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Research Article

Population dynamics and zooplankton-predation impact of the indigenous scyphozoan *Aurelia aurita* and the invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark)

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Abstract

The invasive ctenophore, *Mnemiopsis leidyi*, which had its first mass occurrence in Limfjorden (Denmark) in 2007, and the indigenous common jellyfish, *Aurelia aurita*, were studied from autumn 2008 through summer 2009. By December 2008, both *A. aurita* and *M. leidyi* populations had disappeared for the winter. In 2009, the first *A. aurita* appeared in February and the medusae attained their maximum umbrella diameter by the end of June, when the estimated half-life of copepods was only 1.6 ± 1.1 d. Low densities of *M. leidyi* in early July (< 0.5 m^{-3}) increased to high densities by late August (66.2 to 224.9 ind. m^{-3}). In 2009, the estimated time to clear the central part of Limfjorden (Skive Fjord) of zooplankton by *A. aurita* and *M. leidyi* feeding was between 0.5 d (4 June) and 2.9 d (26 August). During that period, copepods and other mesozooplankton organisms were virtually absent while ciliates were a substantial part of the zooplankton biomass. In "pre-*Mnemiopsis* years", there seems to have been large variability in the grazing impact on zooplankton depending on the seasonal abundance of *A. aurita*. With the addition of the second carnivore *M. leidyi*, however, additional predation pressure caused the zooplankton stocks to be severely depressed throughout 2008 and 2009 when copepods and cladocerans no longer showed the high seasonal peaks in abundance typical of previous years.

Key words: interspecific competition, gelatinous plankton, predation impact, zooplankton

Introduction

The native habitats of the lobate ctenophore, *Mnemiopsis leidyi* (A. Agassiz, 1865), are coastal waters along the east coast of the Americas (Purcell et al. 2001; Sullivan et al. 2001). In the early 1980's, it was introduced to the Black Sea, presumably from ballast water of cargo ships, and a few years later the invasive ctenophore exhibited mass occurrence (Purcell et al. 2001; Shiganova et al. 2001). In 1989, mass occurrences of the ctenophore in combination with over-fishing caused a collapse of the anchovy fishery in the Black Sea (Kideys and Romanova 2001; Purcell et al. 2001; Oguz and Gilbert 2007; Oguz et al. 2008; Mutlu 2009).

More recently during the late summer of 2006, large blooms of *Mnemiopsis leidyi* were observed along the coast of the Netherlands (Faasse and Bayha 2006) and in 2009–2011 along the Belgian coastline (Van Ginderdeuren et al. 2012). Presumably, the invasive ctenophore also had been introduced with ballast water. In

2006, *M. leidyi* was observed in coastal waters to the north and south of Denmark, and soon after had spread into all Danish waters, often in large concentrations (Tendal et al. 2007). Further spread of *M. leidyi* to neighboring waters has been a topic of major concern (Hansson 2006; Javidpour et al. 2006, 2009; Boersma et al. 2007; Storr-Paulsen and Huwer 2008; Lehmann and Javidpour 2010; Hosia and Titelman 2010; Hamer et al. 2011).

Mnemiopsis leidyi was observed for the first time in Limfjorden (Denmark) in 2007 and exhibited mass occurrence in late summer (Riisgård et al. 2007). *M. leidyi* ctenophores were probably brought into Limfjorden from the North Sea via Thyborøn Kanal. Preliminary estimates of the new ctenophore's predation effects were made based on the abundances of *M. leidyi* in Limfjorden in the late summer of 2007 (Riisgård et al. 2007). In August and September 2007, *M. leidyi* was found in every net sample from 9 locations in Limfjorden, whereas the usually predominant common jelly-

fish, *Aurelia aurita* (Linnaeus, 1758), was nearly absent. The population densities of *M. leidyi* were high, up to more than 800 individuals m^{-3} in the innermost part of Limfjorden, whereas the oral-aboral length was small (5 to 15 mm). The live biovolumes were very high (100 and 300 ml m^{-3}) in the central parts of Limfjorden, and thus even greater than those from the Black Sea, where the greatest mean biovolume was about 184 ml m^{-3} in the autumn of 1989 when the zooplankton and fish stocks collapsed (Purcell et al. 2001).

The scyphozoan *Aurelia aurita* has a life cycle with two stages, a pelagic medusa and a benthic polyp (Hamner 1974; Boero et al. 2008). In eutrophic Limfjorden, the polyps apparently thrive and in the early spring, the polyps release ephyrae into the water column that develop into the new generation of medusae (Hansson et al. 2005; Møller and Riisgård 2007a). This results in an annual mass occurrence of *A. aurita* unless they are removed from the fjord system by water exchange, which is strongly influenced by the dominant westerly wind (Møller and Riisgård 2007b). In contrast to this, the ctenophore *Mnemiopsis leidyi* relies on a holopelagic life cycle with sexual reproduction in the water column to increase in number; high fecundity, rapid generation time and (possibly) the ability to self-fertilize may explain its mass occurrences (Baker and Reeve 1974; Purcell et al. 2001; Boero et al. 2008; Javidpour et al. 2010).

In Limfjorden in both 2004 and 2005, dramatic changes in the salinity vertical profiles and subsequent density-driven water exchange coincided with a temporary disappearance of *Aurelia aurita* and the intrusion of a previously unseen hydromedusa species, *Aequorea vitrina* Gosse, 1853, from the North Sea (Møller and Riisgård 2007b,c; Riisgård 2007). Thus, infrequent intrusions of large volumes of high salinity seawater from the North Sea may radically change the composition and density of jellyfish (Møller and Riisgård 2007a, b). The first introduction between 2005 and 2007 of *Mnemiopsis leidyi* was probably also from the North Sea (Riisgård et al. 2007; Tendal et al. 2007).

In the present study, the abundance of *Mnemiopsis leidyi* in Limfjorden was followed from late 2008 throughout 2009. Now, some years after the massive invasion of the much-feared ctenophore into Limfjorden, we report on the abundance and combined zooplankton predation impacts of the invasive ctenophore and the usually predominant indigenous scypho-medusan, *Aurelia aurita*.

Materials and methods

Study area

Limfjorden (Denmark) is a shallow 1575 km^2 water system that connects the North Sea via Thyborøn Kanal in the west with the Kattegat in the east (Figure 1). The average monthly temperature normally ranges from ~1°C (minimum -1.4°C) in January to 19°C (maximum 24.6°C) in August. The yearly average temperature is 9.5°C ± 1.5°C. The mean water depth is about 4.5 m with a maximum depth of 24 m. In the central basin (Løgstør Bredning), the mean depth is about 5.8 m (Wiles et al. 2006; Hofmeister et al. 2009).

The strength of the wind is of great importance for the water exchange in Limfjorden. Westerly wind causes inflow of North Sea water through the Thyborøn Kanal whereas easterly wind results in inflow of Kattegat water at Hals (Dolmer et al. 1999; Wiles et al. 2005; Christiansen et al. 2006; Markager et al. 2006; Hofmeister et al. 2009; Maar et al. 2010; Dolmer and Stenalt 2010). Westerly winds blew for a mean of 220 days per year in 1988 to 2003, which results in considerable water exchange. In 1988–2003, the mean annual net water exchange due to easterly flowing water was 6.4 km^3 input from the North Sea and 9.1 km^3 output to the Kattegat, and the volume of freshwater run-off including net precipitation was 4.5 and 3.5 km^3 in 2003 and 2004, respectively.

