

Interactions between native and alien ctenophores: *Beroe gracilis* and *Mnemiopsis leidyi* in Gullmarsfjorden

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ABSTRACT: We experimentally quantified predation rates between the native North Sea ctenophore *Beroe gracilis* and the introduced *Mnemiopsis leidyi*. A series of incubation experiments with varying *M. leidyi* prey concentrations (0.15 to 2.37 ind. l⁻¹) and sizes (mean oral-aboral length: 5.9 to 20.6 mm) was conducted, and digestion rates were measured. *B. gracilis* fed readily on *M. leidyi* and reproduced on this diet. However, *B. gracilis* were unable to entirely ingest *M. leidyi* approaching their own size, resulting in a size refuge from predation. Larger prey were often partially consumed, and the proportion of prey that was only partially eaten increased with prey size. Observed maximum clearance rates for whole prey were from 0.42 to 0.97 l ind.⁻¹ h⁻¹. Ingestion rates of whole prey increased linearly with prey concentration for the smaller prey, but leveled off at the higher prey concentrations for the larger sizes, indicating handling limitation. The handling limitations probably largely stemmed from digestion time (1.6 to 8.4 h for 4 to 12 mm prey) and gut volume. Applying the determined clearance rates to concurrent *in situ* abundances of *M. leidyi* and *B. gracilis* suggested a slight predation impact on the *M. leidyi* population (overall mortality: 8.8×10^{-4} d⁻¹). The predatory interactions between the 2 species are further complicated by transitional and lobate stage *M. leidyi* being able to feed on young *B. gracilis*.

KEY WORDS: *Mnemiopsis leidyi* · *Beroe gracilis* · Intraguild predation · Predation rates · Invasive species · Gullmarsfjorden

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INTRODUCTION

Marine biological invasions due to human activities are on the increase, and represent a major threat to marine ecosystems because of their potential to alter both the habitat and community structure of the invaded environments (Bax et al. 2003). The ctenophore *Mnemiopsis leidyi* is considered one of the most detrimental invasive species in the pelagic realm, mainly due to the fisheries collapses that coincided with its introduction into the Black Sea in the early 1980s (Kideys 2002) and the Caspian Sea around the turn of the millennium (Stone 2005, Daskalov & Mamedov 2007, Roohi et al. 2009). The invasive *M. leidyi* has been present in the North Sea at least

since 2005 (Oliveira 2007) and has since also been observed in the Baltic Sea (Javidpour et al. 2006). Its appearance has caused concern and received considerable political and research attention, primarily in view of the potential negative effects of large populations of predatory jellyfish on zooplankton and fish larvae. Observations from around the world suggest that human activities resulting in species introductions, overfishing, eutrophication, climate change and habitat degradation could lead to more prominent blooms, as well as sustained biomass increases of jellyfish (reviewed by Mills 2001, Purcell et al. 2007, Richardson et al. 2009). The major concern is that such changes may, due to a positive feedback loop, result in a regime shift towards an undesirable alter-

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nate ecosystem state dominated by jellyfish (Aksnes et al. 2009, Richardson et al. 2009).

In the absence of controlling predators, populations of an invasive species can become a nuisance. In addition to temperature and food availability (Kremer 1994), gelatinous predators such as the ctenophore *Beroe ovata* and the scyphomedusa *Chrysaora quinquecirrha* play an important role in regulating *Mnemiopsis leidyi* populations in its native range along the Atlantic west coast (Purcell et al. 2001 and references therein). Lack of predators probably contributed to the decimation of zooplankton and fish in conjunction with the *M. leidyi* invasions of the Black and Caspian seas, though habitat degradation and overfishing seem to have been the ultimate culprits behind the collapse of commercially important fish stocks there (Daskalov 2002, Gucu 2002, Aksnes 2007). The numbers and adverse effects of *M. leidyi* in the Black Sea have considerably reduced since the subsequent accidental introduction of *B. ovata*, a ctenophore preying on *M. leidyi*, in the late 1990s (Kideys 2002, Bilio & Niermann 2004).

Predatory interactions between gelatinous zooplankton are common (reviewed by Purcell 1991, 1997, Arai 2005), and can be important in structuring the pelagic community; however, rates have rarely been experimentally quantified (but see for example Båmstedt et al. 1994, Purcell & Cowan 1995, Titelman et al. 2007). While neither *Beroe ovata* nor *Chrysaora quinquecirrha* occurs in the NE Atlantic and Baltic areas newly invaded by *Mnemiopsis leidyi*, we hypothesize that other native gelatinous predators may prove important in controlling *M. leidyi* populations. Two *Beroe* species, known to feed almost exclusively on other ctenophores (Swanberg 1974), are native to the North Sea: *B. gracilis* and *B. cucumis*. North Sea *B. gracilis* has been considered a specialist feeding exclusively on *Pleurobrachia pileus* (Greve 1970, Greve & Reinert 1988), and the seasonal population dynamics of these 2 species in the North Sea are closely connected, with *B. gracilis* apparently controlling *P. pileus* populations (Greve 1981, Greve & Reinert 1988). No previous records of *B. gracilis* feeding on *M. leidyi*

exist. In the present study, we experimentally quantified predatory interactions between the co-occurring alien *M. leidyi* and the native *B. gracilis* in Gullmarsfjorden, Sweden.

MATERIALS AND METHODS

Experiments targeting predatory interactions between the ctenophores *Mnemiopsis leidyi* and *Beroe gracilis* were carried out at The Sven Lovén Centre for Marine Sciences, Kristineberg, on the west coast of Sweden from September to October 2009, during a period of simultaneous occurrence of the 2 ctenophores in Gullmarsfjorden.

