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Research article

Invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark) in late summer 2007 - assessment of abundance and predation effects

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Abstract

The invasive ctenophore, *Mnemiopsis leidyi*, was recently observed for the first time in Danish waters where it was widely distributed during the summer of 2007. In certain areas, including Limfjorden, it exhibited mass occurrence. In this study, we assess the abundance of *M. leidyi* in Limfjorden in the late summer of 2007 and give a preliminary evaluation of the predation effects of this ctenophore. On two cruises in August and September, *M. leidyi* was found in every net sample from 9 locations in Limfjorden. The population densities were high, up to more than 800 individuals m^{-3} in the innermost part, but body lengths were small (5 to 15 mm). The bio-volumes were very high (100 and 300 ml m^{-3}) in the central parts of Limfjorden and are even greater than those from the Black Sea, where the greatest mean bio-volume was about 184 ml m^{-3} in the autumn of 1989 when the zooplankton and fish stocks collapsed. The possible ecological consequences of the mass occurrence of this ctenophore are discussed.

Key words: Ctenophora, comb jelly, alien species, jellyfish, zooplankton, *Aurelia aurita*, *Beroe* sp.

Introduction

The native habitats of the invasive lobate ctenophore *Mnemiopsis leidyi* are coastal waters along the Atlantic coast of North and South America (Purcell et al. 2001). In the early 1980s, it was unintentionally brought to the Black Sea in the ballast water of cargo ships and exhibited mass occurrences that peaked in 1989 and coincided with a breakdown of the pelagic fisheries in the Black Sea (Purcell et al. 2001, Shiganova et al. 2001, Kideys and Romanova 2001). *M. leidyi* is a voracious zooplanktivore (e.g. Purcell and Decker 2005), and a catastrophic decrease in zooplankton inevitably influenced the stocks of planktivorous fishes (sprat, anchovy, and horse-mackerel). The catch of those fishes in 1991 was less than one-fifth of that in 1988 (Shushkina et al. 2000). The collapse of fishing in the Black Sea was probably caused by a combination of over-fishing, food competition from the zooplanktivorous ctenophore, and predation of *M. leidyi* on fish eggs and larvae (Bilio and Niermann 2004). Later, the invasive ctenophore spread into the Azov, Marmara, Aegean, and Caspian Seas where similar effects were observed (Shiganova et al. 2001, Kideys and Romanova 2001, Bilio and Niermann 2004, Finenko et al. 2006). In the late summer of 1999, another ctenophore, *Beroe ovata*, also unintentionally carried into the Black Sea, occurred in mass. *B. ovata* consumes other ctenophores, including *M. leidyi*. After *B. ovata* was introduced *M. leidyi* decreased by a factor of almost ten, thus reducing predation pressure on the zooplankton (Shushkina et al. 2000). This has raised the expectation that *B. ovata* may exhibit some control of *M. leidyi*, but it is uncertain whether the predatory capacity of the former is sufficient to control the latter in other than locally favourable conditions (Finenko et al. 2001, Purcell et al. 2001, Bilio and Niermann 2004).

During the late summer of 2006, blooms of *M. leidyi* were observed along the coast of The Netherlands (Faasse and Bayha 2006). Presumably, *M. leidyi* came to the Dutch coast in ballast water. Subsequent expansion of *M. leidyi* into neighbouring waters and far into the Baltic Sea is of major concern (Javidpour et al. 2006, Kube et al. 2007, Boersma et al. 2007, Oliveira 2007, Haslob et al. 2007, Lehtiniemi et al. 2007). The occurrence of *M. leidyi* in Danish waters was recently described by Tendal et al. (2007) who concluded from numerous reports that the ctenophore was widely distributed in all inner Danish waters in the summer of 2007, and in certain areas, including Limfjorden, it exhibited mass occurrence.

In the present study, we assess the abundance of *M. leidyi* in Limfjorden in August and September 2007, and evaluate its possible predation effects on zooplankton.

Materials and Methods

Study area

Limfjorden is not a true fjord, but a 1500 km^2 water system that connects the North Sea via Thyborøn Kanal in the west with the Kattegat in the east (Figure 1). It consists of several basins that are separated by shallow waters or narrow sounds. The average depth is 4.3 m and maximum depth is 28 m. An eastward current brings high salinity (usually > 30 PSU) North Sea water into Limfjorden, which also receives fresh water from the surrounding land area. This results in a salinity gradient from west to east and brackish water conditions in the inner parts (salinities of about 20 to 25 PSU). During summer a thermocline stabilizes this stratification, which is only broken by strong winds (Jørgensen 1980, Møhlenberg 1999, Møller and Riisgård 2007a).

