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Jellyfish and Ctenophores in the Environmentally Degraded Limfjorden (Denmark) During 2014 - Species Composition, Population Densities and Predation Impact

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Abstract

Species composition, population densities and size of jellyfish and ctenophores were recorded during 5 cruises in the heavily eutrophicated Limfjorden in 2014. No or very few ctenophores (*Pleurobrachia pileus*) and jellyfish (*Aurelia aurita*, *Cyanea lamarckii*) were recorded in April and June 2014, whereas in August and September numerous small individuals of the invasive ctenophore *Mnemiopsis leidyi* were found on all 4 locations studied, which were strongly reduced in population density during November. *M. leidyi* exerted a notable predation impact, most pronounced in Løgstør Bredning and Skive Fjord in August when the estimated half-lives of zooplankton were 4.8 and 7.3 d, respectively, and in late September, when the half-life in Skive Fjord was only 2.2 d. Severe oxygen depletion in Løgstør Bredning and Skive Fjord between June and September resulted in a release of nutrients. This was followed by a bloom of the dinoflagellate *Noctiluca scintillans* and a subsequent peak in the abundance of copepods which decreased rapidly after the introduction of *M. leidyi* into Limfjorden from the North Sea (between early April and mid-July) to become virtually absent during the rest of the season. This subsequently resulted in starvation and decay of the *M. leidyi* population. The small predatory ctenophore *Beroe gracilis* was recorded on most locations during August and September 2014 but although *B. gracilis* eats small *M. leidyi*, their low number suggested a negligible predation impact on the *M. leidyi* population. Our present understanding of the many biological and environmental factors that control the species composition, abundance and predation impact of jellyfish and ctenophore populations in Limfjorden are discussed.

Keywords: *Mnemiopsis leidyi*; *Beroe gracilis*; *Pleurobrachia pileus*; *Aurelia aurita*; Predation impact; Hydrography; Zooplankton; Limfjorden; Oxygen depletion; Hypoxia

Introduction

Marine areas experiencing jellyfish and ctenophore blooms seem often to be those that reveal the greatest environmental degradation [1,2]. Limfjorden (Denmark) is heavily eutrophicated and large areas suffer from oxygen depletion each summer which has apparently caused a change "from fish to jellyfish" [3]. The abundance and predation impact of jellyfish and ctenophores in Limfjorden have been described in a number of studies conducted since 2003 [3-10] and recently reviewed [11] which was supplemented with observations from 2012 and 2013.

The common jellyfish *Aurelia aurita* is often very abundant in Limfjorden and may exert a considerable predatory impact on zooplankton and fish larvae. However, the population dynamics of *A. aurita* are not only strongly influenced by the high-salinity water brought into Limfjorden from the North Sea, but also by competition with the invasive ctenophore *Mnemiopsis leidyi* that occurred in Limfjorden for the first time in extremely high numbers in 2007 [12]. It has been suggested that Limfjorden may function as an incubator for *M. leidyi* with the potential to further spread *M. leidyi* into the Kattegat and adjacent Danish waters [9,10]. A recent study [11] reported on two bloom events of ctenophores, *Pleurobrachia pileus* and *M. leidyi*, along with their predators (*Beroe* spp.) in Limfjorden in the autumns of 2012 and 2013, when the previously dominating *A. aurita* was absent. Further it was observed that *B. ovata*, which is *M. leidyi*'s native predator, had now occurred as a new introduced species in Limfjorden.

The aim of the present study was to record the seasonal occurrence patterns of jellyfish and ctenophores in Limfjorden during 5 cruises with the Danish Naval Homeguard in 2014 in order to obtain a better understanding of the biological and environmental factors that control their species composition, population densities and predation impact. Our present knowledge on the complex interplay between biological and environmental factors that control the jellyfish and ctenophore populations in Limfjorden is briefly reviewed and discussed, including the importance of recruitment, life cycles, and hydrographic conditions.

Materials and Methods

Study area

Limfjorden is a Danish shallow-water system with a mean water depth of about 4.5 m that connects the North Sea via Thyborøn Kanal in the west to the Kattegat in the east (Figure 1). A dominating west-easterly wind creates an eastward current that brings highly saline North Sea water into Limfjorden, which also receives freshwater inputs from the surrounding land area and this results in a salinity gradient from west to east [13-17]. Limfjorden is heavily eutrophicated and large

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areas suffer from oxygen depletion each summer [7,13,18], and this has apparently caused the bottom-dwelling fish to disappear and the number of jellyfish and ctenophores to increase [3]. Every year, strong westerly-winds induce about 60 intrusions of North Sea water through Thyborøn Kanal into Limfjorden succeeded by backflow of water into the North Sea on calm days. Annually, about 70 km^3 of North Sea water enter Limfjorden, and approximately 65 % flows eastwards into Løgstør Bredning which additionally receives 3 km^3 freshwater so that about 8.7 km^3 runs eastwards into Kattegat [10]. Inflowing water to Limfjorden mainly comes from the Jutland Coastal Current which flows northwards along the Danish west coast carrying mixed water masses from the English Channel and the southern North Sea [10,19-21].