Experimental animals. Ctenophores were gently hand collected with beakers from a pier outside the laboratory. Only healthy-looking animals were chosen for the experiments, and experimental animals were only used once. Animals were kept at 17 to 18°C (similar to ambient sea temperature at the time of collection) in gently aerated 50 l holding tanks with Gullmarsfjorden water from 32 m depth. Tanks were cleaned, and a portion of the water was changed regularly, resulting in about 30% weekly water renewal. *Mnemiopsis leidyi* were fed *Artemia* sp. ad libitum, with occasional *Centropages typicus* additions. *Beroe gracilis* were fed daily with live or chopped up *M. leidyi*. The *B. gracilis* survived for 6 wk on this diet, and also spawned successfully in the holding tanks. In the end the *B. gracilis* culture crashed, probably due to a sudden outburst of parasites visible in the mesoglea. The *B. gracilis* did not appear to cannibalize each other in the holding tanks. We sometimes saw partial ingestion of one *B. gracilis* by another when both had simultaneously started eating the same *M. leidyi* prey from different directions. The partially ingested conspecific was in all observed cases regurgitated intact.

***Beroe gracilis* feeding on *Mnemiopsis leidyi*.** To estimate feeding rates we carried out a series of incubations with *B. gracilis* feeding on *M. leidyi* at different prey concentrations and sizes (Table 1). Animals from

Table 1. Summary of experimental conditions in feeding incubations. All experiments were conducted using 1 predator per bottle. Size is given as total length for *Beroe gracilis* and oral-aboral length for *Mnemiopsis leidyi*. Data are means (\pm SD). Volume for Expts A to D was 13.5 l and for Expt E was 2.32 l. In the column of initial concentrations the number of replicates is given in parentheses

Expt	Predator	Predator size (mm)	Prey	Prey size (mm)	Initial conc. (ind. l ⁻¹)	Duration (h)
A	<i>B. gracilis</i>	24.3 \pm 0.5	<i>M. leidyi</i>	5.9 \pm 0.9	1.19 (3)	5.1 \pm 1.7
B	<i>B. gracilis</i>	20.4 \pm 2.0	<i>M. leidyi</i>	8.5 \pm 1.6	0.15(2); 0.30 (3); 0.59 (3); 1.19 (2), 2.37 (1)	13.7 \pm 3.4
C	<i>B. gracilis</i>	20.5 \pm 2.9	<i>M. leidyi</i>	12.8 \pm 2.0	0.15(2); 0.30 (3); 0.59 (3); 1.19 (2), 2.37 (1)	13.2 \pm 3.5
D	<i>B. gracilis</i>	23.1 \pm 2.4	<i>M. leidyi</i>	20.6 \pm 2.4	0.15(3); 0.30 (3); 0.59 (3); 1.19 (3)	13.5 \pm 2.6
E	<i>M. leidyi</i>	10.8 \pm 1.1	<i>B. gracilis</i>	1.4 \pm 0.3	2.17 (3), 6.52 (3), 13.04 (4), 26.09 (3)	14.6 \pm 1.6

the holding tanks were acclimatized to experimental water (5 µm filtered Gullmarsfjorden water from 32 m, salinity: 32.7 to 33‰) for 2 to 12 h prior to experiments. Prey ctenophores were first gently added to 13.5 l bottles. The incubations started upon the addition of a single predatory *B. gracilis* to each bottle, after which the bottle was topped and sealed airtight. Bottles were incubated on a rolling table rotating slowly at ~0.5 rpm, in darkness, at 16.9 to 18.2°C for 3.2 to 17 h (12.8 ± 3.3, mean ± SD). At the end of the incubation, the predator was removed and the remaining prey were enumerated. Only incubations during which some, but not all, prey were eaten were used in the subsequent analyses. The fraction of entire prey consumed during these incubations was 0.39 ± 0.17 (mean ± SD). Subsamples of prey were sized (oral-aboral length L_{o-a} , mm) prior to the incubations, while predators were measured (total length L , mm) after the incubations.

Individual clearance rates F (l ind.⁻¹ h⁻¹) were calculated as:

$$F = \frac{V}{tn_{\text{pred}}} \ln\left(\frac{n_{\text{start}}}{n_{\text{end}}}\right)$$

where n_{start} and n_{end} are the number of prey at the beginning and end of the incubation, V is bottle volume (l), n_{pred} is the number of predators (always 1 in our experiments) and t is incubation duration (h). When some of the prey were partly eaten, a search rate (l ind.⁻¹ h⁻¹) was also similarly calculated by replacing n_{end} by the number of undamaged prey remaining at the end of the incubation.

Ingestion I (prey ind.⁻¹ h⁻¹) was calculated as:

$$I = F c_{\text{av}}$$

where c_{av} is the logarithmic average of prey concentration during the incubation (e.g. Kiørboe et al. 1982). For incubation series showing signs of saturation, the maximum clearance rate F_{max} (l ind.⁻¹ h⁻¹) and handling time h (h) were estimated by fitting Holling's disk equation

$$I = \frac{F_{\text{max}} c_{\text{av}}}{1 + F_{\text{max}} h c_{\text{av}}}$$

to the individual ingestion rate data as a function of c_{av} . For non-saturating prey concentrations we also fitted a linear regression, where the slope is a proxy of F_{max} . All curve fitting and associated statistical testing were conducted using SigmaPlot 11.0 and SPSS 16.0.

