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The invasive ctenophore *Mnemiopsis leidyi* poses no direct threat to Baltic cod eggs and larvae

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Abstract

Since its invasion in to the Baltic Sea in 2006, the ctenophore *Mnemiopsis leidyi* has been suspected of serious predation on the early life stages of Baltic cod (*Gadus morhua callarias* L.) due to a temporal and spatial overlap in the most important cod spawning ground, the Bornholm Basin. We conducted laboratory incubation experiments and video observations to quantify feeding rates on Baltic cod eggs and larvae. Ingestion rates increased with cod larvae concentrations up to 8 prey L^{-1}, beyond which ingestion remained constant. Neither *Mnemiopsis* size nor egg concentration (1–16 prey L^{-1}) affected feeding rates on cod eggs. Observed feeding rates pooled from all experiments conducted at nonsaturating prey concentrations were low, with the highest volume-specific clearance on < 4.5-d-old yolk-sac larvae (0.05 ± 0.02 L (mL *Mnemiopsis*)$^{-1}$ h^{-1}), and lower rates on 4.5–8-d-old larvae (0.02 ± 0.02 L (mL *Mnemiopsis*)$^{-1}$ h^{-1}) and eggs (0.02 ± 0.03 L (mL *Mnemiopsis*)$^{-1}$ h^{-1}). When offered *Artemia salina* and cod eggs simultaneously, *Mnemiopsis* passively selected against cod eggs. Video recordings showed that eggs did not trigger the capture response that *Mnemiopsis* shows toward motile prey, and ingested eggs were often ejected (88%, $n = 8$). Applying our clearance rates to in situ abundances of cod eggs, larvae, and *Mnemiopsis* for the peak of the spawning season, we demonstrate that the predation pressure of the invasive ctenophore is negligible. We conclude that *Mnemiopsis* constitutes no direct threat to the Baltic cod population.

During recent decades invasive species have become a major concern due to their direct and cascading effects on marine ecosystems and biodiversity (Carlton and Geller 1993; Graham and Bayha 2007; Molnar et al. 2008). Particularly, the collapse of fisheries that coincided with the invasion of the ctenophore *Mnemiopsis leidyi* in the Black Sea raised major scientific and public attention (Shiganova and Bulgakova 2000; Kideys 2002; Oguz et al. 2008). Deleterious effects of *Mnemiopsis* include predation on eggs and early life stages of fish (Monteleone and Duguay 1988; Cowan et al. 1992; Purcell et al. 1994) as well as competition for food (Purcell 1985; Mills 1995; Bilio and Niermann 2004).

Mnemiopsis leidyi (A. Agassiz, 1865) was first sighted in Northern Europe in 2005 (Oliveira 2007) and has since spread rapidly into the Baltic Sea (Javidpour et al. 2006; Huwer et al. 2008) and the southern North Sea (Boersma et al. 2007). In the Baltic Sea, *Mnemiopsis* overlaps spatially and temporally with Baltic cod (*Gadus morhua callarias* L., 1758), especially in the most important nursery and spawning ground, the Bornholm Basin (Haslob et al. 2007; Huwer et al. 2008). Qualitative observations from the Bornholm Basin have shown *Mnemiopsis* with fish eggs in their guts (Haslob et al. 2007). This has raised serious concern that the invader may decrease local fish stocks and fishery revenues, especially those of Baltic cod (Haslob et al. 2007; Huwer et al. 2008; Storr-Paulsen and Huwer 2008). However, the direct predation rates of *Mnemiopsis* on Baltic cod have not yet been quantified.

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Here we measured the predation rate of *Mnemiopsis* on the early life stages of Baltic cod at the low salinities and temperatures representative of the most important cod spawning area in the Baltic. We applied detailed video observations of the predator–prey interactions to explain observed feeding rates.

Methods

All experiments were conducted at the accredited fish hatchery 'Fonden Bornholm Lakseklækkeri' in Nexø on the island of Bornholm, central Baltic Sea, during late April 2009, matching the physical environment of the central Bornholm Basin spawning area of Baltic cod (7°C, 1013 g L^{-1}; Köster et al. 2005).

Experimental animals—Mnemiopsis leidyi were raised from laboratory-cultured eggs (20°C, 1023 g L^{-1}) from ctenophores originating from the Eastern Skagerrak, southwestern Swedish coast (58°15′N, 11°24′E). Two weeks prior to the experiments the ctenophores were gradually acclimatized to the less saline experimental conditions by successive additions of distilled water to the cultures. *Mnemiopsis* were fed with 1-d-old *Artemia* nauplii reared from cysts, and starved 24 h before the start of experiments and used only once.

Brood stock cod at the fish hatchery 'Fonden Bornholm Lakseklækkeri' originated from the Eastern Baltic spawning grounds. Cod eggs and yolk-sac larvae from several different spawning events were supplied by the hatchery. Eggs were provided within 6 h of spawning, and kept in

Table 1. Summary of experimental conditions of *Mnemiopsis leidyi* feeding on Baltic cod eggs and larvae (7°C, 1013 g L^{-1}). Data are mean ± SD. Prey ages are in days from spawning for eggs and days posthatch for larvae, corrected for average incubation times. L_{o-a} is oral–aboral length. Four experiments were conducted: (A) functional response (FR), (B) prey selection of cod eggs vs. *Artemia salina* (select), (C) clearance as a function of prey age (age), and (D) size-dependent clearance rate (size). Data were pooled and included in subsequent analyses as indicated by superscripts A–D in the replicates column. Controls without predators were performed in parallel with experiments A–D (overall prey loss due to handling: eggs 0.00%, $n = 14$; larvae 0.14%, $n = 13$).