Jellyfish and ctenophores

Jellyfish and ctenophores were collected with a 2 mm-meshed plankton net (mouth-ring diameter = 1.5 m, mouth area = 1.77 m^2) at 4 locations in Limfjorden (Figure 1) during 5 one-day cruises in 2014 with the Danish Naval Homeguard MVH 902 'Manø'. Three hauls per location (haul length ~300 m) were performed at a depth of approximately 1 m at a speed of about 1.5 knots. After the three hauls, the number of medusae and ctenophores in the cod end of the plankton net were counted from sub-samples, and mean population densities were estimated from the densities in the 3 hauls. Further, mean (±SD) sizes were determined to the nearest mm after measuring ctenophore oral-aboral lengths (*L* i.e. distance between mouth and opposite pole) and medusa inter-rhopalia umbrella diameters (*d*) of all, or at least 50 individuals per

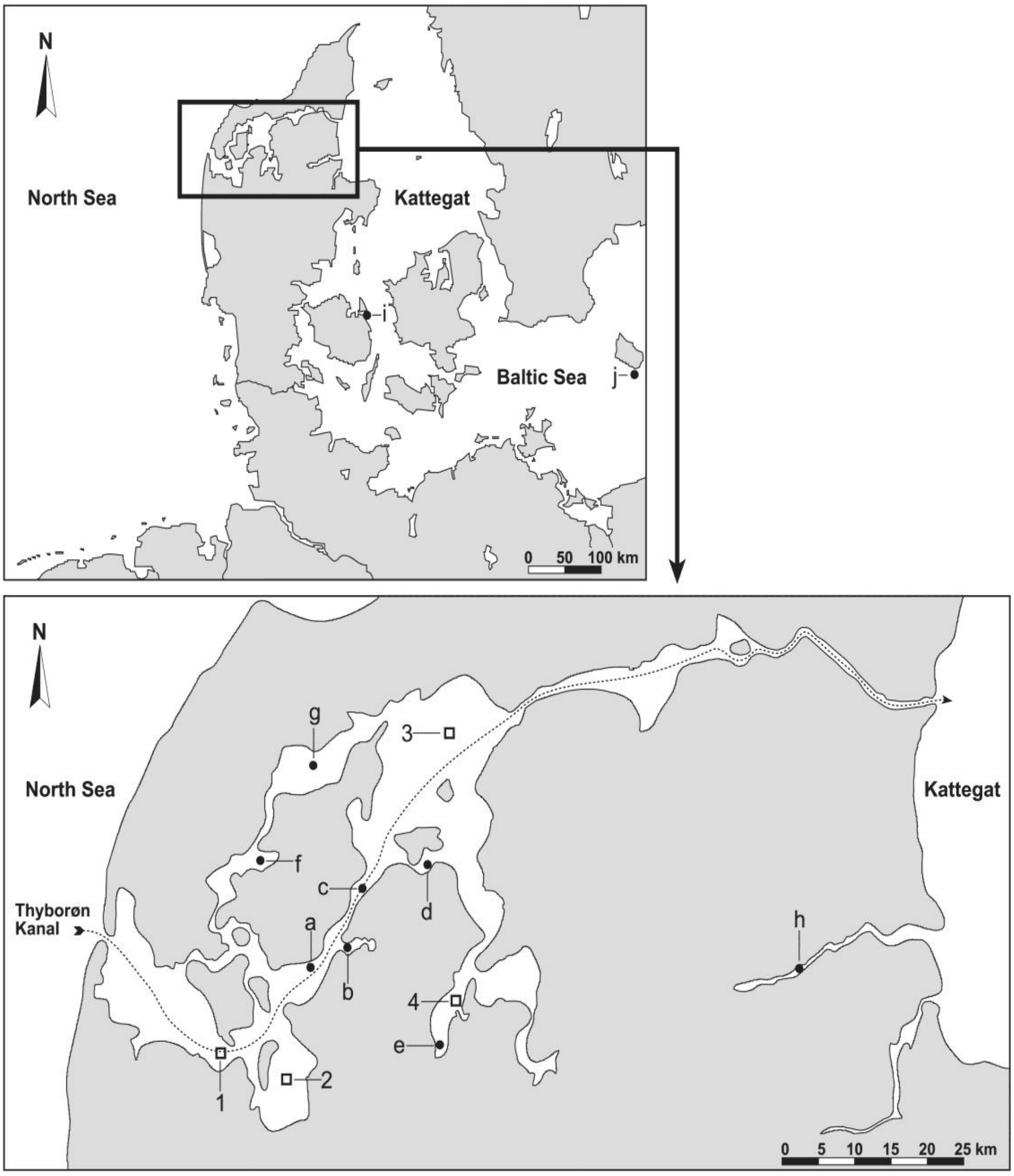


Figure 1: Locations of sampling sites in Limfjorden (Denmark) where jellyfish and ctenophores were collected on cruises during 2014. 1 = Nissum Bredning (56°34'25.80" N, 08°29'41.40" E), 2 = Venø Bugt (56°31'23.40" N, 08°40'27.60" E), 3 = Løgstør Bredning (56°57'09.00" N, 09°03'27.60" E), 4 = Skive Fjord (56°37'15.00" N, 09°05'33.00" E). The path of water exchange between the North Sea in west and Kattegat in the east is indicated by a broken line. Place names: a = Sillerslev, b = Lysen Bredning, c = Glyngøre, d = Branden, e = Skive, f = Dragsted Vig, g = Thisted Bredning, h = Mariager Fjord, i = Kerteminde Fjord/Kertinge Nor, j = Bornholm.

haul. Population clearance rates and predation impact of two species of ctenophores (*Mnemiopsis leidyi*, *Pleurobrachia pileus*) and the moon jellyfish (*Aurelia aurita*) on zooplankton (using copepods as reference) were estimated from recorded population densities using the equations below.

