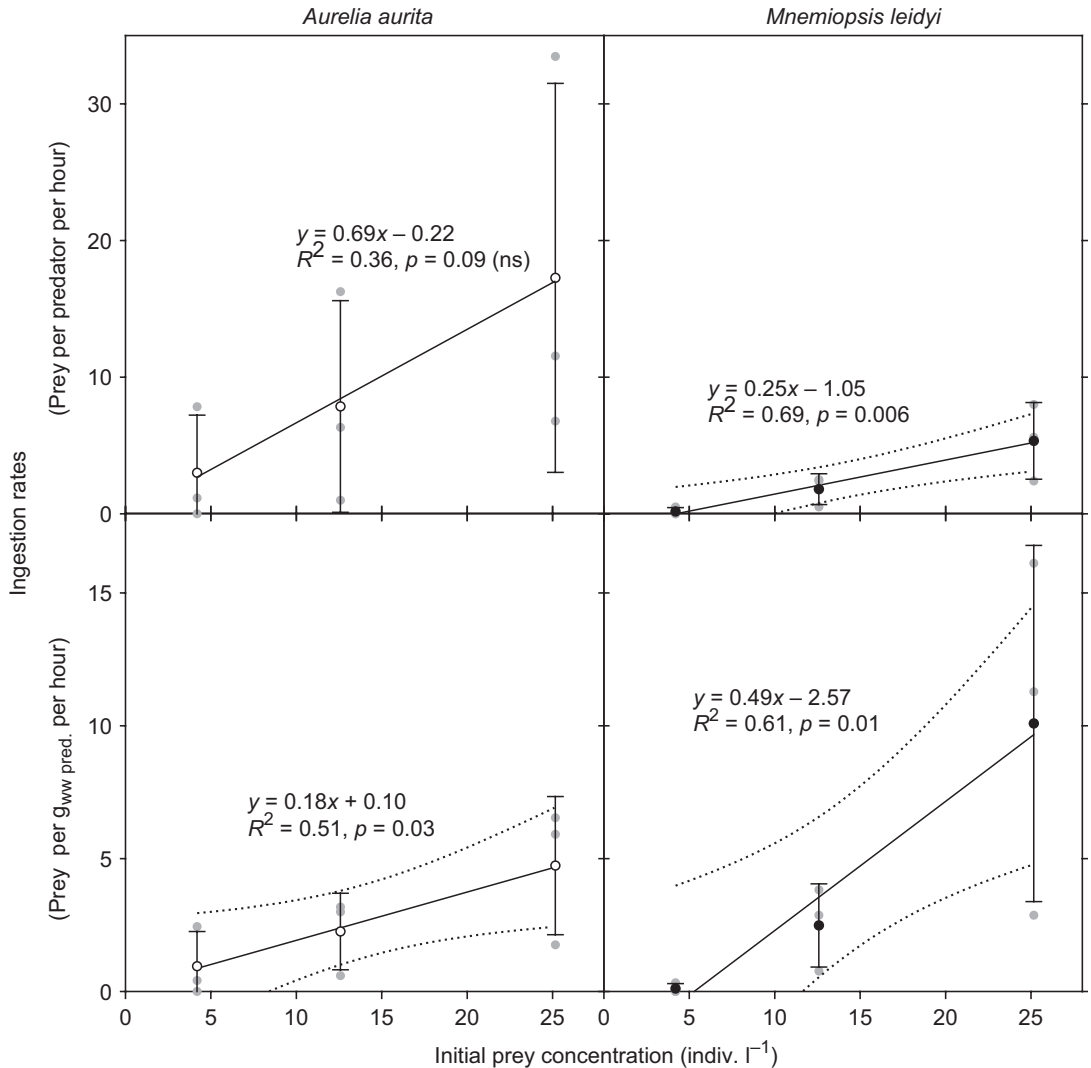
$$F = \frac{V_b}{t \times n_{pred}} \ln \left( \frac{n_{start}}{n_{end}} \right) \quad (1)$$

where  $V_b$  is the bottle volume (l),  $t$  is the incubation time (hours),  $n_{pred}$  is the number of predators per incubation (1 in our experiments), and  $n_{start}$  and  $n_{end}$  are the number of prey at the beginning and the end of the incubation. Incubations were conducted with 10, 30 and 60 prey individuals per bottle, yielding prey concentrations of 4.19, 12.58 and 25.16 indiv.  $l^{-1}$ , respectively. These prey concentrations reflect the autumnal *in situ* values; the long-term average of *Acartia* spp. adult and copepodite density in Tvärminne Storfjärd in September is ~8–11 indiv.  $l^{-1}$  (Viitasalo *et al.* 1995). Three replicates were run for each predator/prey concentration combination. The fraction of prey consumed during the incubations (mean  $\pm$  SD) was  $0.10 \pm 0.08$  for *M. leidyi* and  $0.24 \pm 0.21$  for *A. aurita*. Control incubations without predators indicated a 100% return rate of *Acartia* spp. prey.