Experiment	Prey	Prey conc. (L^{-1})	Prey age (d)	Prey length (mm)	Predator L_{o-a} (mm)	Replicates (n)	Duration (h)
A-FR	eggs	1	1.7±0.6	1.58±0.04(n=53)	12±1.7	$3^{C,D}$	7.8±1.8
		2	1.7±0.6	1.58±0.04(n=53)	12±1.7	$2^{C,D}$	7.8±1.8
		4	1.7±0.6	1.58±0.04(n=53)	12±1.7	$2^{C,D}$	7.8±1.8
		8	1.7±0.6	1.58±0.04(n=53)	12±1.7	$3^{C,D}$	7.8±1.8
		16	1.7±0.6	1.58±0.04(n=53)	12±1.7	5	7.8±1.8
	larvae	2	4.3	4.3±0.4(n=37)	12.5±0.7*	$2^{C,D}$	5.2±0.3
		4	4.3	4.3±0.4(n=37)	12.5±0.7*	$2^{C,D}$	5.2±0.3
		8	4.3	4.3±0.4(n=37)	12.5±0.7*	$2^{C,D}$	5.2±0.3
		16	4.3	4.3±0.4(n=37)	12.5±0.7*	2	5.2±0.3
B-select	eggs and	4	0.9	1.54±0.03(n=36)	13.5±1.7	$9^{C,D}$	16.8±0.5
	Artemia	4	1	0.92±0.09(n=34)	13.5±1.7	$9^{C,D}$	16.8±0.5
C-age	eggs	4	3	1.56±0.02(n=34)	12±1.0	5^{D}	16±1.2
		4	4.8	1.54±0.02(n=23)	12.4±1.1	5^{D}	16.8±0.2
		4	5.9	1.58±0.01(n=16)	11.7±1.8	5^{D}	17.8±0.3
		4	7.5	1.55±0.02(n=22)	11.5±2.6	5^{D}	9.3±0.4
		4	8.5	1.56±0.03(n=26)	11.1±0.6	4^{D}	11.7±0.2
		4	11.5	1.57±0.06(n=63)	10.3±0.7	4^{D}	11.9±0.2
	larvae	4	0–0.5	3.7(n=25)†	10.5±1.0	4^{D}	10.3±0.1
		4	3.3	4.2±0.4(n=17)	11.5±1.5	$5^{D,‡}$	16.9±0.2
		4	6.5	4.6±0.3(n=37)	16.8±5.5	10^{D}	8.7±0.3
		4	8	4.8±0.4(n=35)	11.5±2.0	5^{D}	11.5±0.3
D-size	eggs	4	2.4	1.54±0.01(n=12)	15.2±6.1	15^{C}	5.6±0.5
	larvae	4	5.9	4.3±0.3(n=38)	7.2±2.5*	7^{C}	15.2±0.5
		4	5.4	No data	20.9±3.8	10^{C}	7.8±0.6

* 2–8 predators $bottle^{-1}$.
† Data from Petereit (2004), no SD given.
‡ Four clearance rates included in FR analysis A (4 prey L^{-1}; size 12.4±0.8 mm; 9-mm observation excluded).

separate flow-through systems (7°C, 1013 g L^{-1}) in artificial seawater (Instant Ocean®) from the hatchery circulation system (10-μm–filtered and ultraviolet-light–treated). Cod larvae were not fed, and cohorts were kept separately.

Incubation experiments—We conducted four series of experiments targeting (A) the functional response to prey concentrations (conc.) for *Mnemiopsis* feeding on cod eggs and larvae, (B) potential prey selection, (C) the effect of prey age and, (D) the effects of predator size on the predation rate. The details of the experimental conditions are given in Table 1, while the general experimental protocol is outlined below. When applicable, data from the various experiments were also used in other analyses (Table 1).

Incubations were conducted in wide-mouthed 13.5-liter Nalgene® polycarbonate bottles filled with water from the hatchery system. *Mnemiopsis* were added to each bottle, and allowed to acclimatize until they had fully expanded their lobes. *Mnemiopsis* were incubated individually (in 101 out of 116 bottles) unless otherwise indicated (Table 1).

Cod egg incubations were started with the subsequent addition of prey. In experiments with larvae, the prey was added first and experiments started with the addition of *Mnemiopsis*. They fully expanded their lobes within 2–5 min, corresponding to $< 1.7\%$ of the total incubation time. All prey were picked individually; eggs under a stereomicroscope and larvae by eye. Animals were kept submerged at all times to ensure that both predators and prey were in good condition.