Mnemiopsis leidyi. The following relationship was used for converting oral-aboral length (L, mm) to individual body volume (V, ml ind.$^{-1}$) [8]:

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

The following equation [10,22], was used to estimate the individual clearance rate (Cl_{ind}, l d^{-1}) of *M. leidyi* feeding on copepods as a function of their body volume (V, ml):

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

Pleurobrachia pileus. Clearance rates (Cl_{ind}, l d^{-1}) were estimated from the polar length (L, mm) by using the following equation for ctenophores feeding on copepods [23]:

$$Cl_{ind} = 0.2L^{1.9} \quad \text{Eq (3)}$$

Aurelia aurita. The individual clearance rate (Cl_{ind}, l d^{-1}) of moon jellyfish feeding on copepods was estimated from the mean inter-rhopalia diameter (d, mm) by use of the equation [6]:

$$Cl_{ind} = 0.0073d^{2.1} \quad \text{Eq (4)}$$

The volume-specific population clearance rate of jellyfish and ctenophores (Cl_{pop}, m^3 water filtered by the jellyfish or ctenophore 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 location [10]:

$$Cl_{pop} = Cl_{ind} \times D / 1000 \quad \text{Eq (5)}$$

The time ($t_{1/2}$, d) it takes for a population of jellyfish or ctenophores with known Cl_{pop} to reduce the concentration of prey organisms (copepods) in V = 1 m^3 of water by 50 % (i.e. the half-life of prey) was estimated as [10]:

$$t_{1/2} = \ln 2 / Cl_{pop} \quad \text{Eq (6)}$$

Water chemistry and zooplankton

Water chemistry data (salinity, temperature, dissolved oxygen, chlorophyll *a*) and zooplankton biomass from Løgstør Bredning and Skive Fjord for 2014 were obtained from the "National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environments" (NOVANA) conducted by the Danish Ministry of the Environment. All data were collected and analyzed according to official monitoring guidelines [24]. Water chemistry data were obtained from CTD profiles from the surface to the bottom at the locations. Chlorophyll *a* concentrations at 1 m depth were obtained from the absorbance in spectrophotometric analysis of chlorophyll extracted with ethanol from the algae present in filtered water samples. Zooplankton was collected by using a submersible pump with a minimum capacity of 150 l min^{-1}. The water was pumped up vertically by hauling the pump up at a speed of 0.5 m s^{-1}. Collection of the zooplankton was done by using a 60 µm net at the outlet. The filtered water volume was calculated by using a mechanical flow meter. The filter was rinsed thoroughly and the sample preserved in either 2 to 3 % formalin (pH 8.0 to 8.2) or neutral Lugol's solution. The concentrations (ind. m^{-3}) and biomasses (µg C l^{-1}) of zooplankton species and taxonomic groups were subsequently determined.

Results

Jellyfish and ctenophores

Species composition, population densities and size of jellyfish and ctenophores recorded during 5 cruises in Limfjorden in 2014 are listed in Table 1, along with the estimated half-life of zooplankton for the 3 most abundant species. It is seen that only *Mnemiopsis leidyi* exerted a notable predation impact, most pronounced in Løgstør Bredning and Skive Fjord in August, when the estimated half-life of zooplankton (copepods) were 4.8 and 7.3 d, respectively, and in Skive Fjord in late September when the half-life was 2.2 d. The size distribution of *M. leidyi* at the 4 investigated locations is shown in Figure 2. *M. leidyi* was not observed in Limfjorden during the first 2 cruises, 7 April and 3 June, respectively. But on the 3rd cruise (26 August) the ctenophore was found on all 4 locations, with largest body size (L = 8.6 ± 4.8 mm) and lowest population density (D = 18.5 ± 19.4 ind. m^{-3}) in Nissum Bredning in the western part of Limfjorden. The highest density and smallest size were observed in Løgstør Bredning (D = 158.8 ± 110.7 ind. m^{-3}, L = 4.9 ± 2.1 mm) and Skive Fjord (D = 116.0 ± 25.6 ind. m^{-3}, L = 4.6 ± 1.9 mm). This pattern was somewhat changed one month later on the 4th cruise (23 September), and on the 5th cruise (18 November), when the population density of *M. leidyi* on all locations was strongly reduced. Along with the occurrence of *M. leidyi*, the small predatory ctenophore, *Beroe gracilis* was recorded on most sampling locations during the 3rd and 4th cruise, but not on the 5th cruise when only one large (L = 64 mm) *Beroe* sp. individual was caught (Table 1). From Figure 3 it appears that *B. gracilis* eats small *M. leidyi*, but their low number suggests that the population predation impact of *Beroe gracilis* exerted on *M. leidyi* during 2014 was negligible.