Between the west and east boundaries of Limfjorden there is a permanent horizontal salinity gradient with salinities of 32 to 34 at the connection to the North Sea and 19 to 25 at the connection to the Kattegat. The total water volume in Limfjorden is 7.1 km^3, as compared with the net west-east through-flow of 9.1 km^3 per year. This results in generally short water residence times of 1 to 1.5 months in the winter half-year and about 2 months in the summer half-year. Limfjorden is neither dominated by North Sea water only, nor by riverine freshwater only, but rather by the interaction of both. The water column in Limfjorden switches periodically between stratified and mixed conditions in response to wind forcing (Jørgensen 1980; Møhlenberg 1999; Hansson et al. 2005; Hofmeister et al. 2009).

Occasionally, persistent, strong westerly winds push high salinity North Sea water into the fjord-system, which may cause large variations in the vertical salinity profiles and density-driven flows of bottom and surface water in opposite directions, with lighter (less saline) surface water moving out of the fjord and high-density saline bottom water into the fjord (Figures 5–7 in Møller and Riisgård 2007a). The vertical variations in salinity are generally caused by the interplay of low-density freshwater from the catchment area and near-bottom inflow of high-density saline water. During summer a concomitant thermocline further stabilizes the halocline leading to marked stratification, which can be broken only by strong winds (Jørgensen 1980; Møhlenberg 1999; Wiles et al. 2006; Hofmeister et al. 2009).

Field investigations

Medusae, ephyrae, and ctenophores were collected with a 2-mm-mesh plankton net (1.77-m^2 mouth area) at 4 locations in central Limfjorden during 9 cruises between September 2008 and August 2009 (Figure 1). The net was equipped with a closed cod end bucket to prevent damage of the gelatinous plankton. At each location, 3 hauls were made by obliquely raising the net from the bottom to the surface at a speed of 1.5 knots through a distance of 18.5 m for population density estimates. After each haul, representing a filtered volume of 18.5 m$\times$1.77 m^2 =32.8m^3, the numbers of jellyfish and ctenophores in the sample were estimated by counting live animals from a 1-l subsample from the net-bucket and multiplying those numbers by the total volume of jellyfish and ctenophores in the net-bucket. The mean population densities of jellyfish and ctenophores in each location were estimated from the densities of each species in the 3 hauls. Furthermore, 50 live animals of each species (if that many were in the sample) were measured to estimate the mean (±SD) size (i.e. *A. aurita* umbrella diameter and *M. leidyi* oral-aboral length) at each location. A CTD profile at each station obtained data on chlorophyll *a*, water temperature, and salinity. At each location, 20 l of water was sampled by means of a submersible pump hauled through the water column (see description below) and filtered (60 µm) to obtain a representative sample of the zooplankton species composition in order to estimate the concentrations of the different species. Samples were preserved in Lugol's

solution and transported to the laboratory to be examined with a stereo microscope. All individuals were counted in each filtered 20-l sample to estimate the concentrations (ind. l^{-1}) of the different taxonomic groups (rotifers, mussel veligers, calanoid copepods, harpacticoids, copepod nauplii).

Estimation of clearance rate

(A) *Mnemiopsis leidyi*. The mean size of ctenophores was determined by measuring the distance between mouth and opposite pole (oral-aboral length) on 50 individuals with a Vernier calipers. The following relationship was used for converting oral-aboral length (*L*, mm) and body volume (*V*, ml) (Riisgård et al. 2007):

$$V = 0.0226L^{1.72} \quad \text{Eq. (1).}$$

The following equation was used to estimate the individual clearance rate (Cl_{est}, l d^{-1}) of ctenophores feeding on copepods from the body volume:

$$Cl_{est} = 2.64V \quad \text{Eq. (2).}$$

This equation was derived from empirical estimates as follows: Decker et al. (2004) measured filtration rates (= clearance) of small *M. leidyi* (mean volumes 2.3 (range 1-3) to 3.9 ml (range 1-10)) feeding on adult copepods (*Acartia tonsa*) at about 22°C in 90-l containers as 0.11 l h^{-1} per ml of ctenophore (= 2.64 l d^{-1} ml^{-1}, see Table 1 in Decker et al. 2004). However, recent studies indicate that Eq. (2) may underestimate the clearance rate (Purcell 2009). Subsequently, Granhag et al. (2011) found that the clearance rate (Cl, l h^{-1}) as a function of ctenophore oral-aboral length (*L*, mm) (calculated from gut content of field-collected animals using measured digestion times for the prey-copepod *Acartia* sp.) could be expressed by: $Cl = aL^b = 0.014L^{1.77}$. Likewise, Colin et al. (2010) found that the clearance rate (based on water volume flux between the lobes) as a function of length could be expressed by the equation: $Cl = 0.0011L^{2.07}$. For comparison, the present Eq. (1) and Eq. (2) were used to derive a similar expression: $Cl = 0.002L^{1.7}$. Although the exponents are quite similar, the *a*-values are different. Thus, when using the different equations for a 35-mm ctenophore, the clearance rate is 9 times (7.57 l h^{-1}, Granhag et al. 2011) and 2 times (1.73 l h^{-1}, Colin et al. 2010) higher than the clearance rate of 0.84 ml h^{-1} obtained using the present Eq. (2). Furthermore, the
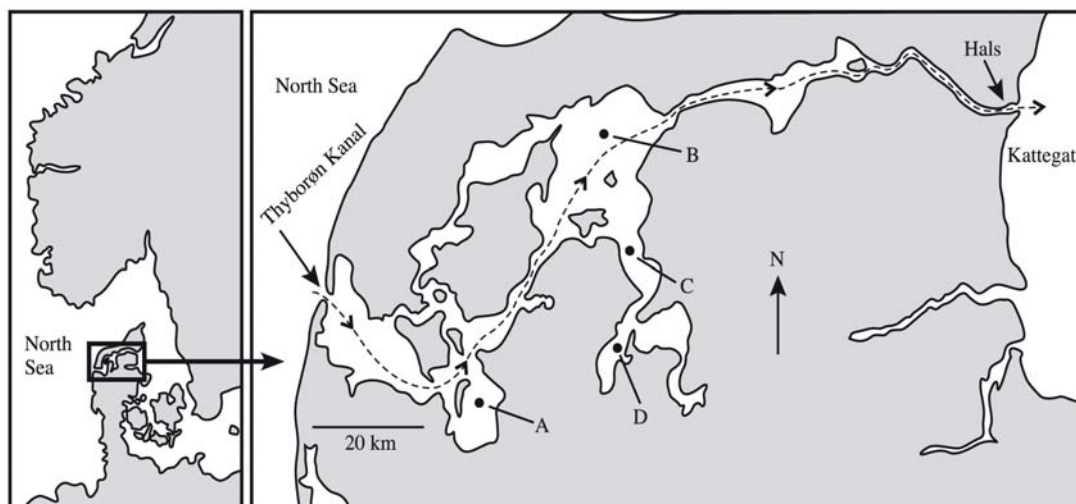
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Figure 1. Locations in Limfjorden where *Mnemiopsis leidyi* and *Aurelia aurita* were collected on 9 cruises in the period September 2008 to August 2009. The main line of water exchange between the North Sea in west and Kattegat in the east is indicated by the broken line (adapted from Jørgensen 1980). A = Venø Bugt (56°31.39N, 08°40.46E), B = Løgstør Bredning (56°57.15N, 09°03.46E), C = Junget Øre (56°47.00N, 09°08.50E), D = Skive Fjord (56°37.25N, 09°05.55E).

clearance rate measured on small ($L = 21 \pm 2$ mm) *Mnemiopsis leidyi* by Madsen and Riisgård (2010) with *Artemia salina* as prey organism was approximately 3 times higher than estimated from Eq. (2). Thus, the present clearance rates based on Eq. (2) may be considered to be conservative estimates of the potential zooplankton (copepod) predation impact exerted by *M. leidyi*.