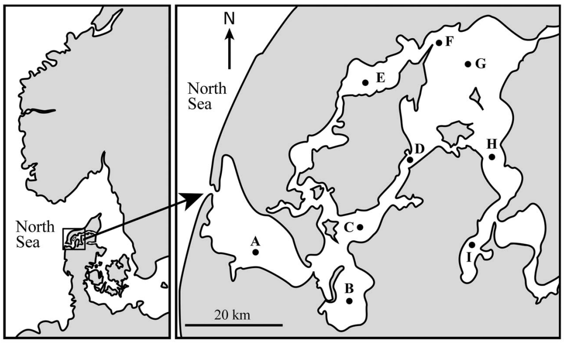

Figure 1. Locations in Limfjorden where *Mnemiopsis leidyi* were collected on two cruises, 7-8 August (A,D,E,F,G,H,I) and 11-12 September (C,D,E,G,H,I) 2007, respectively. A = Nissum Bredning, B = Venø Bugt, C = Kås Bredning, D = Sallingsund, E = Thisted Bredning, F = Feggesund, G = Løgstør Bredning, H = Junget Øre, I = Skive Fjord

The inner parts of the heavily eutrophic Limfjorden therefore, suffer every summer from oxygen depletion in the near-bottom water, which causes large amounts of nutrients (phosphate and ammonia) to be released from the anoxic sediments. This subsequently stimulates a phytoplankton bloom, followed by an increase in zooplankton. A recent study by Møller and Riisgård (2007a) indicated that especially severe cases of oxygen depletion take place in years with mass occurrence of the common jellyfish Aurelia aurita, which consumes zooplankton, allowing the ungrazed algal bloom to settle to the bottom and decompose, resulting in more severe oxygen depletion.

Field investigations

Ctenophores and other jellyfish were collected with a 2 mm-mesh plankton net (1.77 m^2 mouth area) at 9 locations in western and central Limfjorden during two cruises in 2007: 7 to 8 August (water temperature 18-19 °C), and 11 to 12 September (15 °C) (Figure 1). The net was equipped with a closed cod end bucket to prevent damage to the gelatinous plankton. At each location, three hauls were made by raising the net obliquely from the bottom to the surface at a speed of 1.5 knot through a distance of 18.5 m for population density estimates. After each haul, representing a filtered volume of 18.5 m×1.77 m^2 = 32.8 m^3, the number of ctenophores in the sample was estimated by counting live ctenophores from a 1-l subsample from the net-bucket, and multiplying that number by the total volume of ctenophores in the net-bucket. The mean size of the ctenophores was determined by measuring the distance between mouth and opposite pole (oral-aboral length) on 50 individuals with a Vernier caliper. This linear measure is about 65% of the total body length including the oral lobes; oral-aboral length is a more reliable measurement because the lobes are frequently damaged in net hauls.

Predation impact

Estimation of filtration rate. Decker et al. (2004) measured filtration rates (= clearance) of small *M. leidyi* (mean volumes 2.3 - 3.9 ml) feeding on the copepod *Acartia tonsa* at about 22°C in 90 l aquaria as 0.11 l h^{-1} per ml of ctenophore (= 2.64 l d^{-1} ml^{-1}). Thus, the following equation was used to estimate the individual filtration rate (F_{ind}, l d^{-1}) of ctenophores from the mean body volume (V, ml) at each location (Table 1) in the present work:

$$F_{ind} = 2.64V \qquad \text{Eq. (1)}$$

Population filtration rate. The volume-specific population filtration rate (F_{pop}, m^3 water filtered by the ctenophore population in one m^3 water per day = d^{-1}) was estimated as the product of the individual filtration rate (F_{ind}, l d^{-1}) and the population density (D, ind. m^{-3}) for each locality:

$$F_{pop} = F_{ind} \times D/1000 \qquad \text{Eq. (2)}$$

Half-life time of zooplankton. The time it takes for a population of *M. leidyi* to reduce the concentration of zooplankton (copepods) by 50 % (half-life time; e.g. Riisgård et al. 2004, Hansson et al. 2005) was estimated as:

$$t_{1/2} = \ln2/F_{pop} \qquad \text{Eq. (3)}$$

Biometric conversion. Oral-aboral length (L, mm) and body volume (V, ml) were measured on 20 *M. leidyi* ranging from 7 to 31 mm and the following relationship was obtained:

$$V = 0.0226L^{1.72} \; (R^2 = 0.854) \qquad \text{Eq. (4)}$$

Results and Discussion

The ctenophore *M. leidyi* was found in every net sample from the 9 locations in Limfjorden (Figure 1, Table 1). In general, both population density and bio-volume of ctenophores increased from Nissum Bredning in the western part of Limfjorden towards Skive Fjord in the innermost part (Figure 2A, B). The population densities

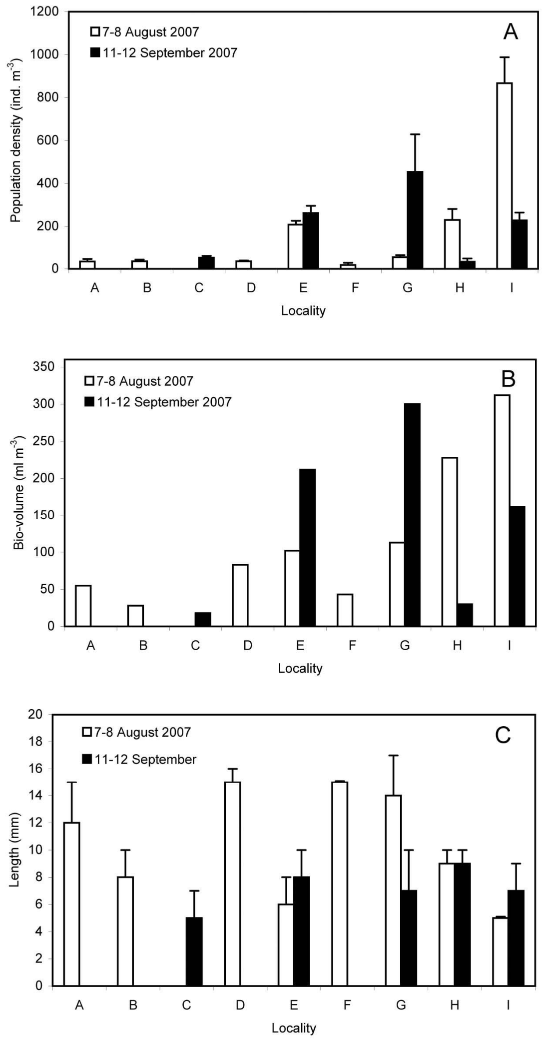

Figure 2. *Mnemiopsis leidyi*: (A) Mean (+ SD) population densities, (B) population bio-volumes, and (C) oral-aboral length (+SD) of ctenophores collected 7-8 August and 11-12 September 2007 from different locations in Limfjorden, Denmark. Locations are identified in Figure 1 and Table 1

generally were high, up to more than 800 individuals m^{-3} in Skive Fjord in August 2007 (Table 1), whereas the body length of the ctenophores at all locations was small, between 5 to 15 mm (Figure 2C) suggesting that no increase in body length had taken place during the about 5 weeks between the two sampling times. Because of water exchange, however, the same population may not have been sampled on the two dates. In Limfjorden, vertical variation in salinity is frequently observed due to freshwater input from the catchment area and to the pronounced near-bottom inflow of high-density saline water from the North Sea. This causes density-driven currents which may influence the distribution and abundance of jellyfish in different parts of Limfjorden (Møller and Riisgård 2007a, b). Thus, for example, at location G (Løgstør Bredning) a pronounced salinity spring-layer was observed at 4-6 m depth on 4 September 2007 (salinity in upper layer = 27; lower layer = 28.5),

Table 1. *Mnemiopsis leidyi* collected during two cruises in Limfjorden in 2007, 8 locations on 7-8 August, and 5 locations on 11-12 September, respectively (see Fig. 1). D = mean (±SD) population density based on 3 hauls; L = mean (±SD, n = 50) body length; estimated individual body volume (cf. equation 4); B = D × V = specific bio-volume of ctenophores; F_{ind} = individual clearance rate; F_{pop} = population clearance rate; $t_{1/2}$ = estimated half-life time