Water chemistry and zooplankton

Figures 4 and 5 show the temperature, salinity, dissolved oxygen and chlorophyll *a* concentrations in Løgstør Bredning and Skive Fjord during 2014. Figure 6 shows vertical profiles of temperature and salinity on selected dates, with full vertical mixing (Figure 6A) and bottom-near intrusion of high-saline North Sea water (Figure 6B) in Løgstør Bredning, and strong stratification due to combined thermo- and haloclines in Skive Fjord (Figure 6C), respectively. The dissolved oxygen concentration in the near-bottom water decreased to zero several times at both locations between June and September. As indicated by high chl *a* concentrations at the two locations (up to 45 µg l^{-1} in mid-August in Skive Fjord, Figure 5), the severe oxygen depletion had resulted in the release of nutrients (ammonium, phosphate) [7] from the anoxic sediment causing an algal bloom which was subsequently followed by a tremendous bloom of the heterotrophic dinoflagellate *Noctiluca scintillans* (Figure 7A). This was again followed by a pronounced peak in the abundance of copepods and their offspring nauplii (Figure 7B). To judge from the population density of *Mnemiopsis leidyi* and the estimated half-life of copepods ($t_{1/2}$ = 4.8 d) in Løgstør Bredning on 26 August 2014 (Table 1) it seems reasonable to suggest that the rapid decrease in the biomass of copepods during late July, and the following absence of zooplankton during the rest of the year was caused by a boom of the invasive ctenophore. As a consequence, it may therefore be suggested that the decrease in population density and the persistent small size of *M. leidyi* during September and November (Table 1) reflect a rapid depletion of prey organisms resulting in starvation and decay.

Discussion

Species composition, population densities and predation impact

The abundance of ctenophores and jellyfish in Limfjorden is characterized by large fluctuations in species composition and population size, and while the yearly development of *Aurelia aurita*

Cruise/Date/Locality	Species	*D* (ind. m^{-3})	*L* (mm)	*d* (mm)	$t_{1/2}$ (d)
Cruise 1, 7 April 2014					
1 Nissum Bredning	*Pleurobrachia pileus*	0.003 ± 0.003	4.1 ± 2.9 (8)		∞
2 Venø Bugt	-				
3 Løgstør Bredning	-				
4 Skive Fjord	-				
Cruise 2, 3 June 2014					
1 Nissum Bredning	*Pleurobrachia pileus*	0.001 ± 0.001	23.0 ± 1.4 (2)		∞
	Aurelia aurita	0.003 ± 0.001		214.8 ± 48.0 (8)	∞
	Cyanea lamarckii	0.003 ± 0.001		66.8 ± 25.3 (8)	
2 Venø Bugt	*Aurelia aurita*	0.001 ± 0.001		212.0 ± 120.2 (2)	∞
3 Løgstør Bredning	*Aurelia aurita*	0.007 ± 0.012		212.5 ± 32.6 (19)	∞
4 Skive Fjord	-				
Cruise 3, 26 Aug 2014					
1 Nissum Bredning	*Mnemiopsis leidyi*	18.5 ± 19.4	8.6 ± 4.8 (50)		15.5
	Beroe gracilis	0.002 ± 0.003	22.0 (1)		
2 Venø Bugt	*Mnemiopsis leidyi*	67.9 ± 50.5	4.5 ± 2.0 (50)		12.9
	Beroe gracilis	0.030 ± 0.019	20.3 ± 5.3 (50)		
3 Løgstør Bredning	*Mnemiopsis leidyi*	158.8 ± 110.7	4.9 ± 2.1 (50)		4.8
	Beroe gracilis	0.002 ± 0.004	13.0 (1)		
4 Skive Fjord	*Mnemiopsis leidyi*	116.0 ± 25.6	4.6 ± 1.9 (50)		7.3
Cruise 4, 23 Sept 2014					
1 Nissum Bredning	*Mnemiopsis leidyi*	38.1 ± 18.1	7.6 ± 2.9 (50)		9.3
2 Venø Bugt	*Mnemiopsis leidyi*	0.2 ± 0.2	6.6 ± 2.0 (50)		∞
	Beroe gracilis	0.001 ± 0.000	20.0 ± 3.6 (3)		
	Aurelia aurita	0.000 ± 0.001		49.0 (1)	∞
	Rhizostoma octopus	0.000 ± 0.001		280.0 (1)	
3 Løgstør Bredning	*Mnemiopsis leidyi*	12.6 ± 5.4	4.3 ± 1.1 (50)		∞
	Beroe gracilis	0.002 ± 0.000	21.5 ± 6.8 (4)		
	Aurelia aurita	0.000 ± 0.001		55.0 (1)	∞
4 Skive Fjord	*Mnemiopsis leidyi*	255.4 ± 116.7	5.8 ± 1.6 (50)		2.2
Cruise 5, 18 Nov 2014					
1 Nissum Bredning	*Mnemiopsis leidyi*	0.5 ± 0.1	15.9 ± 12.7 (50)		∞
	Mnemiopsis leidyi	0.2 ± 0.1	17.8 ± 9.7 (50)		∞
2 Venø Bugt	*Beroe* sp.*	0.000 ± 0.001	64.0 (1)		
3 Løgstør Bredning	*Mnemiopsis leidyi*	6.6 ± 2.9	4.6 ± 1.9 (50)		∞
4 Skive Fjord	*Mnemiopsis leidyi*	19.1 ± 12.2	4.6 ± 1.1 (50)		∞
	Aurelia aurita	0.001 ± 0.002		65.0 (1)	∞