The rates at which *A. aurita* and *M. leidyi* ingested *Acartia* spp. at different prey concentra-

tions were examined both for individual predators and relative to predator wet weight (Fig. 2). No saturation was observed at the used prey concentrations (4.19–25.16 indiv.  $l^{-1}$ ) and a linear regression of ingestion rate on prey concentration was, therefore, used to estimate the clearance rates (Fig. 2) (Holling 1959). Curve fitting and associated statistical testing for ww:BD and ww: $L_{OA}$  relationships as well as feeding rates was done with SigmaPlot 11.0.

We measured the digestion times for several potential *M. leidyi* prey species abundant in the Tvärminne waters. Ctenophores used in the digestion experiments were initially starved overnight in storage aquaria to empty their guts. Each ctenophore was then allowed to feed for one to five minutes in a transparent one-liter bucket with GF/F filtered seawater and a mixture of natural zooplankton prey. A ctenophore was thereafter moved to a small beaker with filtered seawater and the initial number of prey in its gut was noted. Digestion inside the transparent gut of the living animal was followed visually with



**Fig. 2.** Ingestion rates of *Aurelia aurita* and *Mnemiopsis leidyi* feeding on *Acartia* spp. adults and copepodites at 5.7 salinity. Solid lines show linear regressions based on the original data points, indicated by the grey dots. Dotted lines indicate 95%CI for the statistically significant regressions. White and black dots with error bars show mean  $\pm$  SD at different initial prey concentrations. Note that despite the significance levels, linear regression is perhaps not the best fit for the *M. leidyi* data (see text for details).

readings every 10 minutes using a stereo microscope. Digestion time was defined as gut evacuation time from feeding start to the time when no observable prey items remained in the gut. All *M. leidyi* used were in the lobate stage (see Table 1 for sizes).

Utmost care was taken to prevent accidental introduction of *M. leidyi* to the Tvärminne waters. Marked equipment was used for experiments with *M. leidyi*, and all ctenophores, as well as water

that had been in contact with them or used for washing the marked equipment, was disposed of by absorbing in dry earth away from the shore.

## Results

The ww:BD, and ww: $L_{OA}$  relationships ( $y = 0.0007x^{2.326}$ ,  $r^2 = 0.93$ ; and  $y = 0.0003x^{2.446}$ ,  $r^2 = 0.88$ ; respectively) for both species were within

the range found at other locations and salinities (see Fig. 1). The clearance rate estimates (mean  $\pm$  SE) based on the linear regression of ingestion rates and prey concentrations from the experimental incubations were  $0.69 \pm 0.35$  l indiv.<sup>-1</sup> h<sup>-1</sup> ( $p = 0.09$ ) or  $0.18 \pm 0.07$  l g<sub>ww</sub><sup>-1</sup> h<sup>-1</sup> ( $p = 0.03$ ) for *A. aurita* and  $0.25 \pm 0.06$  l indiv.<sup>-1</sup> h<sup>-1</sup> ( $p = 0.006$ ) or  $0.49 \pm 0.15$  l g<sub>ww</sub><sup>-1</sup> h<sup>-1</sup> ( $p = 0.01$ ) for *M. leidyi* (Fig. 2 and Table 2).

As would be expected for a linear, Holling's type I functional response, the mean individual *A. aurita* clearance rates calculated with Eq. 1 did not change with increasing prey concentration (data not shown). However, the individual *M. leidyi* clearance rates seemed to increase with increasing prey concentration (Fig. 3), suggestive of early portions of a sigmoid, type III functional response (Holling 1959).

We found that digestion times measured in salinity 5.7 and 17 °C (Table 1) were of the same order of magnitude as digestion times recorded in higher salinities: in salinity 10–20 at 17 °C, adult *M. leidyi* ( $L_{OA} = 25$  mm) digest copepods (*Acartia tonsa*) in  $1.5 \pm 0.4$  h (Javidpour *et al.* 2009) and in salinity 32 at 20 °C, adult *M. leidyi* ( $L_{OA} = 10$ –18 mm) digest cladocerans (*Penilia avirostris*) in  $2.8 \pm 0.8$  h (Granhag *et al.* 2011). Larval *M. leidyi* in salinity 23–28 at 20 °C digest rotifers in  $0.17 \pm 0.13$  h (Sullivan 2010).