Digestion rates. For non-tentaculate predators, such as *Beroe gracilis*, capable of quickly ingesting intact large prey, a major part of the prey handling time probably corresponds to digestion time. We therefore quantified digestion time on prey ranging from 4 to 12 mm (L_{o-a}). Pairs of a single *Mnemiopsis leidyi* of a

known size and a single *B. gracilis* without visible gut contents, with predator to prey size ratios of <1, were isolated in beakers and monitored continuously. After a feeding event was recorded, gut contents were checked under a dissection microscope ca. every 5 min until complete digestion, indicated by an absence of visible prey tissue in the gut, was recorded. We observed 40 events in total. Predator length was measured after the experiment. Temperature during the digestion experiments was 19.3 ± 0.5°C (mean ± SD).

***Mnemiopsis leidyi* feeding on *Beroe gracilis*.** We also conducted an incubation series in which small lobate *M. leidyi* ($L_{o-a} = 11 \pm 1$ mm, mean ± SD) were allowed to feed on *B. gracilis* larvae ($L = 1.4 \pm 0.3$ mm, mean ± SD) at prey concentrations ranging from 2.2 to 26.1 ind. l⁻¹ in 2.3 l bottles (Table 1). The bottles were incubated on a plankton wheel (0.2 rpm) for 14.6 ± 1.6 h (mean ± SD) in darkness. Our ability to successfully recover *B. gracilis* larvae was tested with controls without predators (return rate >99%). Experimental procedure and estimation of rates were the same as for the incubations with *B. gracilis* feeding on *M. leidyi*.

RESULTS

Beroe gracilis feeding on *Mnemiopsis leidyi*

B. gracilis fed readily on *M. leidyi* both in the holding tanks and during the experiments. Upon encounter with a potential prey, hungry *B. gracilis* attacked and ingested *M. leidyi* smaller than themselves within seconds (see the supplementary video at www.int-res.com/articles/suppl/m422p129_supp/). We qualitatively observed *B. gracilis* feeding on 3 mm (L_{o-a}) tentaculate-stage *M. leidyi* larvae when these were presented as prey. However, smaller (<1 mm), recently hatched larvae did not elicit a feeding response in large (>10 mm) *B. gracilis*, even at direct contact with the mouth. Transitional-stage and small lobate *M. leidyi* were completely ingested, while larger specimens were often partially consumed. In the majority of the partial feeding cases, *B. gracilis* attacked a *M. leidyi* lobe, cleanly biting off as much as they could ingest. The proportion of partially consumed prey increased with prey size, and in the largest prey size group all feeding was partial (Fig. 1). Because of partial feeding, we estimated clearance rates for the consumption of whole prey items, as well as search rates (l ind.⁻¹ h⁻¹) that take into account all encounters ending in complete or partial consumption of prey (Table 2). Since we have no way of knowing whether the complete or partial consumption of prey observed at the end of an incubation is the result of a single encounter or several partial feeding events, these values should be considered conserva-

Table 2. *Beroe gracilis* and *Mnemiopsis leidyi*. Summary of results (mean \pm SD) of *B. gracilis* feeding rates on *M. leidyi*. Significance levels for the fit (after R^2) and for each fitted parameter are given (no asterisk: not significant; * : 0.05 > p \geq 0.01; ** : 0.01 \geq p > 0.001; *** : p < 0.001). Mean digestion time for each prey size group was extrapolated from regression of digestion on length (see Fig. 4). For partially consumed prey a search rate was calculated instead of a clearance rate. Clearance rates used for estimating *in situ* mortality (see Fig. 6) are in **bold**

Prey oral-aboral length (mm)	Whole prey		Whole and partial prey		Digestion time (h prey ⁻¹)
	Linear regression Clearance rate (l ind. ⁻¹ h ⁻¹)	R ²	Search rate (l ind. ⁻¹ h ⁻¹)	R ²	
5.9 \pm 0.9	0.69^a	—	—	—	4.27
8.5 \pm 1.6	0.55	0.86***	0.57	0.81***	5.66
12.8 \pm 2.0	0.42	0.59*	—	—	9.08
20.6 \pm 2.4	—	—	—	—	18.92

Whole prey		Holling II		Whole and partial prey		Digestion time (h prey ⁻¹)
Clearance rate (l ind. ⁻¹ h ⁻¹)	R ²	Clearance rate (l ind. ⁻¹ h ⁻¹)	R ²	Search rate (l ind. ⁻¹ h ⁻¹)	Handling time (h)	
0.97 \pm 0.76	0.33	—	—	1.18 \pm 0.53	1.78 \pm 0.55**	9.08
—	—	2.62 \pm 1.27	—	1.07 \pm 0.45*	3.84 \pm 0.74**	18.92

^aMean of the individual clearance rates obtained from the 3 replicates conducted at a single, presumably non-saturating prey concentration (see Table 1, Expt A)