Bottles were topped, sealed with household film and lids and incubated on a rolling table. The bottles rotated around their longitudinal axis at 0.9 rounds min^{-1}. Based on previous, unpublished feeding measurements, incubation time (5–18 h) and number of predators were set to an expected clearance of 30% of the bottle volume. Experiments were run in darkness to avoid confounding effects of light on larval behavior (Grønkjær and Wienand 1997; Skajaa et al. 2003; Titelman and Hansson 2006). Incubations were terminated by removing the predators; thereafter, remaining prey were enumerated. Cod eggs were concentrated by reverse filtration using a 20-μm Nitex® plankton gauze filter before enumeration. Larvae were not concentrated, but individually counted by eye and removed from the total volume with a white spoon, which offered good contrast to the larvae. Simultaneously incubated controls without predators showed negligible prey losses for both eggs (0.00%, $n = 14$) and larvae (0.14%, $n = 13$) and were, therefore, not corrected for.

After each incubation the *Mnemiopsis* were measured (oral–aboral length, L_{o-a}) to the nearest mm and checked for number of ingested prey. Developmental stages and sizes of cod eggs and larvae in the cohorts were assessed on a daily basis. Images at 6–50× magnification were captured by a Leica DFC290 camera and sizes determined using the software ImageJ (version 1.43n; Rasband 1997–2009).

Ingestion rates (I, prey individual^{-1} h^{-1}) were calculated from differences between initial (C_i) and final (C_f) prey conc. (L^{-1}) as a function of time. Clearance rate (F, L ind.$^{-1}$ h^{-1}) was estimated from experimental observations of prey disappearance over time,

$$F = \left(\frac{V}{n \times t}\right) \times \ln\left(\frac{C_i}{C_f}\right) \quad (1)$$

where V is bottle volume (L), n is number of predators, and t is duration of the incubation (h).

Functional response (A)—To ensure that subsequent experiments were conducted at nonsaturating prey concentrations (securing maximum clearance rates and no handling limitation) we first conducted functional response experiments on both eggs and larvae using predators of similar size (12 ± 1.7 mm and 12.5 ± 0.7 mm, respectively). Prey concentrations ranged from 1 L^{-1} and 2 L^{-1} to 16 L^{-1} for eggs and larvae, respectively (Table 1).

Prey selection (B)—In prey selection experiments we offered 1-d-old *Artemia salina* in combination with freshly spawned cod eggs at the same concentrations (Table 1). Because the swimming and escape abilities of both these prey types are minimal, we expect similar encounter rates. Thus, for no postencounter prey selection we expected $F_{\text{cod egg}} = F_{Artemia}$.

Effect of prey age (C)—Clearance as a function of prey age was examined using prey from several cohorts, as well as utilizing clearance measurements conducted at nonsaturating food concentrations from other experiments (Table 1). To ensure comparable data, all clearance rates were standardized to *Mnemiopsis* volume (L [mL *Mnemiopsis*]$^{-1}$ h^{-1}). L_{o-a} (mm) was converted to volume (V, mL) using the empirically determined relation for *Mnemiopsis* in Limfjorden, Denmark (Riisgaard et al. 2007):

$$V = 0.0226 \times L_{o-a}^{1.72} \quad (2)$$

Effect of predator size (D)—Size-dependent clearance experiments on both eggs and larvae were conducted by using different-sized predators, and different prey cohorts, at a prey concentration of 4 L^{-1}. The data set was supplemented with clearance rates from other experiments for nonsaturated prey concentrations (1–8 L^{-1}), such that the size range in the entire analysis became 4.5 mm to 26 mm L_{o-a} (n = 62 for eggs and n = 47 for larvae; Table 1).

Behavioral observations—To qualitatively assess predator behavior upon prey encounter, silhouette video recordings in darkness were conducted with a black and white analog camera in 1-liter or 8-liter aquaria. Collimated light was provided by an infrared diode shining through a condenser lens and pointing toward the camera. The behavior of free-swimming *Mnemiopsis* with cod eggs at very high prey concentrations or with cod larvae were monitored. *Mnemiopsis* generally captures nonmotile prey that have been entrained in the feeding current on the tentillae. In contrast, motile prey, such as copepods, elicit a rapid closure of the lobes and such prey are primarily captured on the inner surfaces of the lobes (Waggett and Costello 1999). Both the fraction of lobe closing responses by *Mnemiopsis* and the fraction of prey retained on the lobes or tentillae after prey touch were measured.

Three *Mnemiopsis* that had fed on cod eggs during the incubation experiments were subsequently followed for several days to investigate the fate of ingested cod eggs and to estimate digestion times. The animals were placed individually in 2-liter aquaria at 7°C and observed during the digestion or ejection process for up to 3 d. To investigate whether cod eggs could be digested at higher temperatures, similar to those at which experiments on anchovies have been conducted (i.e., ~ 22°C; Cowan and Houde 1993), one *Mnemiopsis* was monitored in a 2-liter aquarium at 22°C for several hours subsequent to feeding, and photographed at regular intervals.