## Discussion

Comparing our results with experimentally determined clearance rates from the literature, reveals no obvious salinity effects on clearance rates of *Aurelia aurita* and *Mnemiopsis leidyi* — our clearance rates from salinity 5.7 are well within the range reported from higher salinities (Table 2). When comparing our clearance rate

results with those from literature (Table 2), we attempted to maximize comparability of the data by employing the following criteria for inclusion of studies:

1. Since clearance rates of gelatinous predators can differ according to prey type (Purcell 1997, Purcell *et al.* 2001a), we chose studies that used *Acartia* spp. as prey organisms. Nevertheless, this included several species, and differences in their size, behavior or activity could affect the observed clearance rates.
2. We included only studies that estimate clearance rates based on experimental incubations. However, exact setups and methods did vary and, hence, might have affected the resulting clearance rate estimates. Some of the experiments offered several types of prey simultaneously, while we only offered *Acartia* spp. adults and copepodites. Since the used prey concentrations were generally below saturation levels, we would not expect this to have a major effect on the clearance rates for the individual prey species.
3. Since clearance rates depend on predator size, with larger gelatinous predators clearing larger volumes of water (e.g. Kremer 1979, Olesen 1995, Graham and Kroutil 2001, Purcell 2009), we tried to choose studies which covered the approximate size range of our animals. When the compared studies provided equations for clearance rates with respect to size, these were used to calculate what the clearance rate would be for animals equal in size to ours (Table 2).

Despite the above criteria, the published experimentally-estimated clearance rates were found to vary with an order of magnitude

**Table 1.** *Mnemiopsis leidyi* digestion times (mean  $\pm$  SD) for various prey when feeding in salinity 5.7 and 17 °C.  $L_{OA}$  = oral–aboral length (mean  $\pm$  SD),  $n$  = number of replicates.

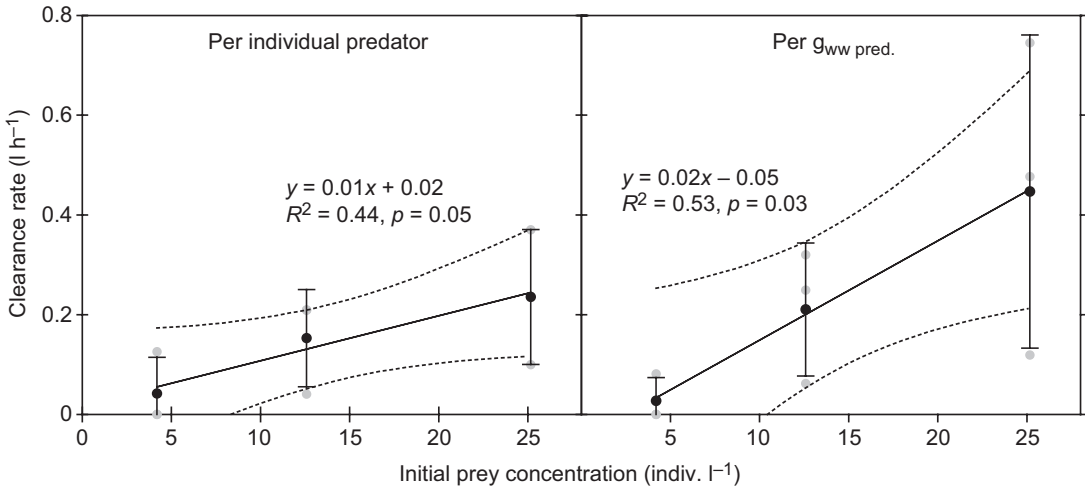
Prey	Prey length ( $\mu$ m)	Number of prey in gut	Digestion times (h)	$L_{OA}$ (mm)	$n$
Rotifers ( <i>Synchaeta</i> sp. & <i>Keratella</i> sp.)	100–200	30–100	$0.5 \pm 0.2$	$10.0 \pm 2.2$	5
Copepods ( <i>Acartia tonsa</i> & <i>A. bifilosa</i> )	~800	1–5	$0.6 \pm 0.2$	$9.8 \pm 2.2$	6
Cladocerans ( <i>Bosmina longispina</i> & <i>Evadne annonyx</i> )	600–800	2–11	$4.8 \pm 3.4$	$10.8 \pm 1.3$	8
Barnacle nauplii	~300	1–2	$0.8 \pm 0.6$	$11.0 \pm 1.0$	5

**Table 2.** Literature values of clearance rates for *Mnemiopsis leidyi* and *Aurelia aurita* feeding on *Acartia* spp. estimated in laboratory incubations. Results from this study are given as the linear regression coefficient  $\pm$  SE and the mean of the individual clearance rates. Where possible, equations and conversions from the paper in question were used to estimate the clearance for a predator equal in size to the average predator in this study. In addition, volume (V) to wet weight (ww) conversion  $ww = 1.017V - 0.122$  (Kremer and Nixon 1976) was used to estimate the clearance rate from Decker et al. (2004). For the studies which did not provide equations for calculation of clearance rates with respect to size, results for the closest predator size range in the study in question are given. Predator size is oral-aboral length for *M. leidyi* and bell diameter for *A. aurita*. Where experimental salinities were not specified, typical regional salinity is given.