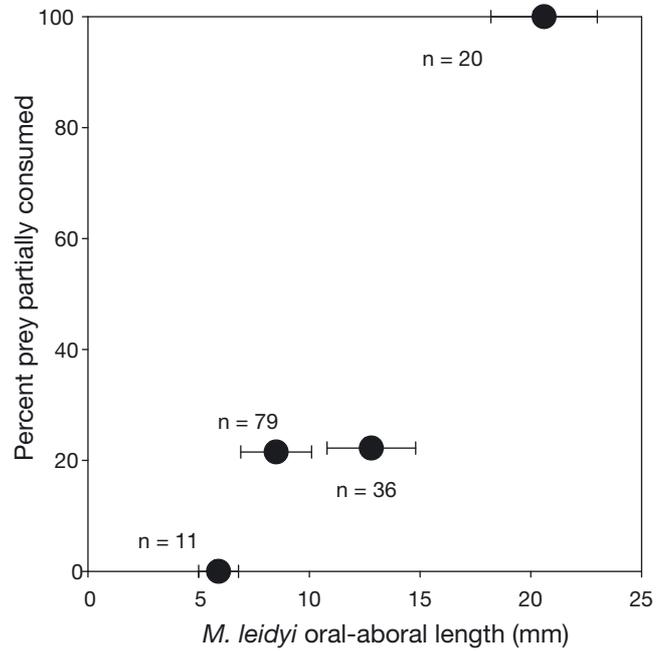


Fig. 1. *Beroe gracilis* and *Mnemiopsis leidyi*. Partial consumption of *M. leidyi* by *B. gracilis* (%) for different prey sizes (mean \pm SD); n is the observed number of feeding events in each size group

Functional response curves (Fig. 2) were estimated both excluding and including partial ingestion.

For the smaller prey (av. L_{o-a} = 8.5 mm), ingestion of whole prey increased linearly with prey concentration through the entire range of concentrations studied (Figs. 2 & 3). For the larger prey sizes (av. L_{o-a} = 12.8 and 20.6 mm), ingestion rates leveled off at higher prey concentrations, suggesting that prey handling was limiting (Fig. 2). The linear regressions, which provided the better fits for the non-saturating prey concentrations for prey sizes 8.5 and 12.8 mm, indicated that F_{max} decreased with prey size (Fig. 2, Table 2). We found no significant effect of predator size (range: 16 to 28 mm) on individual clearance rates (linear regression: R^2 = 0.04, p = 0.306, n = 30).

Digestion rates

Digestion time for prey with L_{o-a} of 4 to 12 mm ranged from 1.6 to 8.4 h prey⁻¹ and increased with prey size (Fig. 4). A partial correlation between prey wet weight and digestion time controlling for predator size confirmed that prey wet weight could explain much of the variation in digestion time (partial r = 0.708, p < 0.001, df = 37), while a partial correlation between predator size and digestion time controlling for prey wet weight indicated predator size was not significant in determining digestion time (partial r = -0.246, p = 0.13, df = 37).

Mnemiopsis leidyi* feeding on *Beroe gracilis

Both transitional stage and adult *M. leidyi* were able to feed on *B. gracilis* larvae (Fig. 5). Larvae were caught with tentilla as well as lobes and were digested

after ingestion. In incubations with small lobate *M. leidyi* as predators, the ingestion rate leveled off to about 1.2 prey ind.⁻¹ h⁻¹ with increasing prey concentrations, yielding an F_{max} of 0.35 l ind.⁻¹ h⁻¹ and a handling time of 0.70 h (Fig. 5).

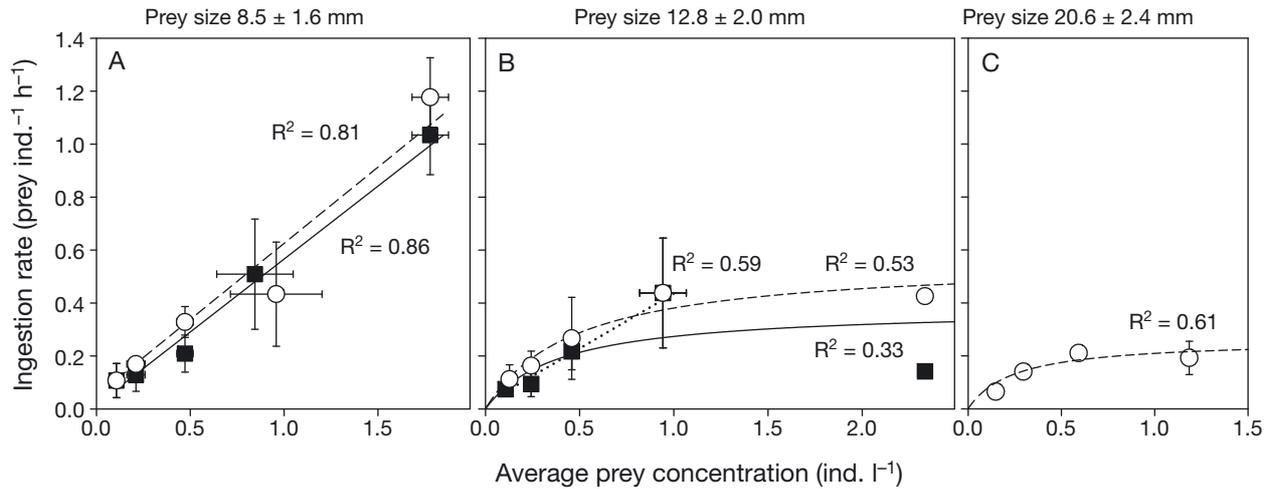


Fig. 2. *Beroe gracilis* and *Mnemiopsis leidyi*. Effect of prey size (oral-aboral length) and concentration on *B. gracilis* feeding on *M. leidyi*. Black squares show ingestion of whole prey items (mean \pm SD); white circles include partial consumption. Incubations are grouped according to initial prey concentration c_0 (see Table 1). Because all consumption in Panel C is partial, the average prey concentration here equals c_0 . Lines fitted on non-averaged data show linear regressions in Panel A; Holling's disk equation was used for the data shown in Panels B and C. Solid lines are for consumption of entire prey items; hatched lines also include partial feeding; the dotted line in Panel B shows linear regression on consumption of entire prey items (non-averaged data) for the non-saturating prey concentrations. For estimates of clearance rates and handling times, see Table 2