Statistical analyses—Statistical analyses were conducted in GraphPad Prism 4.0 and Table Curve 2 dimensional 5.0 with all curve fits and associated significance tests. Plots were generated in Sigma plot 10.0. Functional response experiments (A) were analyzed using linear regressions on nonaveraged raw data in the nonsaturating part of the functional response curves, where the slope proxies the maximum clearance rate. A separate slopes model was used to test for differences between slopes. We used a paired 2-tailed t-test to test for differences in clearance rates on *Artemia* and cod eggs in the selection experiment (B). The effect of larval age on volume-specific clearance rate in experiment C was tested with an ANOVA, and associated Newman–Keuls multiple-comparison post hoc test. Size-dependent clearance (experiment D) was analyzed with power regression analyses on raw data. Differences between regression parameters were tested using separate slopes models (covariance analyses) on log (x + 1)-transformed data. Control treatments without predators were performed and showed negligible prey loss for both cod eggs (0.00%, n = 14) and cod larvae (0.14%, n = 13).

Results

Overall, our results showed that *Mnemiopsis* fed on cod larvae at low rates, while feeding rates on eggs were extremely low and often zero. Across all incubation experiments, *Mnemiopsis* ingested no prey at all in 40% of the incubations with eggs, compared to 15% when larvae were offered. *Artemia* were ingested in 100% of the incubations in which they were offered.

Functional response (A)—The functional response experiment revealed significant differences between ingestion

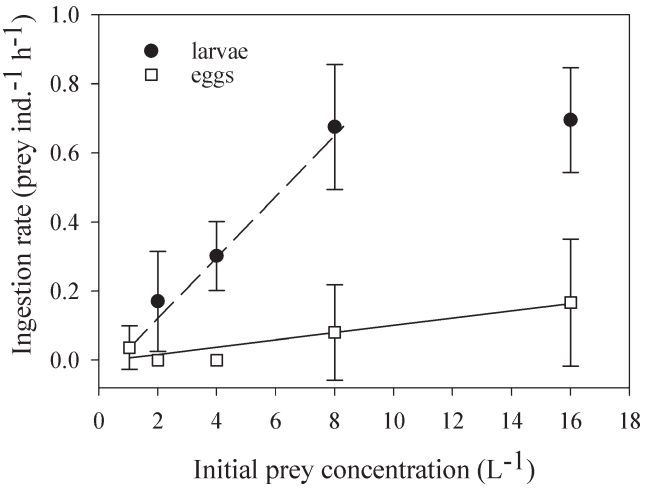

Fig. 1. Functional response of *Mnemiopsis* feeding on Baltic cod eggs and larvae (experiment A; Table 1). Each data point is the mean ± standard deviation for n = 2–6. The regressions for nonsaturating food concentrations using nonaveraged data are $I = 0.088c - 0.056$ ($r^2 = 0.68$, $p = 0.0035$, $n = 10$) for larvae and $I = 0.01c - 0.004$ ($r^2 = 0.25$, $p = 0.058$, $n = 15$) for eggs as prey. The slopes differ from one another (separate slopes model, $F_{21} = 13.78$, $p = 0.0013$).

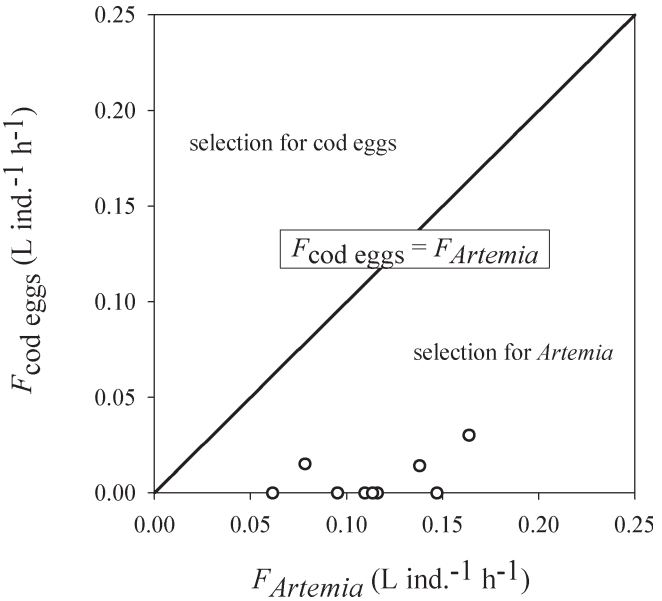

Fig. 2. Clearance rate of individual *Mnemiopsis* (13.5 ± 1.7 mm) on cod eggs and *Artemia* offered simultaneously (experiment B; Table 1). The straight line indicates the predicted equal clearance rates on cod eggs and *Artemia*; data above the line indicate selection for cod eggs, while data below the line indicate selection for *Artemia*. Mean clearance on *Artemia* was 0.114 ± 0.03 L ind.$^{-1}$ h^{-1} while 0.007 ± 0.01 L ind.$^{-1}$ h^{-1} on cod eggs. A 2-tailed paired t-test confirmed the different clearance rates on the two prey types (i.e., negative selection for cod eggs [$t = 10.99$, $p < 0.00001$, df = 8]).

of eggs and larvae (Fig. 1). Ingestion rates of cod eggs were very low at all prey concentrations with no signs of saturation (Fig. 1), generating an average clearance rate of 0.01 ± 0.03 L ind.$^{-1}$ h^{-1}. The slope of the linear regression of cod egg ingestion rate vs. concentration was not significantly different from 0 ($F_{13} = 4.317$, $p = 0.06$). Feeding rates on larvae were higher, and increased with increasing prey concentrations up to 8 L^{-1}, with no further increase at the highest prey concentration tested (16 L^{-1}), yielding an average maximum clearance rate of 0.088 ± 0.02 L ind.$^{-1}$ h^{-1} at nonsaturating prey concentrations (Fig. 1).