(B) *Aurelia aurita.* The following equation was used to estimate the individual clearance rate (Cl_{ind}, l d^{-1}) of jellyfish feeding on copepods from the mean inter-rhopalia diameter (*d,* mm) (Møller and Riisgård 2007b):

$$Cl_{ind} = 0.0073d^{2.1} \quad \text{Eq. (3).}$$

Population clearance rate

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

$$Cl_{pop} = Cl_{ind} \times D/1000 \quad \text{Eq. (4).}$$

Half-life of copepods

The clearance rate of a jellyfish (or a ctenophore) is defined as the volume of water cleared of a certain type of prey organism (e.g. nauplii or adult copepods, mussel veligers, rotifers, brine shrimps) per unit of time (e.g. Madsen and Riisgård 2010; Riisgård and Madsen 2011). In a closed, well-mixed tank with jellyfish and added prey organisms, the reduction in prey concentration as a function of time is exponential (verified as a straight line in a semi-ln plot); therefore, the clearance rate (*Cl*) may be determined by means of the clearance formula (Coughlan 1969):

$$Cl = (V/nt)\ln(C_0/C_t) \quad \text{Eq. (5).}$$

where C_0 and C_t are the prey concentration at time 0 and time *t*, V = volume of water, and n = number of jellyfish. The time ($t_{1/2}$) it takes for a population of jellyfish with a known density (ind. m^{-3}) and known population clearance rate (Cl_{pop}) to reduce the concentration of a certain prey organism in $V = 1$ m^3 of water by 50 % can be obtained from Eq. (5), rewritten as:

$$t_{1/2} = (V/Cl_{pop})\ln[C_0/(C_0/2)] = \ln2/Cl_{pop} \quad \text{Eq. (6).}$$

Eq. (6) expresses the half-life of a certain prey organism and when used in field studies (e.g. Olesen et al. 1994; Hansson et al. 2005; Møller and Riisgård 2007b; Riisgård et al. 2007, 2010), it is assumed that the population clearance rate is constant (i.e. no satiation, no effect of temperature, etc.) and that the water is well-mixed.

To estimate the combined predation impact of the jellyfish and ctenophore populations, with population clearance rates of Cl_{pop1} and Cl_{pop2}, respectively, the total half-life of copepods was estimated as:

$$tot\text{-}t_{1/2} = \ln2/(Cl_{pop1} + Cl_{pop2}) \qquad \text{Eq. (7)}.$$

Zooplankton biomass

Data on biomass of zooplankton in Skive Fjord in the years 1997, 2001, 2003, 2007, 2008, and 2009 were obtained from the Danish national monitoring program, Environment Centre Ringkøbing, Danish Ministry of the Environment. According to the official monitoring guidelines, 20 l of water was sampled by means of a submersible pump (150 l min^{-1}) as equally-sized subsamples taken from bottom to surface of the water column by hauling the pump up at 0.5 m s^{-1}. The sampled water was filtered (60 μm) to obtain a representative sample of the zooplankton species composition. Samples were preserved in basic Lugol's solution and examined in the laboratory by Orbicon A/S in order to estimate the concentration and biomass (μg C l^{-1}) of the different taxonomic groups: polychaete larvae, bivalve and gastropod veligers, barnacle nauplii, copepods, cladocerans, rotifers, and ciliates (Miljøcenter Ringkøbing 2008).

Results

Data from the two cruises in late 2008 indicated that both the *Aurelia aurita* medusa and the *Mnemiopsis leidyi* ctenophore populations had mostly disappeared before December (Tables 1 and 2, Figure 2). In 2009, the first *A. aurita* ephyrae appeared in February and the first medusae in April. In June-July, the medusae had attained their maximum umbrella diameter of 129 ± 34 mm in Venø Bugt and 92 ± 16 mm in Skive Fjord, respectively (Table 2, Figure 2). The maximum density of *A. aurita* was 14.8 ± 0.8 ind. m^{-3} observed in Skive Fjord in early June. After this, both the umbrella diameters and the population densities of *A. aurita* decreased at all locations studied.

The shortest half-life for copepods (only $t_{1/2}$ = 0.5 d) was observed in June in Skive Fjord when medusae were abundant. At all locations in Limfjorden in July 2009, the half-lives were very low (mean ± SD = 1.6 ± 1.1 d, range 0.5 to 3.6 d, Table 2). In the same period the observed

zooplankton concentrations were low and the chlorophyll *a* concentrations high in the central parts of Limfjorden (Figure 2).

Low densities (≤0.5m^{-3}) of *Mnemiopsis leidyi* at all locations in early July 2009 had changed dramatically by August, with moderate densities (1.4 to 131.5 ind.m^{-3}) early and high densities late in the month (66.2 to 224.9ind.m^{-3}) (Table 1, Figure 2). Conspicuous decreases in the *Aurelia aurita* densities apparently coincided with rapid increases in *M. leidyi* densities in late August 2009, when the high ctenophore bio-volume (135 ml) and short copepod half-life ($t_{1/2}$ = 2 d) were first notable in Venø Bugt (Table 1). Figure 3 shows that this was true in Løgstør Bredning (location B), but in Skive Fjord (location D) the medusa decrease preceded the increase of *M. leidyi*, in Junget Øre (location C) the medusa density did not change much as *M. leidyi* increased, and in Venø Bugt (location A) the medusae were never abundant. The density of *M. leidyi* was high in Venø Bugt (A) for the first time in late August 2009 (Figure 3), and ctenophore density were already high in Løgstør Bredning (B) at the beginning of August.

Densities of *Aurelia aurita* were higher in the inner stations of Limfjorden (B, Løgstør Bredning; C, Junget Øre; and D, Skive Fjord) than at the station nearest the North Sea (A, Venø Bugt). By contrast, densities of *Mnemiopsis leidyi* usually were highest at the outer-most station A (Figures 2 and 3). Predation of *M. leidyi* on copepods in Skive Fjord was negligible until late August when the combined ctenophore-medusa predation became important ($tot\text{-}t_{1/2}$ ~2.9 d, Table 2).

In 2009, when the estimated combined predation ($tot\text{-}t_{1/2}$) of *Aurelia aurita* and *Mnemiopsis leidyi* in Skive Fjord was between 0.5 d (4 June) and 2.9 d (26 August) (Table 2), copepods and other meso-zooplankton organisms were virtually absent, while ciliates made up a substantial part of the zooplankton biomass (Figure 4). In 2008 and 2007, *M. leidyi* also was present, zooplankton was reduced in Limfjorden, by in comparison, zooplankton was extremely abundant in 1997 when the ctenophore was absent (Figure 4).

Possible interspecific competition, when *Aurelia aurita* and *Mnemiopsis leidyi* were in the same water mass, and shortage of food may explain why the ctenophores remained small, only 6 to 9 mm in late August (Table 1) at all locations in Limfjorden. This suggestion is supported by the low observed zooplankton

Table 1. *Mnemiopsis leidyi* collected during cruises in Limfjorden in 2008 and 2009 on 4 locations (see Figure 1). D = mean (±SD) population density; L = mean (±SD, n = 50, or all sampled individuals) body length; estimated individual body volume, cf Eq (6); $B = D \times V$ = specific bio-volume of ctenophores; Cl_{ind} = individual clearance rate; Cl_{pop} = population clearance rate; $t_{1/2}$ = estimated half-life ($t_{1/2} > 3$ weeks are indicated by ∞). A = Venø Bugt, B = Løgstør Bredning, C = Junget Øre, D = Skive Fjord (Figure 1).