* *Beroe ovata* or *cucumis*

Table 1: Ctenophore and jellyfish species collected during 5 cruises in Limfjorden in 2014. *D* = mean (± SD) population density; *L* = mean (± SD, *n* = number of measured individuals) oral-aboral length of ctenophores; *d* = mean (± SD, *n*) inter-rhopalia diameter of medusae; $t_{1/2}$ = estimated half-life of copepods (cf. Eq. 6; $t_{1/2}$ > 3 weeks are indicated by ∞).

populations depends on benthic polyps, incoming water from the North Sea seems to be responsible for a yearly reinvasion by *Mnemiopsis leidyi* and other ctenophore species from the North Sea, and the present study supports the hypothesis that the North Sea serves as a refuge from where *M. leidyi* reinvades Limfjorden [10,11].

No or only very few ctenophores (*Pleurobrachia pileus*) and jellyfish (*Aurelia aurita*, *Cyanea lamarckii*) were recorded during the first two cruises in April and June 2014, and *Mnemiopsis leidyi* was first recorded on the 3rd cruise in late August (Table 1). However, the present first author (HUR) observed *M. leidyi* at a number of sites in Limfjorden (Sillerslev, Lysen Bredning, Glyngøre, Branden ; Figure 1) between 25 and 28 June 2014. Therefore, *M. leidyi* must have entered Limfjorden with North Sea water through Thyborøn Kanal between 7 April and 25 July. In the period between the 2nd and 3rd cruise, salinity increased in the bottom-near water (from 25.5 to 27.9 psu) in Løgstør Bredning during the period 17 June to 1 July (Figures 5B and 7B). This is also coincident with the observation of the North Sea scyphomedusa *Rhizostoma octopus* which is frequently brought into Limfjorden in the autumn months [11]. The Jutland Coastal Current which carries mixed water masses from the English Channel and the southern North Sea gives rise to seawater inflows into Limfjorden, which also explains the occasional re-introduction of the hydromedusa *Aequorea vitrina* in Limfjorden where it is not able to establish a surviving population [6,8].

Differences in the life-history strategies of jellyfish and ctenophores are important for understanding the often strong variations in species composition and population dynamics. The scyphozoan *Aurelia aurita* has a life cycle which includes a pelagic medusa and a benthic polyp stage. Medusae reproduce sexually and larval development is followed by the disappearance of medusae in late autumn. After settlement, planula larvae metamorphose into polyps to pass the winter. In the early spring, the polyps produce ephyrae that are released into the water column to develop into a new generation of medusae [4,25]. In contrast