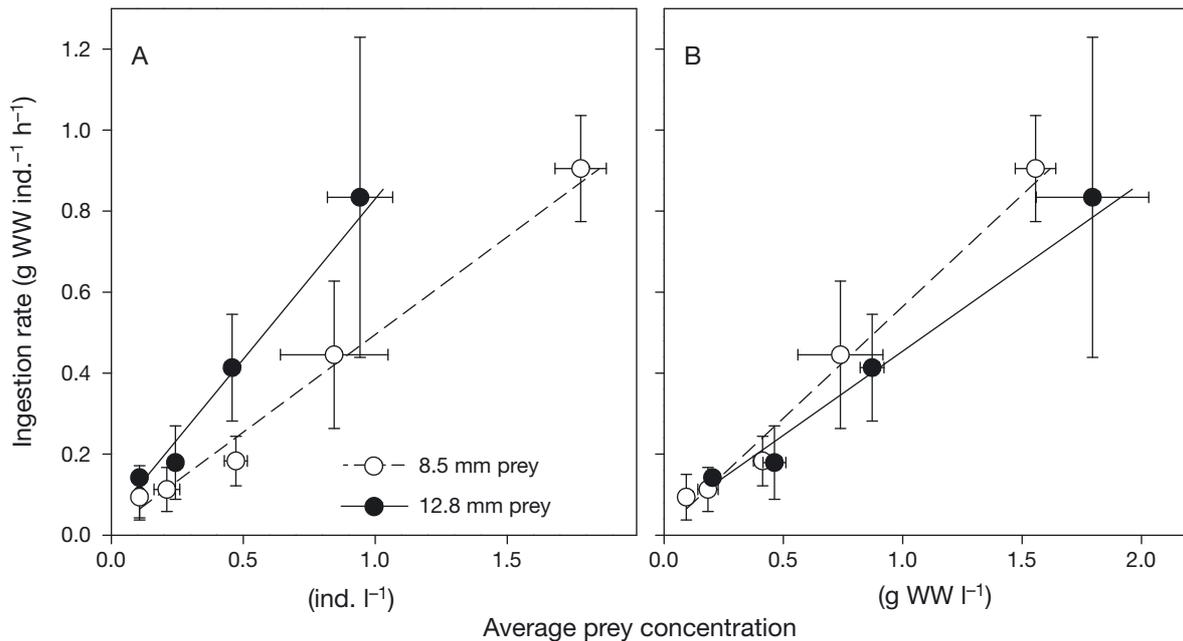


Fig. 3. *Beroe gracilis* and *Mnemiopsis leidyi*. *B. gracilis*' ingestion of 8.5 and 12.8 mm (mean oral-aboral length) *M. leidyi* in terms of wet weight, non-saturating concentrations of completely consumed prey only; prey concentration is given in terms of (A) individuals and (B) wet weight per liter. Linear regressions are for 8.5 mm prey (hatched line; $p < 0.001$, $R^2 = 0.86$) and for 12.8 mm prey (solid line; $p = 0.016$, $R^2 = 0.59$). Wet weight was converted according to $g\ WW = 0.015(mm\ L_{0-a})^{1.9}$ (L. Friis Møller unpubl. data)

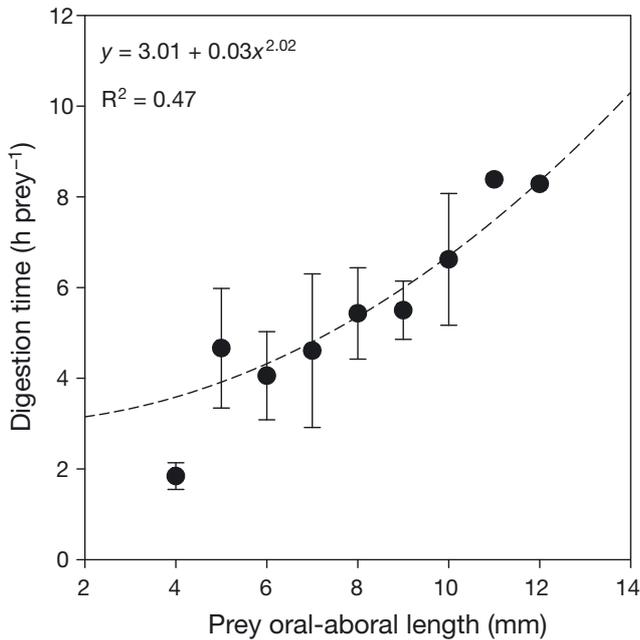


Fig. 4. *Beroe gracilis* and *Mnemiopsis leidyi*. *B. gracilis* digestion time (mean \pm SD) increases with oral-aboral length of *M. leidyi* prey at $19.3 \pm 0.5^\circ\text{C}$ (mean \pm SD) ($n = 40$, $R^2 = 0.47$, $p < 0.001$)