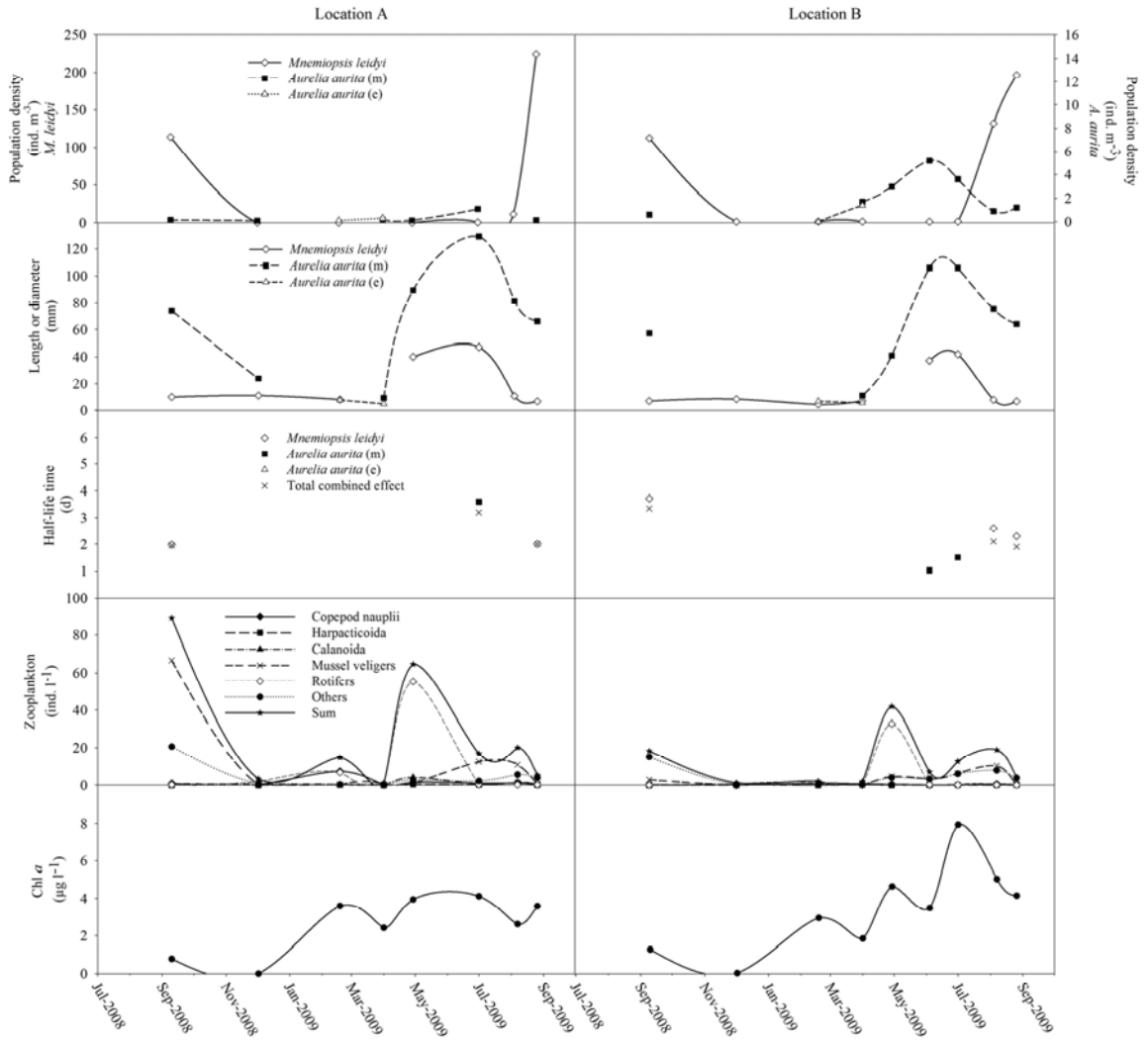| Cruise/Date/Locality	D (ind. m^{-3})	L (mm)	V (ml ind.$^{-1}$)	B (ml m^{-3})	Cl_{ind} (l d^{-1})	Cl_{pop} (d^{-1})	$t_{1/2}$ (d)
Cruise 1							
10 Sept 2008							
A	114 ± 70	10 ± 3	1.17	133	3.1	0.351	2.0
B	112 ± 8	7 ± 2	0.63	71	1.7	0.186	3.7
C	23 ± 9	9 ± 4	0.96	22	2.5	0.057	12.1
D	196 ± 118	5 ± 3	0.40	78	1.1	0.206	3.4
Cruise 2							
2 Dec 2008							
A	0.002 ± 0.003	11 ± 0	1.40	0.003	3.7	0.00001	∞
B	0.1 ± 0.1	8 ± 3	0.87	0.1	2.3	0.0002	∞
C	14 ± 2	6 ± 2	0.52	7	1.4	0.02	∞
D	32 ± 8	7 ± 3	0.66	21	1.8	0.06	12.4
Cruise 3							
18 Feb 2009							
A	0.001 ± 0.001	8	0.81	8.1×10^{-4}	2.1	1.4×10^{-6}	∞
B	0.01 ± 0.01	4 ± 1	0.28	2.8×10^{-3}	0.8	6.5×10^{-6}	∞
C	0.1 ± 0.1	4 ± 0	0.28	2.0×10^{-2}	0.7	5.4×10^{-5}	∞
D	0.01 ± 0.01	4 ± 2	0.24	2.4×10^{-3}	0.6	7.6×10^{-6}	∞
Cruise 4							
1 April 2009							
A	0	0	0	0	0	0	∞
B	0.003 ± 0.01	7	0.64	1.9×10^{-3}	1.7	4.8×10^{-6}	∞
C	0	0	0	0	0	0	∞
D	0	0	0	0	0	0	∞
Cruise 5							
29 April 2009							
A	0.001 ± 0.002	40 ± 0	13.00	0.01	34.0	3.2×10^{-5}	∞
B	0	0	0	0	0	0	∞
C	0	0	0	0	0	0	∞
D	0	0	0	0	0	0	∞
Cruise 6							
4 June 2009							
A	-	-	-	-	-	-	-
B	0.03 ± 0	37 ± 4	11.43	0.4	30.2	0.001	∞
C	0	0	0	0	0	0	∞
D	0	0	0	0	0	0	∞
Cruise 7							
1 July 2009							
A	0.5 ± 0.2	47 ± 8	17.11	9	45.2	0.023	∞
B	0.02 ± 0.04	42 ± 4	14.00	0.3	37.0	0.001	∞
C	0	0	0	0	0	0	∞
D	0.01 ± 0.02	50 ± 0	18.89	0.2	49.9	0.001	∞
Cruise 8							
4 Aug 2009							
A	11.3 ± 4.9	11 ± 12	1.31	15	3.5	0.039	17.7
B	131.5 ± 42.4	8 ± 6	0.77	101	2.0	0.269	2.6
C	2.5 ± 0.3	16 ± 11	2.63	7	7.0	0.017	∞
D	1.4 ± 1.2	24 ± 9	5.31	7	14.0	0.019	∞
Cruise 9							
26 Aug 2009							
A	224.9 ± 63.4	7 ± 5	0.60	135	1.6	0.354	2.0
B	196.3 ± 42.9	7 ± 4	0.59	116	1.6	0.309	2.3
C	87.9 ± 36.3	6 ± 3	0.42	37	1.1	0.098	7.0
D	66.2 ± 13.4	9 ± 5	0.99	66	2.1	0.173	4.0

Figure 2. Population density (ind. m^{-3}) and size (mm) of *Mnemiopsis leidyi* and *Aurelia aurita* ephyrae (e), and medusae (m) in Limfjorden during the study period, September 2008 to August 2009 [from left to right: Venø Bugt (Location A, Figure 1), Løgstør Bredning (Location B, Figure 1)]. Estimated half-life of copepods (specified for species, stage, and joint for *M. leidyi* and *A. aurita*) are shown along with measured zooplankton density (ind. l^{-1}) and chlorophyll *a* concentration (µg l^{-1}). Note top-right outside scale for *A. aurita*.

concentrations, the high chlorophyll *a* concentrations in the central parts of Limfjorden, and the rather small maximum umbrella diameters of 89 ± 15 to 129 ± 34 mm of *A. aurita* in July 2009 (Figure 2, Table 2), before it became smaller when deprived of food ("regressing until it resembles a diminutive adult", cf. Hamner 1974).