Predator	Prey	Predator size (mm)	Salinity	Clearance rate (l indiv. <sup>-1</sup> h <sup>-1</sup> )	Container size (l)	Prey conc. (indiv. l <sup>-1</sup> )	Predators per container	Temp. (°C)	Location	Reference
<i>M. leidyi</i>	<i>A. biflosa</i> & <i>A. tonsa</i>	9.6 $\pm$ 1.5	5.7	0.25 $\pm$ 0.06; 0.14	2,385	5–30	1	17	N Baltic	this study
<i>M. leidyi</i>	<i>A. clausi</i> & <i>A. tonsa</i>	9.6*	6–10	0.06	5	100	5	21	Caspian Sea	Finenko et al. 2006
<i>M. leidyi</i>	primarily <i>A. tonsa</i>	9.6*	10–14	0.06 $\pm$ 0.01	22–95	22–95	12	~21–23	US east coast	Decker et al. 2004
<i>M. leidyi</i>	<i>Acartia tonsa</i>	11.6–12.7 $\pm$ 1.1–1.8	20	0.6 $\pm$ 0.4	60	3.3	~12	12.4	Denmark	Madsen and Riisgaard 2010
<i>A. aurita</i>	<i>A. biflosa</i> & <i>A. tonsa</i>	37.3 $\pm$ 6.9	5.7	0.69 $\pm$ 0.35; 0.90	2,385	5–30	1	17	N Baltic	this study
<i>A. aurita</i>	<i>Acartia tonsa</i>	37.3*	15–18	1.11	1.2	42 or 83	1 (to 30)	15	Denmark	Olesen 1995
<i>A. aurita</i>	<i>Acartia tonsa</i>	37.3*	20	0.61	70–85	5–110	5	15	Denmark	Møller and Riisgaard 2007
<i>A. aurita</i>	<i>Acartia tonsa</i>	28.1–32.8	20	1.1 $\pm$ 0.2	60	3.3	?	12.4	Denmark	Riisgaard and Madsen 2011

\* Clearance-rate values for predator size equal to our mean size extrapolated from equations given in the papers. Our *M. leidyi* mean size is covered by the length range examined by Finenko et al. (2006), and corresponds with the very lowest end of the size range included in Decker et al. 2004 according to conversions to wet weight. Our *A. aurita* mean size is covered by the medusa diameter ranges studied by Olesen (1995) and Møller and Riisgaard (2007).





**Fig. 3.** Clearance rate as a function of prey concentration for *Mnemiopsis leidyi* feeding on *Acartia* spp. adults and copepodites. Solid lines show linear regressions on the original data points, indicated by the grey dots. Black dots with error bars are mean  $\pm$  SD at different initial prey concentrations, dotted lines are 95% CIs.

(0.06 to 0.6 l indiv.<sup>-1</sup> h<sup>-1</sup>, Table 2). *Mnemiopsis leidyi* with the highest experimentally determined clearance rates (0.6  $\pm$  0.4 l indiv.<sup>-1</sup> h<sup>-1</sup> from salinity 20, Madsen and Riisgård 2010) were also the largest. Their average volume was roughly 1.65 ml, while the average volume of our ctenophores was  $\sim$ 0.89 ml [calculated from the  $w\text{w}:L_{\text{OA}}$  regression with the conversion  $w\text{w} = 1.01(\text{volume}) - 0.122$  (Kremer and Nixon 1976)]. Assuming that the relationship between clearance rates and volume within this size-range is approximately linear and applying a correction for the 1.85 times larger volume in Madsen and Riisgård (2010) would give an estimated clearance rate of 0.32 l indiv.<sup>-1</sup> h<sup>-1</sup> for a 0.89 ml ctenophore — a result much more comparable to our 0.25 l indiv.<sup>-1</sup> h<sup>-1</sup>. Even after this adjustment, the *M. leidyi* clearance rates from the present study and that from Madsen and Riisgård (2010) are 2–5 times higher than those measured by Finenko *et al.* (2006) and Decker *et al.* (2004). The *A. aurita* clearance rates from literature also vary, although to a lesser degree (Table 2). The smaller variation could be partly due to the much smaller geographic range and range of environmental parameters encompassed by the *A. aurita* studies included in the comparison (Table 2).