Prey selection (B)—In the prey selection experiments all *Mnemiopsis* were actively filtering as indicated by their feeding on *Artemia* (0.114 ± 0.03 L ind.$^{-1}$ h^{-1}; Fig. 2). Simultaneous clearance on eggs was 16 times lower than clearance on *Artemia*, but similar to rates obtained in the functional response experiment for cod eggs (Figs. 1, 2). The differing clearance rates on the two prey types clearly demonstrated that *Mnemiopsis* passively selected *Artemia* nauplii over cod eggs (Fig. 2).

Effect of prey age (C)—There was no significant effect of egg age on the rate at which they were cleared (ANOVA: $F_{8,53} = 1.74$, $p = 0.11$) and data were, therefore, pooled. The pooled overall average volume-specific clearance on cod eggs was 0.02 ± 0.03 L (mL *Mnemiopsis*)$^{-1}$ h^{-1} (Fig. 3). Larval age affected clearance rates, with higher clearance on < 4.5-d-old yolk-sac larvae (0.05 ± 0.02 L [mL *Mnemiopsis*]$^{-1}$ h^{-1}) compared to 4.5–8-d-old larvae (0.02 ± 0.02 L [mL *Mnemiopsis*]$^{-1}$ h^{-1}; Fig. 3). Feeding rates on cod eggs and 4.5–8-d-old larvae were similar (ANOVA: $F_{4,89} = 0.75$, $p = 0.56$; Fig. 3). Generally, mean clearance rates on cod larvae were lower than those on *Artemia* (Fig. 3).

Effect of predator size (D)—Because larval age affects clearance rates (Fig. 3) we separated the predator-size–dependent clearance-rate observations into clearance on young (< 4.5 d posthatching) and older (4.5–8 d post-hatching) cod larvae (Fig. 4A). The narrow predator size range (9–13.3 mm, $n = 15$) in incubations with the younger larvae did not allow for testing for size dependency. For older larvae, however, clearance rates increased with predator size to a power of 1.74 ± 0.51 (Fig. 4A). Given that predator volume scales with length to a power of 1.72 (Riisgaard et al. 2007), clearance rates on cod larvae scale almost perfectly isometrically with predator volume. Thus, the use of predator volume-normalized clearance rates removes any effect of predator size and is adequate for comparison of clearance rates among differently sized *Mnemiopsis*. When feeding on cod eggs the size scaling was only to a power of 0.6, but not significant (Fig. 4B).

Behavioral observations—Nonmotile cod eggs rarely triggered a lobe-closing response in *Mnemiopsis*, even when clearly touching the capture sites (*see* Web Appendix, www.aslo.org/lo/toc/vol_56/issue_2/0431a.wmv). *Mnemiopsis* did not react to cod egg encounters in > 95% of the video observations (n = 63 for 7 *Mnemiopsis* L_{o-a} = 12.0–16.2 mm). *Mnemiopsis* reacted more often with lobe closing to fish larvae (20.0%, n = 70 for six *Mnemiopsis* L_{o-a} =

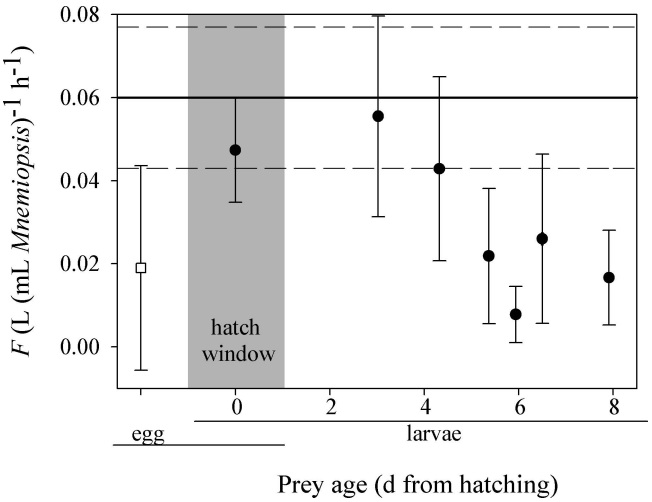

Fig. 3. *Mnemiopsis* volume-specific clearance rate as a function of prey age for data obtained at nonsaturating food concentrations (experiment C; Table 1). Rates on eggs were pooled from experiments A, B, and D ($n = 62$). Clearance on larvae varied with larval age (ANOVA: $F_{6,40} = 5.752$, $p = 0.0002$), forming two clusters of < 4.5-d-old and 4.5–8-d-old larvae (Newman–Keuls post hoc test, $p > 0.05$). At 7°C Baltic cod eggs hatch within 12 ± 1 d postfertilization and the grey box indicates this hatch window. The solid (mean) and dashed (± SD) lines indicate volume-specific clearance on *Artemia* from experiment B.