Between 1 July and 7 August 2009, new cold high-salinity water came into Limfjorden from the North Sea, thus increasing the salinity in the western part of the fjord (Venø Bugt) from 29.5 to 31 in the upper 5 m and somewhat higher in the deeper water (Figure 5). The salinity and

temperature of the water was uniform from surface to bottom on 26 August due to wind mixing, except in Skive Fjord, which remained stratified due to freshwater from the River Skive Å. The obvious trends of higher salinities in the surface waters in the west (Venø Bugt) to lower salinities in the east (Skive Fjord) and markedly higher salinities deeper in the water column indicated that cold high-salinity water from the North Sea replaced a considerable part of the less saline water in the central and innermost parts of Limfjorden between 1 July and 26 August 2009.
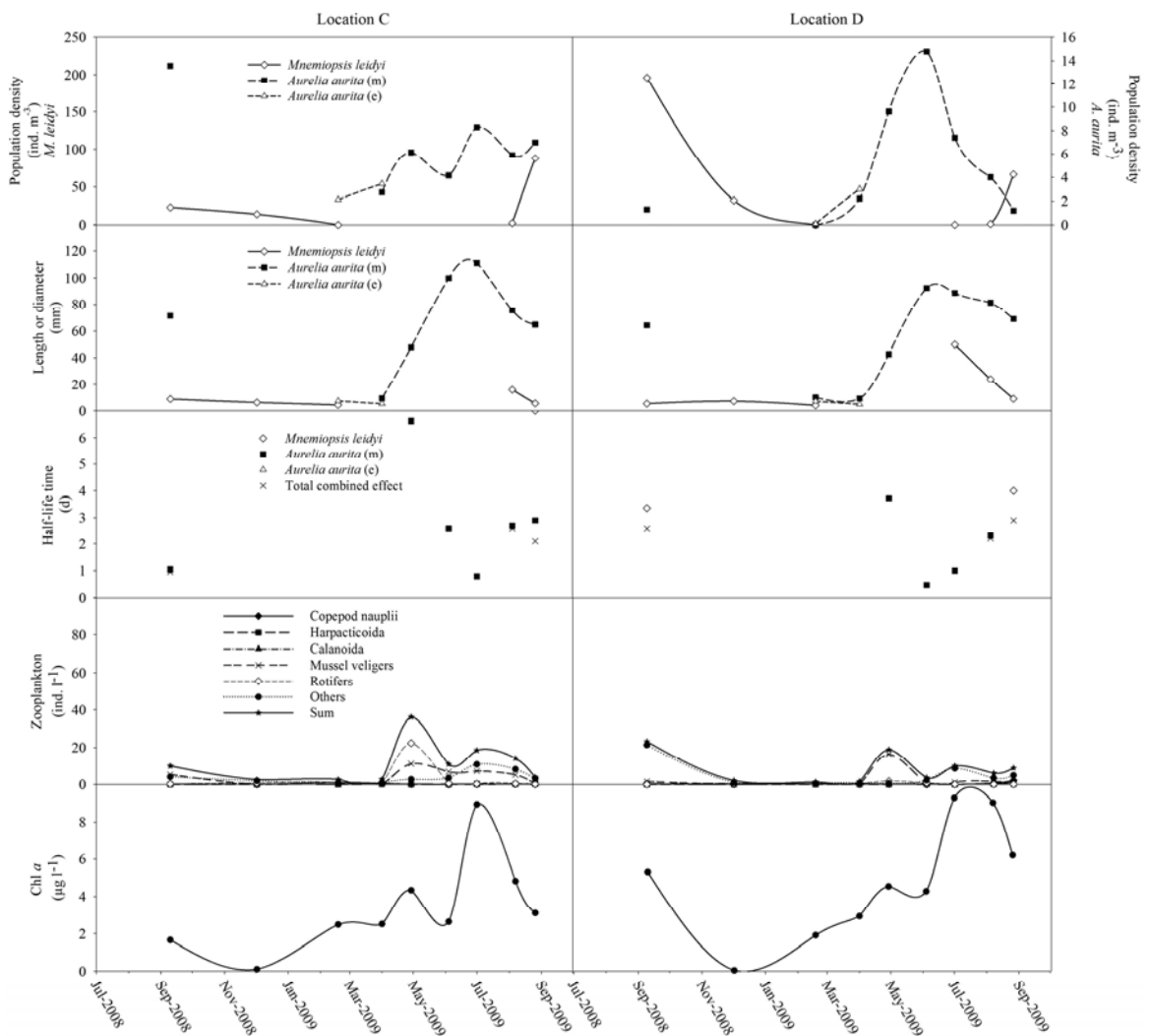
Figure 2 (continued) Population density (ind. m^{-3}) and size (mm) of *Mnemiopsis leidyi* and *Aurelia aurita* ephyrae (e), and medusae (m) in Limfjorden during the study period, September 2008 to August 2009 [from left to right: Junget Øre (Location C, Figure. 1), Skive Fjord (Location D, Figure. 1)]. Estimated half-life of copepods (specified for species, stage, and joint for *M. leidyi* and *A. aurita*) are shown along with measured zooplankton density (ind. l^{-1}) and chlorophyll *a* concentration (µg l^{-1}). Note top-right outside scale for *A. aurita*.

Discussion

In the present study, competition for zooplankton prey between the ctenophores and medusae must be considered as an explanation for the replacement of *Aurelia aurita* medusae by *Mnemiopsis leidyi* ctenophores in Limfjorden, but water exchange may also have brought in *M. leidyi*.

In the shallow Limfjorden, the polyp stage of *Aurelia aurita* produces a large number of ephyrae in the early spring, resulting in a large population of medusae that may control the zooplankton during summer and autumn (Hansson et al. 2005; Møller and Riisgård 2007a, b). The density of *A. aurita* in Limfjorden from late February to late August 2003 was high and stable over time; during those 6 months medusa densities varied between 0.6 and 3 ind. m^{-3} (Hansson et al. 2005). They combined medusa abundance estimates with clearance rates of individual *A. aurita* to calculate the potential jellyfish-induced mortality on prey in Limfjor-

Table 2. *Aurelia aurita* (medusae) collected during cruises in Limfjorden in 2008 and 2009 on 4 locations (see Figure 1). D = mean (±SD) population density; d = mean (±SD) umbrella diameter, Cl_{ind} = individual clearance rate; Cl_{pop} = population clearance rate; $t_{1/2}$ = estimated half-life ($t_{1/2}$ > 3 weeks are indicated by ∞). Estimated joint-predation impact by *A. aurita* and *Mnemiopsis leidyi* has been expressed as total half-life of copepods = tot-$t_{1/2}$. A = Venø Bugt, B = Løgstør Bredning, C = Junget Øre, D = Skive Fjord (Figure 1).