Temperature, container effects and nutritional state of the predators are all known to

affect clearance rates and could contribute to the observed variation in the experimentally estimated clearance rates. However, although *M. leidyi* metabolic rates are sensitive to temperature and tend to increase with it within the range included in our comparison (Kremer 1979, Purcell *et al.* 2001a), the highest rates we found in the literature were from the lowest temperature in the comparison (Table 2). For *A. aurita*, our experimental temperature (17 °C) was close to the regional optimum in northern-temperate waters (Olesen 1995, Møller and Riisgård 2007). All *A. aurita* studies compared stem from this region, but no connection is apparent between clearance rates and experimental temperature.

Clearance rates of gelatinous predators are reduced in small containers and a minimum container-volume/predator-volume ratio of 2500:1 is recommended for experiments (Purcell 2009). Our containers complied with this recommendation for *M. leidyi*; an average ctenophore volume of 0.89 ml yields a ratio of 2680:1. In the case of *A. aurita*, we could be underestimating clearance rates due to container effects. The average wet-weight estimate for *A. aurita* in our experiments was 3.44 g. Assuming a 1:1 wet-weight/displacement-volume ratio, this would give an estimated container-volume/jellyfish-volume ratio of 693:1. Ours is not the only study in the comparison to possibly suffer from container effects. Olesen

(1995) used 1.2-l containers for the clearance rate incubations, which resulted in the highest estimates in our comparison (Table 2).

It should be noted that when the linear regression model, or type I functional response, is applied to the data from the *M. leidy* incubations, the intercepts are considerably below zero, implying that this is perhaps not the best way to model the functional response at these prey concentrations. While *A. aurita* exhibited a straightforward type I functional response with a stable average individual clearance rate over the range of prey concentrations used in our incubations, individual *M. leidy* clearance rates showed a significant increase with prey density and seemed to approximate the early portions of a type III functional response (Figs. 2 and 3) (Holling 1959). This kind of a sigmoid functional response would be expected if higher prey density for some reason stimulated increased search behavior or, in this case, filtration activity by the predator (Hassell et al. 1977). If this were indeed the case for *M. leidy*, it would have consequences for its predatory impact at lower prey concentrations. However, we cannot rule out that our observations may be simply an artifact of small container volumes, short incubation times and few replicates.

While many gelatinous predators are able to maintain initially high clearance rates throughout a wide range of prey concentrations due to their large gut volume, sustained ingestion rates are ultimately limited by the time it takes to digest the prey (Hansson and Kiørboe 2006, Mazlum and Seyhan 2007). Starved *M. leidy* have initially high clearance rates, which level off after a few hours (Reeve et al. 1989). Our predators were starved prior to the relatively short incubations, thus longer incubations could have revealed lower, sustained clearance rates.

Digestion time of ctenophores varies with several factors including prey type, prey size, temperature, and amount of prey in the gut (Purcell 1997, Martinussen and Båmstedt 1999, 2001, Mazlum and Seyhan 2007). However, we did not find salinity to have a notable effect, giving us no reason to assume that the sustained clearance rates at low salinities would be markedly different to those from higher salinities.

The native species, *A. aurita*, seems to be able to both reproduce in the northern Baltic Sea and feed at rates comparable to those observed at higher salinities. Nevertheless, individuals of *A. aurita* from the northern Baltic Sea are likely to be occurring close to their distributional limits. It has been suggested that *A. aurita* has only extended its reproductive area to the northern parts of the Baltic during the last century, in conjunction with a trend of increasing salinity (Segerstråle 1952). While salinity differences in the range of 17.5–35 have been found to have little or no effect on *A. aurita* growth rate and efficiency (Båmstedt et al. 1999), it would be interesting to see how the growth efficiency and reproductive success of *A. aurita* from the much lower salinities of the northern Baltic compare.