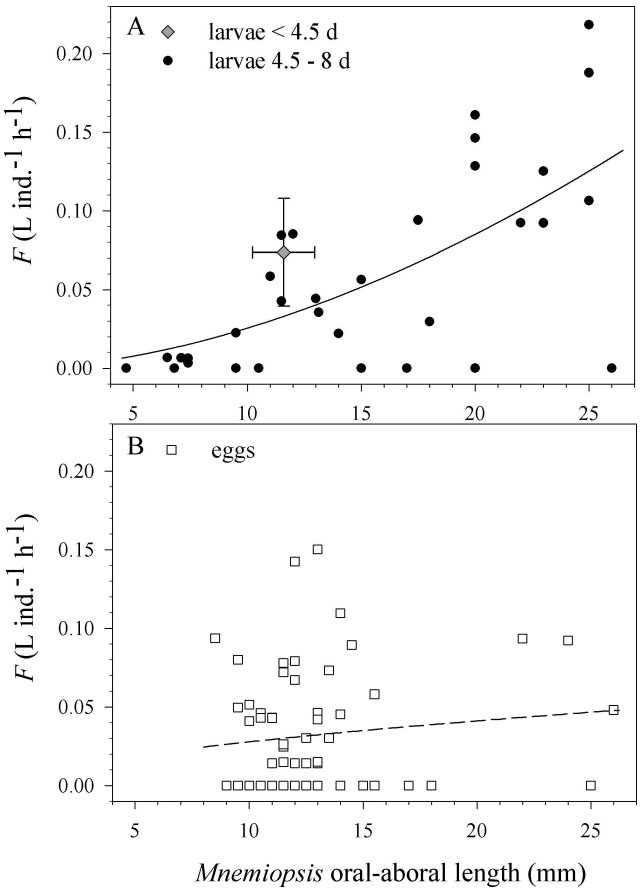

Fig. 4. *Mnemiopsis* clearance rate on (A) cod larvae, and (B) eggs as a function of size (experiment D; Table 1). (A) $F_{larvae} = 0.0005 \times L_{o-a}^{1.74}$ for L_{o-a} of 4.5–26 mm ($r^2 = 0.43$, $p < 0.0001$, $n = 32$). The exponent (1.74 ± 0.51) differs from 0 ($p < 0.0001$). Data for young larvae (< 4.5 d) are mean ± SD ($n = 15$) and excluded from the regression. (B) $F_{egg} = 0.008 \times L_{o-a}^{0.6}$ ($r^2 = 0.01$, $p = 0.389$, $n = 62$), the exponent 0.6 ± 0.6 did not differ from 0 ($p = 0.42$).

12.7–17.7 mm). More surprisingly, the cod eggs were not retained on the inner lobes or the tentillae after contact (0%, $n = 63$). We observed the ingestion of eight fish larvae out of 70 contacts (11.4%) for six *Mnemiopsis*. Three *Mnemiopsis* that had fed on cod eggs during the incubation experiments actively ejected seven out of eight eggs and the regurgitation process lasted on the order of 3 d at 7°C.

To investigate whether cod eggs could be digested at higher temperatures, *Mnemiopsis* were followed for several hours subsequent to feeding at 22°C (Fig. 5). The ejection of five out of six ingested eggs took around 2 h for a 25-mm L_{o-a} animal. In contrast, cod larvae were successfully digested within minutes and no ejection was observed.

Discussion

We demonstrate experimentally that feeding rates of the invasive ctenophore *Mnemiopsis* on cod eggs and larvae are extremely low and often zero, at environmental conditions relevant to the major spawning grounds of the Baltic Sea. *Mnemiopsis leidyi* has been present in northern European waters since 2005 (Javidpour et al. 2006; Boersma et al. 2007; Oliveira 2007). Our results sharply contrast with those obtained from other native and invaded habitats, outside northern Europe, where predation rates and predation potential of *Mnemiopsis* on ichthyoplankton are reported to be high (Cowan and Houde 1993; Rilling and Houde 1999; Purcell and Arai 2001). For example, extrapolations from laboratory experiments reveal that *Mnemiopsis* was the major source of ichthyoplankton mortality in the coastal Cape Cod area, USA, where it accounted for 10–65% and 3–65% of the daily Bay Anchovy egg and larvae mortality, respectively (Table 2; Monteleone and Duguay 1988). Due to such findings, and based on an observed spatial and temporal overlap of *Mnemiopsis* and cod eggs and larvae in its major spawning area, it has been speculated that *Mnemiopsis* poses a serious mortality threat to recruits of the commercially most important fish species in the Baltic Sea (Haslob et al. 2007; Huwer et al. 2008; Storr-Paulsen and Huwer 2008).