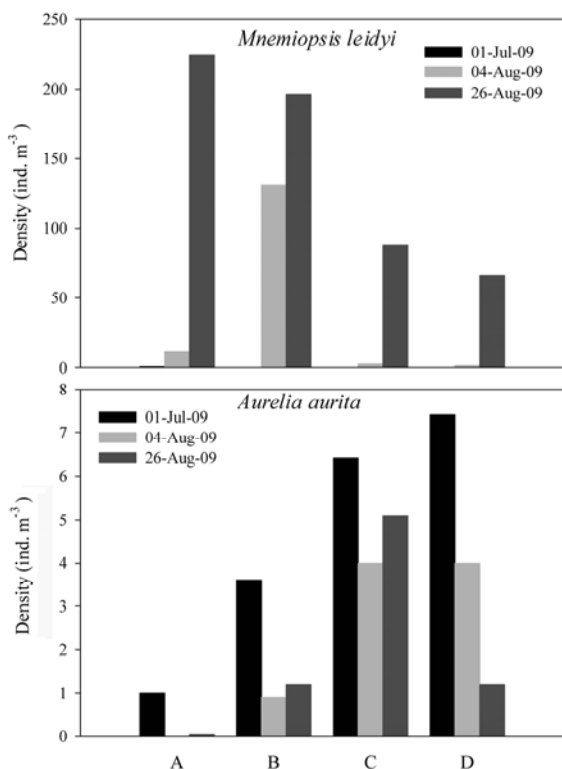| Cruise/Date/Locality	D (ind. m^{-3})	D (mm)	Cl_{ind} (l d^{-1})	Cl_{pop} (d^{-1})	$t_{1/2}$ (d)	tot-$t_{1/2}$ (d)
Cruise 1						
10 Sep 2008						
A	0.1 ± 0.1	74 ± 22	61.0	0.004	∞	2.0
B	0.6 ± 0.2	57 ± 1	35.8	0.020	∞	3.4
C	11.6± 2.7	72 ± 5	57.3	0.663	1.1	1.0
D	1.3 ± 0.7	64 ± 2	45.7	0.061	11.4	2.6
Cruise 2						
2 Dec 2008						
A	0.002 ± 0.003	24	5.8	$1.1×10^{-5}$	∞	∞
B	0	0	0	0	∞	∞
C	0	0	0	0	∞	∞
D	0	0	0	0	∞	12.4
Cruise 3						
18 Feb 2009						
A	0	0	0	0	∞	∞
B	0	0	0	0	∞	∞
C	0	0	0	0	∞	∞
D	0.001 ± 0.002	10	0.9	$8.1×10^{-7}$	∞	∞
Cruise 4						
1 April2009						
A	0.1 ± 0.1	9 ± 1	0.8	$6.0×10^{-5}$	∞	∞
B	1.7 ± 0.5	11 ± 1	1.1	0.002	∞	∞
C	0.9 ± 0.3	9 ± 1	0.8	0.001	∞	∞
D	2.2 ± 1.4	9 ± 1	0.8	0.002	∞	∞
Cruise 5						
29 April 2009						
A	0.03 ± 0.03	89 ± 7	91.4	0.003	∞	∞
B	3.0 ± 0.7	41 ± 5	17.8	0.053	13.1	13.1
C	4.2 ± 1.6	48 ± 2	24.6	0.105	6.6	6.6
D	9.6 ± 3.4	43 ± 1	19.4	0.186	3.7	3.7
Cruise 6						
4 June 2009						
A	-	-	-	-	-	-
B	5.2 ± 1.1	106 ± 24	130.4	0.674	1.0	1.0
C	2.3 ± 0.1	100 ± 18	115.5	0.267	2.6	2.6
D	14.8 ± 0.8	92 ± 16	98.0	1.447	0.5	0.5
Cruise 7						
1 July 2009						
A	1.0 ± 0.2	129 ± 34	198.3	0.191	3.6	3.2
B	3.6 ± 1.1	106 ± 19	130.4	0.464	1.5	1.5
C	6.4 ± 3.5	111 ± 16	143.9	0.923	0.8	0.8
D	7.4 ± 0.8	89 ± 15	89.9	0.667	1.0	1.0
Cruise 8						
4 Aug 2009						
A	0	0	0	0	∞	17.7
B	0.9 ± 0.3	75 ± 1	63.6	0.055	12.5	2.1
C	4.0 ± 0.6	76 ± 2	64.3	0.254	2.7	2.6
D	4.0 ± 0.8	81 ± 14	75.1	0.302	2.3	2.2
Cruise 9						
26 Aug 2009						
A	0.04 ± 0.04	66 ± 14	48.4	0.002	∞	2.0
B	1.2 ± 0.4	64 ± 15	45.2	0.056	12.5	1.9
C	5.1 ± 2.0	65 ± 13	46.5	0.236	2.9	2.1
D	1.2 ± 0.5	69 ± 15	53.1	0.065	10.6	2.9

Figure 3. Population densities of *Mnemiopsis leidyi* and *Aurelia aurita* at 4 locations in Limfjorden, from west (A, Venø Bugt, Figure 1) to east (D, Skive Fjord, Figure 1) from 1 July to 26 August 2009.

den. The estimated half-lives as a consequence of predation on cirripede larvae were very short; for example, in Skive Fjord, half-lives were from 0.9 d in May to 0.5 d in August 2003. By contrast, half-lives estimated from predation on copepods (*Acartia tonsa*) were 21 d in May and 14 d in August (Tables 3 and 4 in Hansson et al. 2005).

The consistent densities of *Aurelia aurita* in Limfjorden between late February and late August 2003 observed by Hansson et al. (2005) were opposite to the pattern seen in Skive Fjord in the present study where medusa densities decreased from 14.8 to 1.2 ind. m^{-3} between 4 June and 26 August (Figure 2, Table 2). The incursion of cold, high-salinity water from the North Sea into Limfjorden (Figure 3) may have carried ctenophores into the fjord system from the North Sea while medusae were flushed out into the Kattegat, as previously described by Møller and Riisgård (2007a, c). This suggests that mass occurrence of large *A. aurita* in

Limfjorden may occur in years with relatively little water exchange, allowing the density and predation impact of *A. aurita* to remain constant and high. Conversely, in years with a pronounced water exchange, *A. aurita* may be flushed out into the Kattegat and, since 2007, replaced by *Mnemiopsis leidyi* from the North Sea where the ctenophore may survive the winter.

Clearance rates for ephyrae and small medusae of *Aurelia aurita* feeding on various prey organisms differ considerably, depending on the size and stage of the predator as well as type and size of prey (Riisgård and Madsen 2011). The mean clearance rates on natural prey (copepod nauplii and adults, 22 to 37 %, and mussel veligers, 14 to 30 %) were considerably lower than on *A. salina* nauplii. Riisgård and Madsen (2011, Table 7 therein) also compared clearance rates for small (about 40 mm umbrella diameter) *A. aurita* medusae offered *Artemia salina* as prey, with rates from literature for medusae of comparable size offered fish larvae (capelin and cod, yolk-sac), and it was found that fish larvae were cleared with rates comparable to *A. salina* (3.8 l h^{-1}), namely between 3.0 l h^{-1} (de Lafontaine and Leggett 1988) and 5.0 l h^{-1} (Titelman and Hansson 2006). Compared to those clearance rates, "mixed zooplankton" (Båmstedt 1990), rotifers (*Brachionus plicatilis*, Olesen 1995), copepods (*Acartia tonsa*, Møller and Riisgård 2007c), and ciliates (*Balanion* sp., Stoecker et al. 1987) were cleared with rates of 1.4, 1.2, 0.7, and 0.15 l h^{-1}, respectively. In the present study, the clearance rate of copepods (*A. tonsa*), cf. Eq. (2), was used to express the potential predation impact of *A. aurita*. But because the clearance of "mixed zooplankton" is twice the rate we used, it suggests that the half-lives were conservative estimatesof the potential zooplankton predation impact exerted by *A. aurita* in Limfjorden.