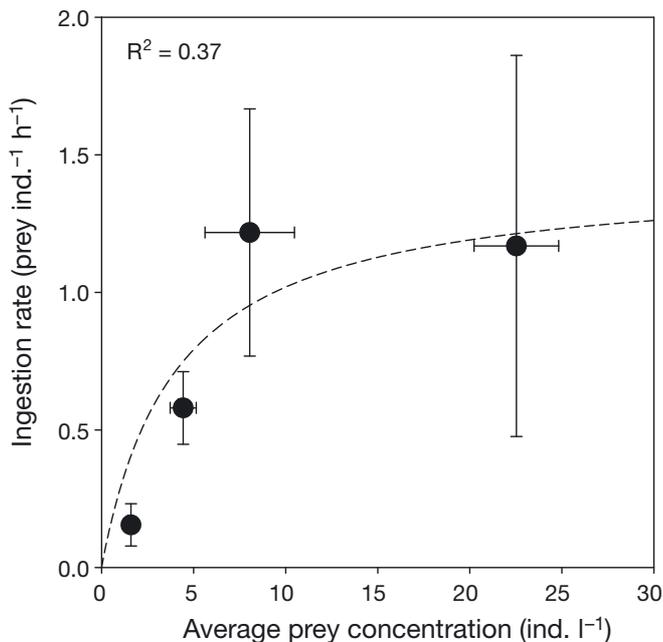


Fig. 5. *Beroe gracilis* and *Mnemiopsis leidyi*. Functional response of *M. leidyi* (11 mm mean oral-aboral length) feeding on *B. gracilis* larvae. Incubations are grouped according to initial prey concentration. Means (\pm SD) are shown for ingestion rate and average prey concentration during incubation. Line represents Holling's disk equation fitted to non-averaged data ($R^2 = 0.37$, $p = 0.028$)

DISCUSSION

North Sea *Beroe gracilis*, previously considered a specialist feeder on *Pleurobrachia pileus* (Greve 1970, Greve & Reiners 1988), feeds readily on the introduced *Mnemiopsis leidyi* and reproduces successfully on this diet. *B. gracilis* may be able to utilize *M. leidyi* as prey throughout their development. Young *B. gracilis* are able to feed on young *P. pileus* of suitable size (Greve 1970), and, since larval lobate and cydippid ctenophores are similar in size and morphology, they can probably also prey on *M. leidyi* larvae. We also observed larval *B. gracilis* attaching to adult *M. leidyi*. It remains unclear whether the larvae were indeed feeding, as no wounds could be detected on *M. leidyi* under a stereomicroscope. However, Greve (1970) described a similar behavior with *B. gracilis* larvae attaching themselves to *P. pileus* and called it 'a kind of temporary ectoparasitism'.

Reversal of roles

The association between *Mnemiopsis leidyi* and *Beroe gracilis* populations is not straightforward, as the predatory interactions between the 2 species are size dependent and their roles may be interchanged. We found that transitional-stage and larger *M. leidyi* can in turn ingest and digest larval *B. gracilis* (Fig. 5). The ingestion rate increased up to 8 prey l⁻¹ and leveled out at ca. 1.2 prey ind.⁻¹ h⁻¹ (Fig. 5). The functional response of similarly sized *Bolinopsis infundibulum* (Sørnes & Aksnes 2004) and *M. leidyi* (Hansson et al. unpubl. data) feeding on *Artemia salina* nauplii does not level out until ca. 200 prey l⁻¹. However, by prey volume, *M. leidyi* reaches saturation at similar concentrations: 7.4 mm³ l⁻¹ for *B. gracilis* prey at a saturation concentration of 10 ind. l⁻¹ and 7.8 mm³ l⁻¹ for *A. salina* nauplii at a saturation concentration of 200 ind. l⁻¹ (assuming prey volumes of 0.74 mm³ for 1.4 mm *B. gracilis* larvae and 0.039 mm³ for 0.7 mm *A. salina* nauplii). This suggests that gut volume is an important part of the handling limitation in *M. leidyi*.

Predation of *Beroe* spp. larvae by abundant *Mnemiopsis leidyi* could preempt predation pressure by reducing *B. gracilis* numbers before they reach a size at which they are able to reproduce and feed on *M. leidyi*. Similar dynamics with switching of roles have been observed for other gelatinous prey-predator pairs such as *Aurelia aurita* and *Cyanea capillata* (Gröndahl 1988, Titelman et al. 2007), as well as *Aequorea victoria* and *Clytia gregaria* (Pennington 1990). However, such effects are, in this case, probably minor, as they have not been reported from other areas where *Beroe* sp. and *M. leidyi* co-occur.

Role of prey size

The impact of *Beroe gracilis* predation on *Mnemiopsis leidyi* depends on prey size. Most importantly, *B. gracilis* are unable to completely ingest *M. leidyi* approaching their own size (Fig. 1). *M. leidyi* thus experience a size refuge from predation by *B. gracilis* in the North Sea, where *B. gracilis* typically grows to about 3 cm (Greve 1970), while *M. leidyi* can approach 7 cm in oral-aboral length (M. Haraldsson et al. unpubl. data). When feeding on *Pleurobrachia pileus*, *B. gracilis* discards prey larger than itself (Greve 1975). However, the lobate form of *M. leidyi* is much more vulnerable to partial feeding than the compact ovoid shape of *P. pileus*, and large *M. leidyi* prey were partially consumed rather than rejected. Partial feeding behavior, where macrociliary teeth are used to bite off pieces of prey, is common in beroids and has also been observed for *B. cucumis* (Falkenhaus & Stabell 1996) and *B. ovata* (Swanberg 1974) feeding on lobate ctenophores.