*Mnemiopsis leidy* seems to be able to relatively quickly adapt to low salinities without negative effects on feeding rates. Digestive processes also seemed to be at least superficially unaffected by the low salinity. However, we did not observe reproduction at salinity 5.7 and 17 °C. While this may have been due to the relatively small size of our ctenophores, laboratory experiments have also confirmed strongly reduced reproduction at salinity 6 (Jaspers et al. 2011). Niche analyses based on present distribution of *M. leidy* suggest that it may be able to survive but not reproduce under northern Baltic salinity and temperature conditions (Lehtiniemi et al. 2012). It is feasible that even though the ctenophores are able to ingest and digest prey at normal rates, the combination of low ambient salinity and suboptimal temperatures imposes metabolic costs which prohibit allocation of energy to reproduction. *Mnemiopsis leidy* in the low salinity environments of the Caspian Sea (Finenko et al. 2006) and the Baltic (Javidpour et al. 2006) also tend to be smaller and have shorter lobes as compared with their conspecifics from higher salinities. These morphological differences, as well as the lower fecundity of the Caspian Sea *M. leidy*, may be due to low salinity (Finenko et al. 2006). Nevertheless, lower salinities and smaller size have not prevented *M. leidy* from decimating zooplankton prey populations in the Sea of Azov and the Caspian Sea (Shiganova and Bulgakova 2000, Roohi et al. 2010).



## Concluding remarks

Our results suggest that the feeding rates, and thus potential predatory impact, of *Aurelia aurita* and *Mnemiopsis leidyi* are not markedly affected by low salinity (< 6) of the northern Baltic Sea. This is, to our knowledge, the first study exploring the effect of such low salinity on the feeding rates of euryhaline gelatinous predators. The results should, however, be considered preliminary and interpreted cautiously due to the low number of replicates and large variance. Varying experimental setups and environmental conditions also hinder proper comparisons between studies from different salinities. Hence, more rigorous experiments with identical setups at different salinities would be needed to uncover possible subtle effects. The effect of low salinity on the reproductive success of the species is also of utmost importance for the potential ecological role of the gelatinous predators. Low salinity probably prevents successful *M. leidyi* reproduction and establishment in the northern Baltic Sea (Jaspers *et al.* 2011, Lehtiniemi *et al.* 2012), but experiments on the reproductive potential of the local *A. aurita* are lacking (but see Holst & Jarms 2010). *A. aurita* is a common member of the autumnal plankton community and could contribute to the natural zooplankton population decrease in autumn (e.g. Viitasalo *et al.* 1995). The Baltic Sea also suffers from several environmental issues (Vahtera *et al.* 2007) that have been indicated as potentially favoring jellyfish, including eutrophication (Arai 2001), deteriorated light conditions (Eiane *et al.* 1999) and low oxygen levels (Purcell *et al.* 2001b, Ekau *et al.* 2010). Nevertheless, the ecology and potential role of gelatinous zooplankton in the northern Baltic ecosystem remains virtually unstudied (but see Segerstråle 1951, Vuorinen 1987).

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## References

- Arai M.N. 2001. Pelagic coelenterates and eutrophication: a review. *Hydrobiologia* 451: 69–87.
- Barz K., Hinrichsen H.-H. & Hirche H.-J. 2006. Scyphozoa in the Bornholm Basin (central Baltic Sea) — the role of advection. *J. Mar. Syst.* 60: 167–176.
- Båmstedt U., Lane J. & Martinussen M.B. 1999. Bioenergetics of ephyra larvae of the scyphozoan jellyfish *Aurelia aurita* in relation to temperature and salinity. *Mar. Biol.* 135: 89–98.
- Decker M.B., Breitbart D.L. & Purcell J.E. 2004. Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. *Mar. Ecol. Prog. Ser.* 280: 163–172.
- Eiane K., Aksnes D.L., Bagoien E. & Kaartvedt S. 1999. Fish or jellies — a question of visibility? *Limnol. Oceanogr.* 44: 1352–1357.
- Ekau W., Auel H., Portner H.O. & Gilbert D. 2010. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences* 7: 1669–1699.
- Finenko G.A., Kideys A.E., Anninsky B.E., Shiganova T.A., Roohi A., Tabari M.R., Rostami H. & Bagheri S. 2006. Invasive ctenophore *Mnemiopsis leidyi* in the Caspian Sea: feeding, respiration, reproduction and predatory impact on the zooplankton community. *Mar. Ecol. Prog. Ser.* 314: 171–185.
- Gorokhova E. & Lehtiniemi M. 2010. Reconsidering evidence for *Mnemiopsis* invasion in European waters. *J. Plankton Res.* 32: 93–95.
- Gorokhova E., Lehtiniemi M., Viitasalo-Frösén S. & Haddock S.H.D. 2009. Molecular evidence for the occurrence of ctenophore *Mertensia ovum* in the northern Baltic Sea and implications for the status of the *Mnemiopsis leidyi* invasion. *Limnol. Oceanogr.* 54: 2025–2033.
- Graham W.M. & Kroutil R.M. 2001. Size-based prey selectivity and dietary shifts in the jellyfish, *Aurelia aurita*. *J. Plankton Res.* 23: 67–73.
- Granhag L., Møller L.F. & Hansson L.J. 2011. Size-specific clearance rates of the ctenophore *Mnemiopsis leidyi* based on *in situ* gut content analyses. *J. Plankton Res.* 33: 1043–1052.
- Hansson H.G. 2006. Ctenophores of the Baltic and adjacent seas — the invader *Mnemiopsis* is here! *Aquat. Inv.* 1: 295–298.
- Hansson L.J. & Kiørboe T. 2006. Effects of large gut volume in gelatinous zooplankton: ingestion rate, bolus production and food patch utilization by the jellyfish *Sarsia tubulosa*. *J. Plankton Res.* 28: 937–942.
- Haslob H., Clemmesen C., Schaber M., Hinrichsen H., Schmidt J., Voss R., Kraus G. & Köster F. 2007. Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. *Mar. Ecol. Prog. Ser.* 349: 303–306.
- Hassell M.P., Lawton J.H., Beddington J.R. 1977. Sigmoid functional responses by invertebrate predators and parasitoids. *J. Anim. Ecol.* 46: 249–262.
- Hirst A.G. & Lucas C.H. 1998. Salinity influences body