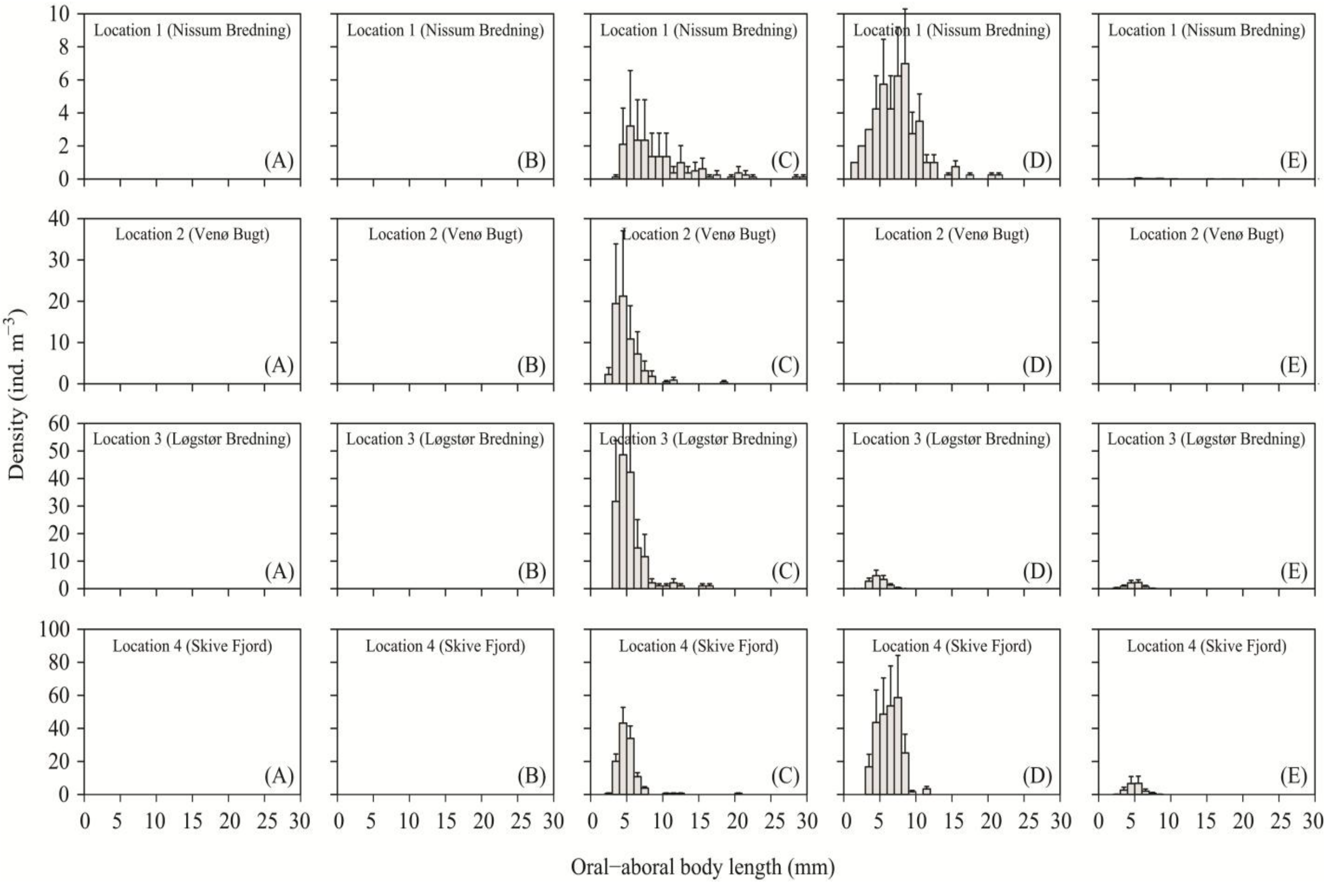
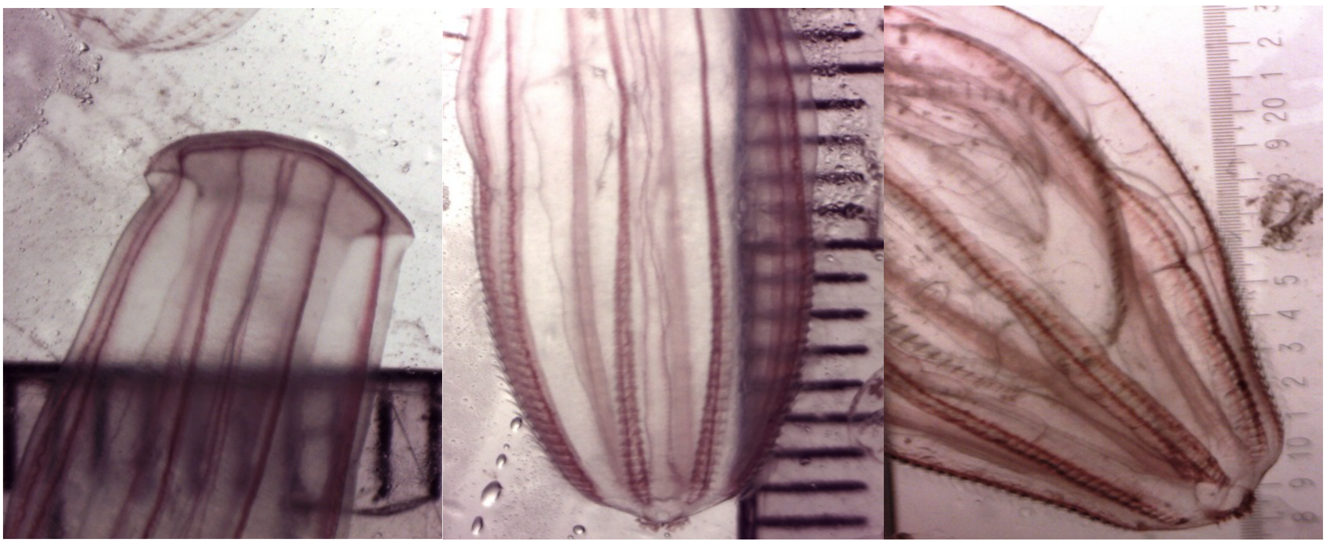


Figure 2: *Mnemiopsis leidyi*. Oral-aboral length distribution at 4 investigated locations in Limfjorden on A) 07 April B) 3 June, C) 26 August, D) 23 September and E) 18 November 2014. Average sizes for each mm size category are displayed (± SD for 3 replicate samples at each location).



A B C

Figure 3: *Beroe gracilis* & *Mnemiopsis leidyi*. Ctenophores captured in net hauls in Limfjorden 26 August 2014. (A) oral end of *B. gracilis*, note a prey organism (*M. leidyi*) close to the left corner; scale: 1.0 mm. (B) aboral end of *B. gracilis*; scale: 1.0 mm. (C) *B. gracilis* with prey organism (*M. leidyi*) in the gastrovascular cavity; scale: 0.1 mm. Photos: Hans Ulrik Riisgård.