The use of "half-life" has been established in previous publications (Olesen et al. 1994; Hansson et al. 2005; Møller and Riisgård 2007b; Riisgård et al. 2007, 2010), which indicates the time to reduce the standing stock of a certain type of zooplankton organisms (usually copepods) by 50 %. Because reproduction also is occurring, during the half-life, populations may not actually be reduced by 50%. Copepods have generation times (i.e. time from egg to maturity) of about 2 to 3 weeks, depending on temperature, e.g. Gillooly (2000), which compared to the
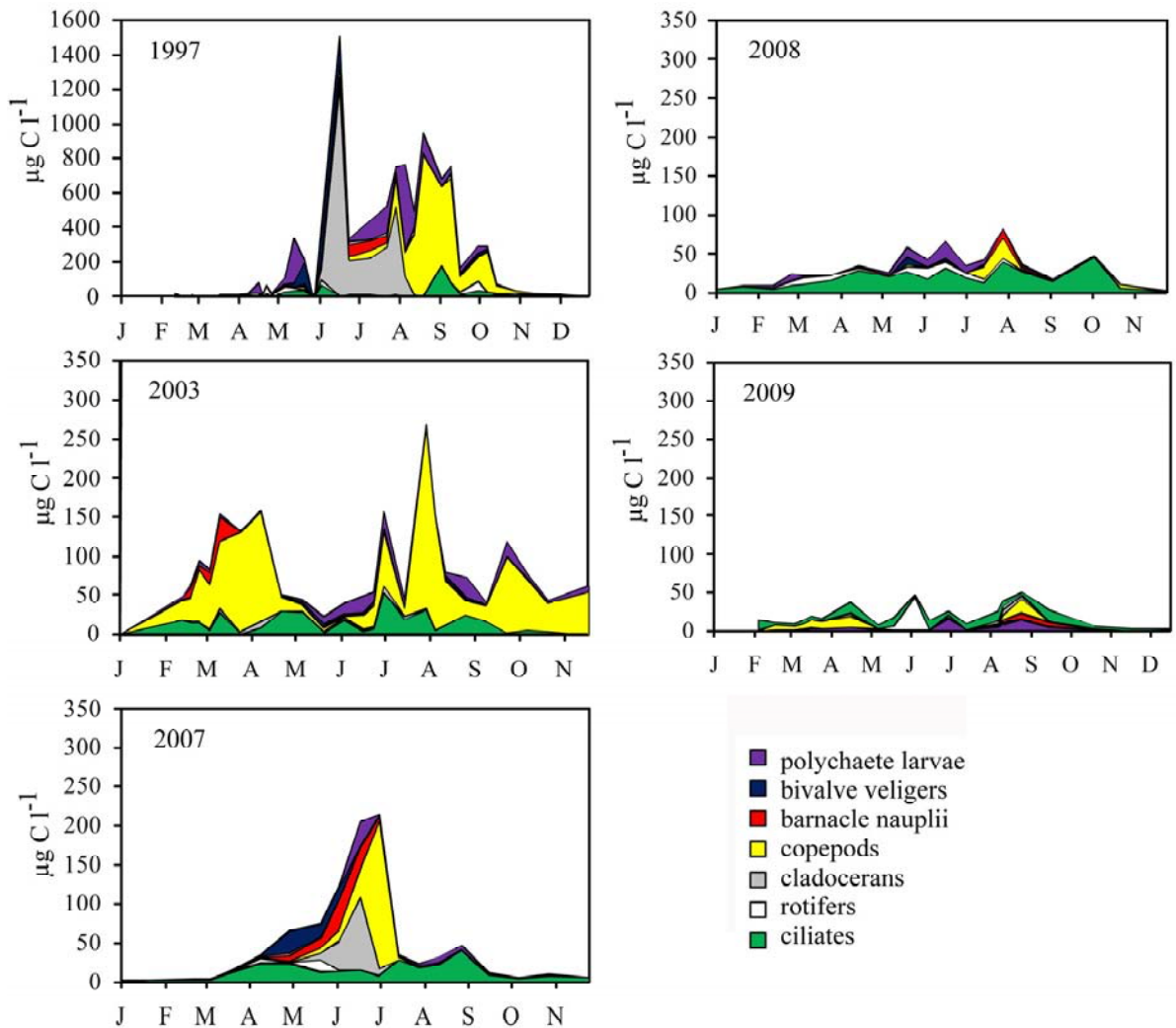
Figure 4. Biomass of zooplankton in Skive Fjord (Figure 1, Location D) in 1997, 2003, 2007, 2008, and 2009. Note the different y-scale in 1997.

combined half-lives of one to a few days during June-August estimated in the present work (Table 2), justifies the use of the term "half-life" in the present study. Because the zooplankton densities were low (Figures 2 and 5) and the summer maxima of chlorophyll *a* concentrations, the short half-lives reliably reflect that predation on zooplankton was high and that the jellyfish populations were food limited. This is also consistent with the observation that ciliates, which are poorly retained by both medusae and ctenophores (e.g. Stoecker et al. 1987; Båmstedt 1990; Waggett and Sullivan 2006), dominate the biomass of zooplankton (Figure 4).

The prey-capture efficiency and clearance rates of *Mnemiopsis leidyi* also differ considerably depending on stage (cydippid, transitional, lobate) and size of the predator, and on type and size of prey organism (Costello 1998; Costello et al. 1999; Purcell et al. 2001; Sullivan and Gifford 2004, 2007; Rapoza et al. 2005; Waggett and Sullivan 2006; Haddock 2007). This is important for understanding the predation impact on various zooplankton taxa where this ctenophore may occur in large numbers (Purcell et al. 2001, 2005; McNamara et al. 2010). In the adult lobate stage, *M. leidyi* has two methods of catching prey that function synergistically,
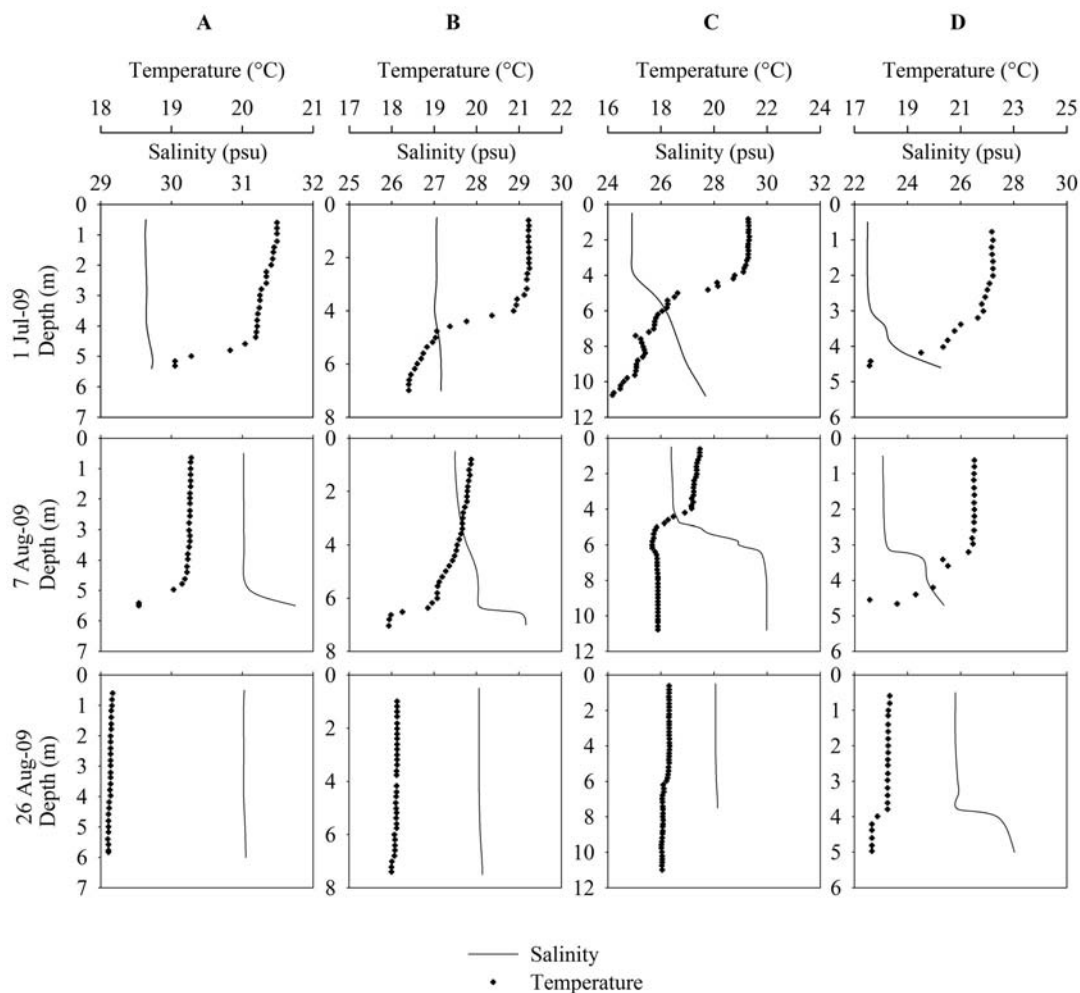
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Figure 5. Salinity and temperature profiles at the 4 studied locations (A, B, C, D) in Limfjorden (Figure 1) on 1 June 7, August, and 26 August 2009. Water depths are indicated by the extent of the temperature profiles.