Because of the impressive regenerative abilities of *Mnemiopsis leidyi* (Henry & Martindale 2000), losing a lobe is rarely fatal. *M. leidyi* that escape capture by jellyfish predators, but lose tissue in the process, regenerate the lost parts in a few days (Kreps et al. 1997, Hosia & Titelman 2010). Nevertheless, the wounded ctenophores suffer reduced fitness due to allocation of energy to healing and regeneration rather than to growth and reproduction. A severed lobe is also likely to affect feeding efficiency and reproductive output, as both the prey capture surface and the length of the meridional canals used for reproduction decrease (Purcell & Cowan 1995). The wounded individual can also become more susceptible to further predation, both because of reduced swimming performance and because exudates from the wounded prey may stimulate intensified search behavior by predators. *Beroe cucumis* responds to *Bolinopsis infundibulum* extracts by increased swimming (Falkenhaus & Stabell 1996), and we also observed that *B. gracilis* increased cruising activity when bits of *M. leidyi* were added to the holding containers.

No handling limitations were apparent when *Beroe gracilis* were feeding on *Mnemiopsis leidyi* considerably smaller than their own size (cf. Fig. 2). The *B. gracilis* cruised around actively searching for prey, and small *M. leidyi* could be rapidly ingested upon encounter (see supplement). For larger prey, however, handling limitations became more apparent with increasing prey size. The handling time h estimated from Holling's disk equation is influenced by prey pursuit, capture, ingestion and digestion time. Comparing h with the quantified digestion time for *B. gracilis* feeding on *M. leidyi* suggests that handling limitations

largely stem from digestion (Table 2), the duration of which increased with prey size (Fig. 4). While we do not know the exact digestion times for partial feeding on the largest prey, we can expect these to be generally high because *B. gracilis* often seemed to engulf as much of the attacked lobe as they could before biting it off. Other processes may also have contributed to the longer handling times of large prey, although they are probably of less importance. For example, the ingestion process may take longer for larger prey, and while the process of biting off a piece of lobe with the macrociliary teeth (Swanberg 1974) was relatively quick, it still increases prey handling time compared to swallowing a prey whole.

For all prey sizes, the extrapolated digestion time was much longer than the estimated h (Table 2). This is because it is available gut space rather than the ongoing digestion process per se that limits further feeding (Hansson & Kiørboe 2006), so that multiple prey can be handled simultaneously. We, for example, observed a *Beroe gracilis* ingesting one transitional-stage *Mnemiopsis leidyi* and then, upon encounter, ingesting a second one within minutes, so that both were undigested and clearly visible in the gut. A relatively large portion of the observed digestion time was often spent on the last poorly digestible morsels, possibly prey gut contents egested at the end of the digestion process (Swanberg 1974), which would be unlikely to hinder further feeding.

Linear regressions provided the best fit for functional response under limiting prey concentrations for prey with mean L_{0-a} of 8.5 and 12.8 mm (Fig. 2, Table 2). The maximum observed ingestion rate in terms of numbers of prey was more than twice as high for the smaller of these prey size groups (Fig. 2). However, ingestion rates in terms of wet weight, and thus energetic gain, were similar when feeding on the 2 prey size groups (Fig. 3). The similarity of the functional response curves (Fig. 3) for the 8.5 and 12.5 mm L_{0-a} size groups would be further increased if partial feeding was also taken into account. For the 12.5 mm L_{0-a} prey size group, further increases in prey concentration invoked handling limitations (Fig. 2). Assuming *Beroe gracilis* feeding is limited by gut volume, we could expect handling limitations at prey concentrations exceeding our experimental maxima (i.e. 2.37 ind. l⁻¹), also for 8.5 mm prey (Fig. 2).

Ecological relevance

It is quite common for gelatinous species to feed on one another (reviewed by Purcell 1991, 1997, Arai 2005). For example, *Beroe gracilis*' congener *B. ovata* has been shown to exert control on the *Mnemiopsis lei-*

dyi populations in the NW Atlantic (Purcell et al. 2001 and references therein) and in the Black Sea (Kideys 2002, Stone 2005). Estimated clearance rates (based on equations in Finenko et al. 2003) for 2 to 10 cm sized *B. ovata* feeding on *M. leidy* in the Black Sea are ca. 0.11 to 0.14 l ind.⁻¹ h⁻¹. This is somewhat lower than our figures for *B. gracilis* (Table 2). Predation by *B. cucumis* has, in turn, been implicated in population reductions of the lobate *Bolinopsis infundibulum* along the Norwegian coast (Falkenhaus 1996). In the North Sea, *B. gracilis* itself controls *Pleurobrachia pileus* populations (Greve 1981, Greve & Reiners 1988). However, *B. gracilis* is smaller than the other mentioned *Beroe* species capable of controlling populations of large lobate ctenophores, and its small size relative to *M. leidy* affects the dynamics between these 2 species.

Little quantitative data for feeding amongst jellies is to be found in the literature (but see e.g. Strand & Hamner 1988, Purcell & Cowan 1995, Titelman et al. 2007), making it difficult to assess potential mortality in field populations. We applied our feeding rates to concurrent *in situ* abundances of *Mnemiopsis leidy* and *Beroe gracilis* at a nearby monitoring station (Släggö, Gullmarsfjorden), taking into account their vertical and size distributions (Fig. 6; M. Haraldsson et al. unpubl. data). *B. gracilis*-induced mortality on the entire *M. leidy* population was only $8.8 \times 10^{-4} \text{ d}^{-1}$, when calculated as $\mu_{\text{pop}} = \sum(\mu_{id} c_{id} s_d) / \sum(c_{id} s_d)$, where μ_{id} is the mortality and c_{id} is the concentration of prey size group i in depth stratum d , and s_d is the height of the sampled depth stratum (see Fig. 6 legend for details). The overall mortality was much reduced by the large portion of the *M. leidy* population that was too big for complete ingestion by *B. gracilis*. Mortality from *B. gracilis* predation was highest close to the surface, where the fraction of oversized prey was smallest and *B. gracilis* was most abundant. The fraction of *M. leidy* too large to be consumed by *B. gracilis* increased with depth, with all individuals below 30 m safe from complete ingestion.