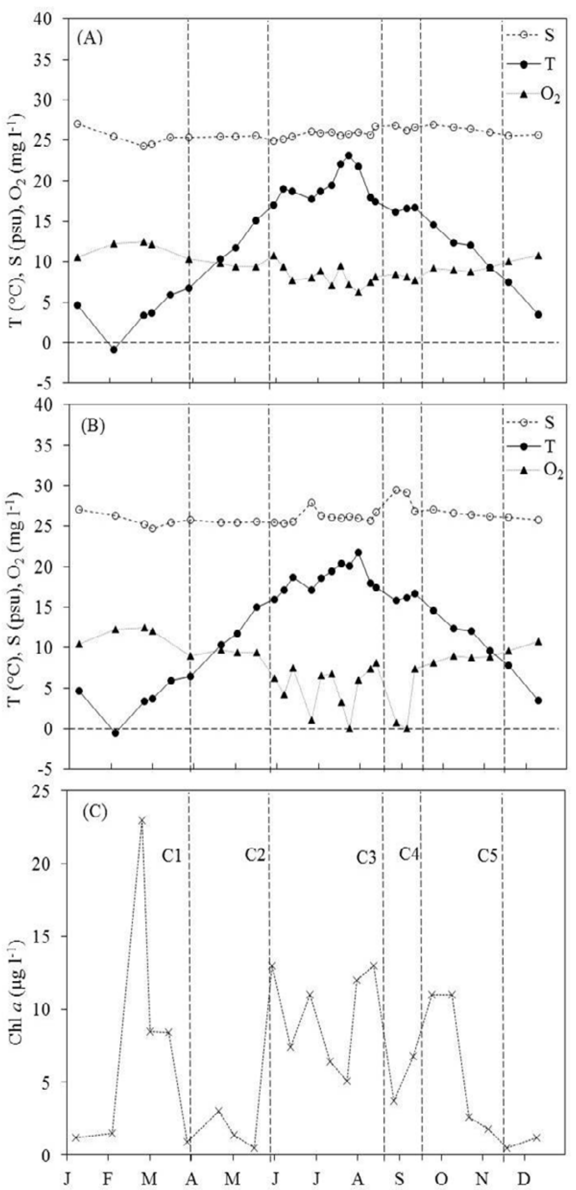


Figure 4: Løgstør Bredning 2014. (A) Temperature (T), salinity (S) and oxygen (O) in the top water layer (0.8 m below the surface), and (B) in the bottom water layer (0.3 to 0.4 m above the bottom). (C) Chlorophyll *a* (Chl *a*, µg l^{-1}) measured at a depth of 1 m. Punctured vertical lines (labelled C1-C5) signify the date of each of the 5 cruises carried out in the present study.

to this, the ctenophore *Mnemiopsis leidyi* relies on a holoplanktonic life cycle. *M. leidyi* is a self-fertilizing hermaphrodite, releasing eggs and sperm in the ambient water where fertilization occurs [26-29]. Thus, high fecundity and rapid generation times during the whole season may explain the ability of *M. leidyi* (and *Pleurobrachia pileus*) to occur in large numbers in Limfjorden [11]. However, unless a major fraction of *A. aurita* ephyrae are washed out of Limfjorden in the early spring, this may also result in a mass occurrence [7] and interspecific competition with *M. leidyi* [9]. The conspicuously few *A. aurita* observed in the present study as well as in the two preceding years [11] indicates that moon jellyfish populations in Limfjorden may currently experience the process of being outcompeted by the more numerous and faster reproducing *M. leidyi*, which could, on the long-term, also lead to a disappearance of local *A. aurita* polyps. However, alternative explanations are also possible, but especially improved understanding of polyp ecology seems necessary for understanding fluctuations in jellyfish numbers [2,30-33].

The abundance of ctenophores and jellyfish in Limfjorden is characterized by often large fluctuations in species composition and population size [11]. While the yearly development of *Aurelia aurita*