which enables the ctenophore to capture a wide range of zooplankton taxa. Capture via auricular flow-field entrainment is thought to function in the capture of non-motile (e.g. fish eggs) and slowly swimming prey (e.g. mussel veligers). Capture of highly-motile prey (e.g. copepods) is accomplished when prey collide with the interior of the oral lobes (Waggett and Costello 1999). Larson (1987) showed that slowly-swimming prey such as veligers are captured more frequently than adult copepods. This agrees with capture efficiencies found in a study by Madsen and Riisgård (2010), in which mussel veligers were captured most efficiently (maximum clearance rate = 100%), rotifers (*Brachionus plicatilis*) and adult copepods (*Acartia tonsa*)

less efficiently (70 and 47%, respectively), and *A. tonsa* copepod nauplii were captured with only 14 % efficiency. The predation impact of lobate *M. leidyi* was estimated at about one-third of clearance rates on copepods measured by Madsen and Riisgård (2010), suggesting that our estimated predation impact of ctenophores on copepods may be a conservative estimate of the potential zooplankton predation impact of lobate *M. leidyi* in Limfjorden. In addition, the predation impact of the tentaculate ctenophore larvae was not assessed. Although *Aurita aurita* and *M. leidyi* capture different prey types with different relative efficiencies, the two predators feed on the same broad spectrum of zooplankton (i.e. dietary overlap). This indicates that

interspecific competition for prey would occur when they inhabit the same water mass and when prey is limiting. The situation in Limfjorden may be compared to strong competition and food shortage explaining the small size of medusae in the shallow *A. aurita*-dominated Kertinge Nor (Denmark) where the medusae usually obtain a maximum umbrella diameter of only 3 to 5 cm (Olesen et al. 1994; Riisgård et al. 1995, 2008, 2010).

Both the separate ($t_{1/2}$) and the combined (tot-$t_{1/2}$) predation impacts of *Aurelia aurita* and *Mnemiopsis leidyi* may be evaluated by inspection of Figure 4. Before the invasion of *M. leidyi*, the density of *A. aurita* was very low in 1997 and very high in 2003 (Figure 4 in Møller and Riisgård 2007a). That was clearly reflected in the biomass of zooplankton for those two years, specifically, in 1997, the zooplankton biomass was very high compared to 2003. In 2007 when *A. aurita* was almost absent, large numbers of *M. leidyi* were observed for the first time in midsummer and early autumn and the estimated half-life of copepods in Skive Fjord was <1 d (Riisgård et al. 2007). As a consequence, the copepods, cladocerans, and other mesozooplankton were completely eliminated by the end of July, and only ciliates remained during the rest of the season. Thus, in "pre-*Mnemiopsis* years" there seems to have been large variation in the grazing impact of zooplankton, and consequently, in the chlorophyll *a* concentrations, depending on the seasonal abundance of *A. aurita*. With the arrival of *M. leidyi*, however, this second carnivore added sufficient additional predation pressure to severely depress the zooplankton stocks throughout the year in 2008 and 2009 when copepods and cladocerans no longer showed the high seasonal peaks in abundance they did before *M. leidyi*.

In coastal waters where *Mnemiopsis leidyi* is native (e.g. Narragansett Bay and Chesapeake Bay on the north east coast of the USA), a number of studies have previously described the patterns of abundance (reviewed in Kremer 1994), timing and sizes of blooms (Sullivan et al. 2001), predation impacts, and relationships between the ctenophore and native jellyfish (e.g. Cowan and Houde 1993; Purcell et al. 1994, 2001; Purcell and Decker 2005). In the Narragansett Bay, *M. leidyi* is near the northern limit of its distribution and here, according to records from 1950 to 1979, it typically bloomed later in the summer compared to spring or early

summer blooms in warmer southern waters (Kremer 1994; Sullivan et al. 2001). But due to increasing water temperatures in Narragansett Bay (about 2°C from 1950 to 1999), the ctenophore's seasonal range has expanded to include springtime blooms during the 1980s and 1990s (Sullivan et al. 2001). Because springtime blooms of *M. leidyi* may impact fish recruitment directly by predation of fish eggs (e.g. Purcell et al. 1994), Sullivan et al. (2001) calculated predation rates on fish eggs in Narragansett Bay using published data on clearance rates of *M. leidyi* on fish eggs together with ctenophore abundance. At one collecting site in mid-July the density was 300 ctenophores m^{-3} (17 mm average length) which were estimated to clear 1,110 to 15,000 l m^{-3} d^{-1}, and Sullivan et al. (2001) concluded that "few eggs would be expected to survive this high abundance of ctenophores".

These observations suggest that the temporal patterns of abundance, bloom size, and predation impact of *Mnemiopsis leidyi* in Limfjorden may be comparable to the bloom peak performance of the invasive ctenophore in its native waters. But it seems unlikely that this ctenophore can survive the winter in Limfjorden, although this possibility cannot be excluded near the bottom in certain deeper (up to 25 m) areas, as suggested by Storr-Paulsen and Huwer (2008) and Javidpour et al. (2009), and therefore it may depend on seasonal recruitment from the North Sea. Fasse and Bayha (2006) suggested that the southern North Sea and its estuaries "may serve as a reservoir of *M. leidyi* and a yearly source of new immigrants to the colder waters", such as Limfjorden; however, Costello et al. (2006) found *M. leidyi* in most net samples in a shallow embayment (Greenwich Cove in Narragansat Bay, USA) even during winter ice cover and concluded that these ctenophores probably "inoculate the main region of the bay" in the spring.

Accurate quantitative estimates of abundance and distribution of *Mnemiopsis leidyi* may be problematic when based upon conventional net sampling, or even oblique net tows as in the present study, because the ctenophore may be concentrated either near the surface or at the bottom (Costello and Mianzan 2003). In the last case, the present sampling technique would probably not capture the ctenophore. Future studies, possibly using underwater-video and scuba diving may reveal if *M. leidyi* survives the winter near the bottom in the deeper parts of Limfjorden.

Our study emphasizes the crucial importance of studying the interplay between hydrography and population dynamics of medusae and ctenophores in order to understand their presence and densities and also their zooplankton-predation impacts, which can affect the whole pelagic food web, as illustrated here by very low biomass of grazing zooplankton and high chlorophyll *a* concentrations.

Acknowledgements

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