The *in situ Beroe gracilis* size at Släggö was $16.1 \pm 5.2 \text{ mm}$ (mean \pm SD), the mean size thus being close to the smallest predator sizes used in our experiments. We did not consider *B. gracilis* size in the *in situ* mortality rate estimations because we found no effect of size on individual clearance rates in our experiments. Nevertheless, it may be assumed that *B. gracilis* towards the lower range of the *in situ* size spectrum would have been able to completely ingest only the smaller size fractions of *Mnemiopsis leidy*, further diminishing the actual *in situ* mortality.

Despite significant feeding on *Mnemiopsis leidy* in the experiments, *Beroe gracilis* was thus at the time of our study unlikely to significantly reduce the *M. leidy* population *in situ*. However, this was only a momen-

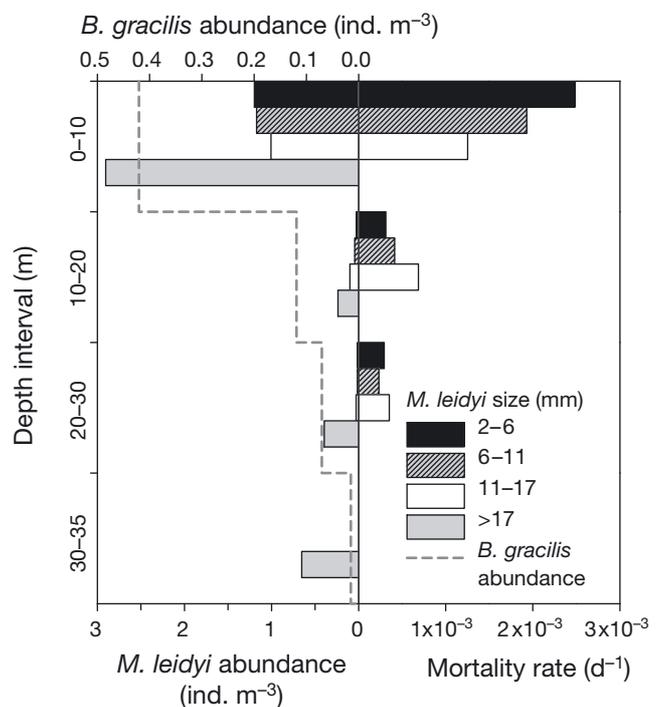


Fig. 6. *In situ* abundances of >2 mm ctenophores (M. Haraldsson et al. unpubl. data) and predation-induced mortality for different depths and prey sizes at Släggö station (58.15° N, 11.26° W, 14 September 2009). Bars: *Mnemiopsis leidy*; dashed line: *Beroe gracilis*. *M. leidy* prey are divided into oral-aboral length categories roughly corresponding to the ones used in our incubations, and size-specific clearance rates (in bold, Table 2) were applied to these groups. Clearance rate estimates from linear regression were used for calculations for prey sizes 8.5 and 12.8 mm because the *in situ* abundances of *M. leidy* were well below limiting prey concentrations. We assumed that no *M. leidy* of >17 mm are consumed entirely. Prey mortality rates μ (d^{-1}) were calculated separately for each prey size group i in each depth stratum d as $\mu_{id} = F_i P_d c_{id} / c_d$, where F_i ($\text{ind. l}^{-1} \text{ d}^{-1}$) is the size-specific clearance rate, P the predator concentration (ind. l^{-1}) and c the prey concentration (ind. l^{-1}). We assumed equal encounter rates for the different prey sizes and therefore calculated μ_{id} as proportional to the fraction of prey in each size class. An oblique tow with a 300 μm Multinet (Hydrobios) equipped with a flow meter was used to sample the ctenophores

tary glimpse, and the effect will vary as the relative abundances and size ranges of the 2 species change over time.

The spatial and temporal occurrences of the 2 species in the North Sea do overlap to a large degree, and the invasive ctenophore could thus become an attractive and important prey for *Beroe gracilis*. In addition to *B. gracilis*, other native gelatinous predators may turn out to have an impact on *Mnemiopsis leidy* populations, thus helping to avoid in this region the problems experienced in the Ponto-Caspian region. The other North Sea beroid, *B. cucumis*, can grow to >10 cm in length and is assumed to primarily feed on

the native lobate *Bolinopsis infundibulum* (Greve 1970, Falkenhaus & Stabell 1996), similar to *M. leidy* in size. With *B. cucumis* as a predator, *M. leidy* would thus probably not experience the same size refuge as with *B. gracilis*. We observed *B. cucumis* feeding on *M. leidy* in captivity, but did not have enough animals for experimentation. There are also several species of scyphomedusae native to the North Sea, most notably *Cyanea* spp. and *Chrysaora hysoscella*, which are able to feed on *M. leidy* (Hosia & Titelman 2010). The sheer numbers of *M. leidy* in the Skagerrak, Kattegat and other North Sea locations make it an important potential prey item for any native predator of gelatinous zooplankton in these regions.

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