Locality	Position	D (ind. m^{-3})	L (mm)	V (ml ind.$^{-1}$)	B (ml m^{-3})	F_{ind} (l d^{-1})	F_{pop} (d^{-1})	$t_{1/2}$ (d)
Cruise I 7-8 August 2007								
A Nissum Bredning	56°36.05N 08°24.89E	34 ± 12	12 ± 3	1.62	55	4.3	0.145	4.8
B Venø Bugt	56°31.39N 08°40.46E	35 ± 8	8 ± 2	0.81	28	2.1	0.074	9.3
D Sallingsund	56°46.62N 08°53.30E	35 ± 4	15 ± 1	2.37	83	6.2	0.219	3.2
E Thisted Bredning	56°55.20N 08°44.25E	208 ± 18	6 ± 2	0.49	102	1.3	0.269	2.6
F Feggesund	56°58.51N 08°55.19E	18 ± 10	15 ± 0	2.4	43	6.3	0.114	6.1
G Løgstør Bredning	56°57.15N 09°03.46E	54 ± 10	14 ± 3	2.1	113	5.5	0.299	2.3
H Junget Øre	56°47.00N 09°08.50E	230 ± 51	9 ± 1	0.99	228	2.6	0.601	1.2
I Skive Fjord	56°37.25N 09°05.55E	867 ± 121	5 ± 0	0.36	312	1.0	0.824	0.8
Cruise II 11-12 Sept. 2007								
C Kås Bredning	56°39.40N 08°42.38E	52 ± 8	5 ± 2	0.35	18	0.9	0.048	14.4
E Thisted Bredning	56°55.20N 08°44.25E	262 ± 34	8 ± 2	0.81	212	2.1	0.560	1.2
G Løgstør Bredning	56°57.15N 09°03.46E	454 ± 175	7 ± 3	0.66	300	1.7	0.791	0.9
H Junget Øre	56°47.00N 09°08.50E	33 ± 15	9 ± 1	0.92	30	2.4	0.080	8.6

but one week later on 11 September the salinity was 27.5 from surface to bottom, indicating that horizontal movement of water masses (and ctenophores) had occurred between the two dates.

Ctenophore bio-volumes were high in the central parts of Limfjorden, between about 100 and 300 ml m^{-3} (Figure 1, Table 1). These values may be compared to the Black Sea with average bio-volumes of up to about 40 ml m^{-3} in 1988, and to the greatest mean bio-volume of about 184 ml m^{-3} in the autumn of 1989 (Purcell et al. 2001).

Individual clearance rates estimated for the small ctenophores in Limfjorden (mean oral-aboral lengths of 5 -15 mm and volumes of 0.4 - 2.4 ml) ranged from 0.9 to 6.3 l d^{-1}, and averaged 3.0 ± 2.1 l d^{-1} (Table 1). Purcell et al. (2001) pointed out that clearance rates of *M. leidyi* increase with container size and could be seriously underestimated in < 20 l aquaria; therefore, we believe these rates to be representative of clearance rates in situ. An important additional food source for small *M. leidyi* is microplankton (e.g. Sullivan and Gifford 2004). We have estimated clearance rates of *M. leidyi* feeding on microplankton from their equation for ctenophores 1 to 15 mm in length. These rates for clearance of micro-plankton (mean 2.2 ± 0.8 l ind^{-1} d^{-1}) were similar to the above rates for copepods.

The ctenophore population was estimated to filter copepods from 5% to 80% of the water column daily (mean 34.3 ± 27.8% d^{-1}). The estimated half-life times of zooplankton (copepods) were very short (~1 day) at certain locations, and relatively short (mean 4.4 ± 4.3 d) at most other locations (Table 1). In Chesapeake Bay, USA, copepod densities were very low when *M. leidyi* clearance rates were estimated to be 20-45% d^{-1} (Purcell and Decker 2005). In the Black Sea, *M. leidyi* was estimated to consume as much as 30-40% d^{-1} of the mesozooplankton and 23-25% d^{-1} of the microzooplankton (Finenko et al. 2006). High clearance rates by ctenophores occurred in both locations when predators of the ctenophores were in low abundance. Thus, the clearance rates we estimated suggest that *M. leidyi* predation could seriously affect zooplankton populations in Limfjorden.