- weight quantification in the scyphomedusa *Aurelia aurita*: important implications for body weight determination in gelatinous zooplankton. *Mar. Ecol. Prog. Ser.* 165: 259–269.
- Holling C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist* 91: 293–320.
- Holst S. & Jarms G. 2010. Effects of low salinity on settlement and strobilation of scyphozoa (Cnidaria): Is the lion's mane *Cyanea capillata* (L.) able to reproduce in the brackish Baltic Sea? *Hydrobiologia* 645: 53–68.
- Ivanov V.P., Kamakin A.M., Ushivtzev V.B., Shiganova T., Zhukova O., Aladin N., Wilson S.I., Harbison G.R. & Dumont H.J. 2000. Invasion of the Caspian Sea by the comb jellyfish *Mnemiopsis leidyi* (Ctenophora). *Biol. Invasions* 2: 255–258.
- Jaspers C., Møller L.F. & Kiørboe T. 2011. Salinity gradient of the Baltic Sea limits the reproduction and population expansion of the newly invaded comb jelly *Mnemiopsis leidyi*. *PLoS ONE* 6: e24065, doi:10.1371/journal.pone.0024065.
- Javidpour J., Molinero J.C., Lehmann A., Hansen T. & Sommer U. 2009. Annual assessment of the predation of *Mnemiopsis leidyi* in a new invaded environment, the Kiel Fjord (Western Baltic Sea): a matter of concern? *J. Plankton Res.* 31: 729–738.
- Javidpour J., Sommer U., Shiganova T. 2006. First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. *Aquat. Inv.* 1: 299–302.
- Kramp P.L. 1937. *Polyppdyr (Coelenterata) II. Gopler. Danmarks fauna 43*. G.E.C. Gads forlag, Copenhagen.
- Kremer P. 1979. Predation by the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode-Island. *Estuaries* 2: 97–105.
- Kremer P. & Nixon S. 1976. Distribution and abundance of the ctenophore, *Mnemiopsis leidyi* in Narragansett Bay. *Estuar. Coast. Mar. Sci.* 4: 627–639.
- Lehtiniemi M., Lehmann A., Javidpour J. & Myrberg K. 2012. Spreading and physico-biological reproduction limitations of the invasive American comb jelly *Mnemiopsis leidyi* in the Baltic Sea. *Biol. Invasions* 14: 341–354.
- Leppäranta M. & Myrberg K. 2009. *Physical oceanography of the Baltic Sea*. Springer-Verlag, Berlin–Heidelberg–New York.
- Lucas C.H. 2001. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia* 451: 229–246.
- Madsen C.V. & Riisgård H.U. 2010. Ingestion-rate method for measurement of clearance rates of the ctenophore *Mnemiopsis leidyi*. *Aquat. Inv.* 5: 357–361.
- Martinussen M.B. & Båmstedt U. 1999. Nutritional ecology of gelatinous planktonic predators. Digestion rate in relation to type and amount of prey. *J. Exp. Mar. Biol. Ecol.* 232: 61–84.
- Martinussen M.B. & Båmstedt U. 2001. Digestion rate in relation to temperature of two gelatinous planktonic predators. *Sarsia* 86: 21–35.
- Mazlum R.E. & Seyhan K. 2007. Gastric emptying, clearance rate, feeding periodicity and food consumption of the Black Sea jelly fish, *Mnemiopsis leidyi* (Agassiz). *Indian J. Mar. Sci.* 36: 59–64.
- Møller L.F. & Riisgård H.U. 2007. Feeding, bioenergetics and growth in the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina*. *Mar. Ecol. Prog. Ser.* 346: 167–177.
- Olesen N.J., Frandsen K. & Riisgård H.U. 1994. Population dynamics, growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. *Mar. Ecol. Prog. Ser.* 105: 9–18.
- Olesen N.J. 1995. Clearance potential of jellyfish *Aurelia aurita*, and predation impact on zooplankton in a shallow cove. *Mar. Ecol. Prog. Ser.* 124: 63–72.
- Palmén E. 1953. Seasonal occurrence of ephyrae and subsequent instars of *Aurelia aurita* (L.) in the shallow waters of Tvärminne, S. Finland. *Arch. Soc. 'Vanamo'* 8: 122–131.
- Purcell J.E. 1997. Pelagic cnidarian and ctenophores as predators: selective predation, feeding rates, and effects on prey populations. *Ann. Inst. Oceanogr. Paris* 73: 125–137.
- Purcell J.E. 2009. Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. *Hydrobiologia* 616: 23–50.
- Purcell J.E., Shiganova T.A., Decker M.B. & Houde E.D. 2001a. The ctenophore *Mnemiopsis* in native and exotic habitats: U.S. estuaries versus the Black Sea basin. *Hydrobiologia* 451: 145–176.
- Purcell J.E., Breitbart D.L., Decker M.B., Graham W.M., Youngbluth M.J. & Raskoff K.A. 2001b. Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. *Coastal Estuarine Stud.* 58: 77–100.
- Reeve M.R., Syms M.A. & Kremer P. 1989. Growth dynamics of a ctenophore (*Mnemiopsis*) in relation to variable food supply. I. Carbon biomass, feeding, egg production, growth and assimilation efficiency. *J. Plankton Res.* 11: 535–552.
- Remane A. 1934. Die Brackwasserfauna. *Zool. Anz.* 7 (Suppl): 34–74.
- Riisgård H.U. & Madsen C.V. 2011. Clearance rates of ephyrae and small medusae of the common jellyfish *Aurelia aurita* offered different types of prey. *J. Sea Res.* 65: 51–57.
- Roohi A., Kideys A.E., Sajjadi A., Hashemian A., Pourgholam R., Fazli H., Khanari A.G. & Eker-Develi E. 2010. Changes in biodiversity of phytoplankton, zooplankton, fishes and macrobenthos in the Southern Caspian Sea after the invasion of the ctenophore *Mnemiopsis leidyi*. *Biol. Invasions* 12: 2343–2361.
- Schaber M., Haslob H., Huwer B., Harjes A., Hinrichsen H.-H., Köster F.W., Storr-Paulsen M., Schmidt J.O. & Voss R. 2011. The invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea: seasonal phenology and hydrographic influence on spatio-temporal distribution patterns. *J. Plankton Res.* 33: 1053–1065.
- Schneider G. & Behrends G. 1998. Top-down control in a neritic plankton system by *Aurelia aurita* medusae — a summary. *Ophelia* 48: 71–82.
- Segerstråle S.G. 1951. The recent increase in salinity off the coasts of Finland and its influence upon the fauna. *J. Cons. Int. Explor. Mer.* 17: 103–110.
- Segerstråle S.G. 1952. The recent increase in salinity off the