Feeding on fish larvae—Previous studies of *Mnemiopsis* predatory interactions with fish eggs and larvae have demonstrated higher clearance rates than in our study, but those studies have exclusively been conducted at much higher temperatures (Table 2). Respiration rates and energetic demand increase dramatically with temperature for *Mnemiopsis* ($Q_{10} = 4$, for 10.3–24.5°C; Kremer 1977), and similar differences in predation rates are to be expected. One low-temperature study of *Mnemiopsis* reports similar feeding rates on copepods at 8°C (Miller 1970) as those that we observed on 4.5–8-d-old cod larvae at 7°C (Table 2). However, low temperature effects on

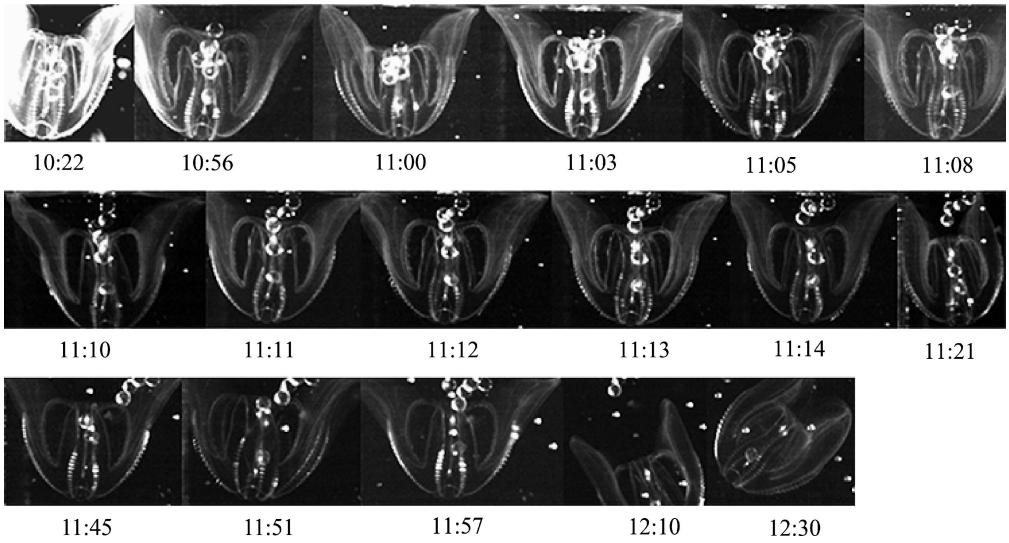

Fig. 5. Sequence of pictures following a *Mnemiopsis* (25-mm L_{o-a}) ejecting cod eggs at 22°C, 1013g L^{-1} over ~ 2 h. Time of the day is indicated below each picture, sequence from upper left (six eggs ingested) to lower right (one egg left in stomach). The *Mnemiopsis* had been incubated under extremely high prey concentrations.

feeding rates have been neglected in the evaluation of the potential implications of *Mnemiopsis* so far.

In general, differences in clearance rates, such as those observed here between young and older larvae, can usually be explained by differing predator or prey behaviors. Predators like *Mnemiopsis* detect the hydrodynamic signals produced by actively swimming prey items, and normally react with a capture response upon perception in their encounter zone (Costello et al. 1999). The hydrodynamic signal of the prey depends on prey speed, size, and behavior (Kiørboe et al. 1999). On the other hand, prey may perceive the flow field produced by the predator and attempt to escape. However, escape ability differs with prey types (Kiørboe et al. 1999; Waggett and Costello 1999), and also with different development stages of fish larvae, including cod, whose survival in interactions with other gelatinous predators increases during their development (Bailey and Batty 1984; Titelman and Hansson 2006). For example, old yolk-sac anchovy larvae have lower mortality rates than younger ones in interactions with *Mnemiopsis* (Table 2; Monteleone and Duguay 1988), maybe due to increasing predator perception and escape abilities of the larvae. Similarly, we found that clearance on young yolk-sac cod larvae (0–4.5 d posthatch) was 2.5× higher compared to that on older larvae. In general, cod larvae are quite passive and yolk-sac larvae do not engage in active search behavior (Skajaa et al. 2003). However, older cod larvae are generally better escapers, probably because they are able to sustain relatively higher swimming speeds about 4 d after hatching (Yin and Blaxter 1987). Therefore, decreasing feeding rates of *Mnemiopsis* on cod larvae during their early development may be explained by differing stage-specific abilities of the prey.

Feeding on fish eggs—Mnemiopsis fed on cod eggs only at very low rates, if at all (Fig. 1). Nonmotile cod eggs produce negligible hydrodynamic signals and have no ability to escape. If all contacted prey were captured, clearance rates on cod eggs should theoretically equal the volume encounter rate produced by the flow field of the *Mnemiopsis*. However, our experiments demonstrated a clear negative, passive selection of cod eggs when offered in combinations with poorly escaping *Artemia*. In accordance with the rate measurements, our video recordings revealed that the capture response in *Mnemiopsis* was not triggered by encounters with nonmotile cod eggs (*see* Web Appendix). We repeatedly observed *Mnemiopsis* swimming through dense patches of eggs without responding. This may suggest that encountered cod eggs were not perceived by *Mnemiopsis*, but in some cases entrained in the feeding current and accidentally ingested without the normally observed capture response (Costello et al. 1999). In corroboration with our experimental results an experiment conducted at extreme prey densities (50 L^{-1}) each of copepods and a mix of fish eggs (0.8–1.5 mm) at 8°C demonstrated almost no feeding on fish eggs (0.003 ± 0.5 eggs h^{-1}; Hamer et al. 2011).