More knowledge about the effect of *M. leidyi* size on water processing and retention efficiencies of different types and different sizes of prey organisms (Waggett and Costello1999, Waggett and Sullivan 2006, Sullivan and Gifford 2007) is needed to more precisely assess the actual predation impact of this ctenophore in Limfjorden; the generally small size of *M. leidyi* in Limfjorden (5 to 15 mm body length, Table 1) further emphasizes this lack of knowledge.

Mass occurrences of *M. leidyi* in Limfjorden in August-September 2007 appear to have impacted the zooplankton biomass; the lack of ctenophore growth during the 5 weeks between the two cruises supports this suggestion. Furthermore, high concentrations of chlorophyll "a" measured in September in Junget Øre (9.9 µg l^{-1}) and Skive Fjord (22.0 µg l^{-1}), which may be compared to only 2.0 µg l^{-1} in Nissum Broad, might indicate reduced grazing by zooplankton in the central parts of Limfjorden. Zooplankton data (available in January 2008) collected by the environmental authorities may clarify this.

In some years, high densities of the common jellyfish *Aurelia aurita* have been observed in Limfjorden, especially in Skive Fjord (Møller and Riisgård 2007a). Recent studies show that the predation effect of the jellyfish on zooplankton may be particularly pronounced in Skive Fjord in July and August (Hansson et al. 2005, Møller and Riisgård 2007a, b). In August 2003 when *A. aurita* was blooming, the estimated half-life time of zooplankton was only 5 to 12 h, coincident with low concentrations of zooplankton and high chlorophyll "a" concentrations. This indicates that high densities of jellyfish may prevent the zooplankton from rapidly grazing down the blooming phytoplankton (Møller and Riisgård 2007a).

During the two cruises reported here, very few *A. aurita* were observed, except in Skive Fjord in September 2007 when the density was 0.4 medusae m^{-3} and the mean umbrella diameter 9.7 ± 3.0 cm. This density is low when compared to 2.4 medusae m^{-3} with a mean umbrella diameter of 14.6 ± 2.9 in late August 2003 (Møller and Riisgård 2007b) before *M. leidyi* was present. This may indicate that *M. leidyi* competed with *A. aurita* for food in 2007 and partly assumed this scyphozoan's trophic role in the ecosystem. Similarly, in the Black Sea, the concentration of *A. aurita* doubled when predation by *M. leidyi* on zooplankton decreased after the invasion of *B. ovata* in 1999 (Shushkina et al. 2000). Numerous species of gelatinous zooplankton consume ctenophores, especially scyphomedusae. Large *M. leidyi* are able to escape after contact with the tentacles of *Chrysaora quinquecirrha* medusae; however, most small ctenophores were caught (Kreps et al. 1997), and these medusae control *M. leidyi* population in Chesapeake Bay, USA (Purcell and Decker 2005). We observed that the scyphomedusae *Cyanea capillata* and *C. lamarckii* easily captured and consumed *M. leidyi*, and therefore, these jellyfish may be critically important predators of *M. leidyi* in Danish waters.

The native habitats of *M. leidyi* are temperate to subtropical estuaries (Purcell et al. 2001), where it is eaten by *B. ovata*. In September, only a few 2 to 3 cm long *Beroe* sp. were captured in Løgstør Bredning and Kås Bredning, suggesting that *M. leidyi* predators were not yet abundant in Limfjorden. Thus it remains to be seen if the two species of *Beroe* occurring in Danish waters, *B. cucumis* and *B. gracilis*, will take the role as predators of *M. leidyi*, or if an invasion of *B.*

ovata is required to promote recovery of Limfjorden from the effects of the *M. leidyi* invasion.

The distribution and winter survival of *M. leidyi* is restricted by low temperatures (< 2°C) (Purcell et al. 2001, Purcell 2005); however, because of global warming, the mean summer temperature of surface water (July-November) has increased about 2.3°C (from 13.0 to 15.3°C) and bottom water about 1°C (from 11.1 to 12.1°C) in the inner Danish waters during the period 1975-2006 (Harley Bundgaard Madsen, Environmental Center Odense, pers. comm.). Additionally, *M. leidyi* finds winter refugia in shallow embayments with limited water exchange (Costello et al. 2006). Consequently, *M. leidyi* may survive the coming winter in Danish waters and subsequently damage the fish populations in spring 2008 by eating their food and their eggs and newly hatched larvae.

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