- Finnish coast — a probable consequence of the climatic change — and its biological bearing. *Fennia* 75: 55–58.
- Shiganova T.A. & Bulgakova Y.V. 2000. Effects of gelatinous plankton on Black Sea and Sea of Azov fish and their food resources. *ICES J. Mar. Sci.* 57: 641–648.
- Sullivan L.J. 2010. Gut evacuation of larval *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). *J. Plankton Res.* 32: 69–74.
- Vahtera E., Conley D.J., Gustafsson B.G., Kuosa H., Pitkänen H., Savchuk O.P., Tamminen T., Viitasalo M., Voss M., Wasmund N., Wulff F. & Tamminen T. 2007. Internal ecosystem feedbacks enhance nitrogen-fixing cyanobacteria blooms and complicate management in the Baltic Sea. *Ambio* 36: 186–194.
- Viitasalo M., Vuorinen I. & Saesmaa S. 1995. Mesozooplankton dynamics in the northern Baltic Sea — implications of variations in hydrography and climate. *J. Plankton Res.* 17: 1857–1878.
- Vuorinen I. 1987. Is the ctenophore *Pleurobrachia pileus* important in the ecosystem of the Bothnian Sea? *Memoranda Soc. Fauna Flora Fennica* 63: 91–96.
- Wikström D.A. 1932. Beobachtungen über die Ohrenqualle (*Aurelia aurita* L.) in den Schären SW-Finlands. *Memoranda Soc. Fauna Flora Fennica* 8: 14–17.