In contrast, several authors have demonstrated feeding of *Mnemiopsis* on anchovy eggs (0.7 mm) at higher temperatures (21–27°C; Table 2, references therein). The reason for the different predation rates on eggs of anchovy and cod is not clear, but cannot be explained solely by temperature as *Mnemiopsis* is clearly capable of feeding at these very low temperatures on larvae and *Artemia* (Table 2), as well as on copepods (Miller 1970). Egg size or surface properties may possibly matter, but more detailed studies are necessary to enlighten this.

Eggs were digested at a much lower rate than larvae and the majority of ingested eggs were regurgitated. For cod eggs the ejection process took ~ 2 h at 22°C, while it was on the order of 3 d at 7°C. Similar observations of inhibited digestibility and regurgitation of fish eggs has been described for the ctenophore *Bolinopsis infundibulum*, which ejected undigested plaice eggs after several hours (Gamble 1977). Because of the long duration of the ejection process (days) compared to that of our incubations (hours), we are confident that the egg clearance rates are reliable

Table 2. Published *Mnemiopsis* feeding rates on copepods, fish eggs or larvae, and *Artemia* at different temperatures, recalculated to volume-specific rates (*) if not presented in the original source; predator size shown as oral–aboral length (mm), anchovy (*Anchoa mitchilli*), cod (*Gadus morhua callarias*), and goby (*Gobiosoma bosci*). Only rates from experiments conducted at limited prey concentrations are included.

Prey	Temp. (°C)	Specific clearance (L mL^{-1} h^{-1})	Predator length (mm)	Volume (L)	Reference
Copepods	8	0.024	20–50 mm	6	Miller (1970)
Copepods	16.5	0.09	20–50 mm	6	Miller (1970)
Copepods	24.5	0.18	20–50 mm	6	Miller (1970)
Fish eggs					
Anchovy	21–22.7	0.4	37.5–41.7 mm†	750	Cowan and Houde (1990)
Anchovy	23–23.5	0.9	41.7–46.7 mm†	3000	Cowan and Houde (1990)
Anchovy with alternative prey	19.5–22	0.2	41.7 mm†	750	Cowan and Houde (1990)
Anchovy	21–24	0.26	20–25 mm	15	Monteleone and Duguay (1988)
Anchovy	26	0.13±0.06*	66.4 mm†	field‡	Purcell et al. (1994)
Fish	20	0.76	Average: 17.6 mm†	2200	Cowan et al. (1992)
Cod	7	0.02±0.03	8.5–26 mm	13.5	This study
Fish larvae					
Anchovy yolk sac	21–24	0.44	20–25 mm	15	Monteleone and Duguay (1988)
Anchovy 3 d starved	21–24	0.18	20–25 mm	15	Monteleone and Duguay (1988)
Anchovy 5 d starved	21–24	0.53	20–25 mm	15	Monteleone and Duguay (1988)
Anchovy 5 d fed	21–24	0.23	20–25 mm	15	Monteleone and Duguay (1988)
Goby	25	0.3*	49 mm†	3200	Cowan and Houde (1992)
Cod <4.5 d	7	0.05±0.02	4.5–26 mm	13.5	This study
Cod 4.5–8 d	7	0.02±0.02	4.5–26 mm	13.5	This study
Artemia					
A. salina	7	0.06±0.02	13.5±1.7 mm	13.5	This study
A. salina	17.5±1	0.5	13.5 mm	13.5	L. J. Hansson unpubl.

† Length (without lobes) conversion from volume based on equations in Kremer and Nixon (1976).
‡ From gut content analyses.

and not underestimated. The fate of regurgitated eggs remains uncertain, because we did not follow the developmental success of regurgitated eggs. However, while dead eggs tend to become white as proteins denature, the ejected eggs followed by picture sequence remained clear.

In situ predation effect—Our feeding-rate measurements demonstrated that young yolk-sac larvae (< 4.5 d posthatch) represent the most susceptible life stage for predation from *Mnemiopsis*. Cod spawning in the Bornholm Basin takes place from March to September, peaking in May and June around the halocline (Grønkjaer and Wieland 1997). At the depth of the highest densities of cod eggs and yolk-sac larvae, the maximum observed in situ abundance of *Mnemiopsis* in May 2007 was 0.5 ctenophores m^{-3} (Haslob et al. 2007), with a L_{o-a} of 14.4 ± 0.5 mm and cod egg and larvae densities of 4.5 m^{-3} and 0.02 m^{-3}, respectively (H. Haslob pers. comm.). If we apply our measured clearance rates, *Mnemiopsis* would clear at maximum 0.13% of the cod larvae and 0.05% of the cod eggs d^{-1}, respectively. After the yolk-sac stage, cod larvae migrate upwards in the water column for first feeding (Grønkjaer and Wieland 1997), whereby they virtually escape the potential predation by *Mnemiopsis* on later life stages, because *Mnemiopsis* are rarely found at those depths in the Bornholm Basin (own data, unpubl.). Thus, despite the temporal and spatial overlap of *Mnemiopsis* and cod recruits in the most important spawning and nursery area of the Baltic, the direct predation effect of the alien, invasive ctenophore on cod eggs and larvae is negligible.

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