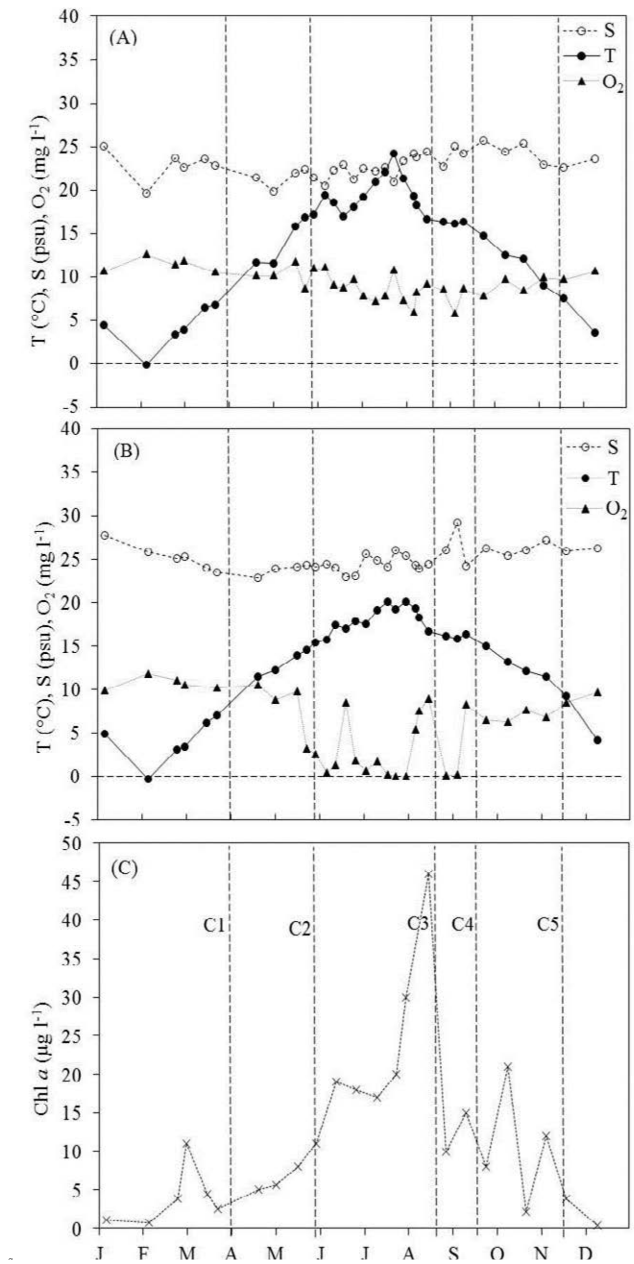


Figure 5: Skive Fjord 2014. (A) Temperature (T), salinity (S) and oxygen (O) in the top water layer (0.8 m below the surface), and (B) in the bottom water layer (0.3 to 0.4 m above the bottom). (C) Chlorophyll *a* (Chl *a*, µg l^{-1}) measured at a depth of 1 m. Punctured vertical lines (labelled C1-C5) signify the date of each of the 5 cruises carried out in the present study.

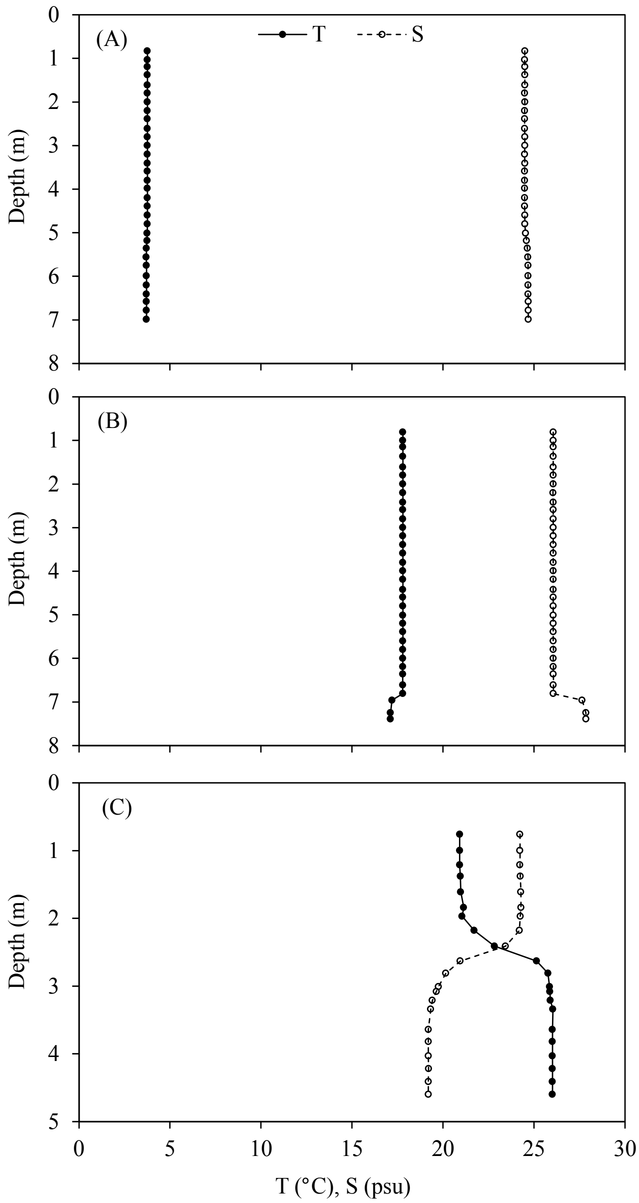


Figure 6: (A) Løgstør Bredning. Vertical profiles of temperature (T, °C) and salinity (S, psu) measured 4 March 2014 which is in between the cruises C1 and C2. (B) Løgstør Bredning. Vertical profiles measured 1 July 2014 (i.e. between cruises C2 and C3 at the time when salinity in the bottom water showed an increase, see Figure 5B). (C) Skive Fjord. Vertical profiles measured 28 July 2014 (i.e. between cruises C2 and C3, a few days before upwelling of anoxic bottom water to the surface as shown in Figure 5).

populations in Limfjorden may largely depend on recruitment via asexual reproduction by local polyps, the incoming water from the North Sea is of decisive importance for the yearly reinvasion by *Mnemiopsis leidyi* and other ctenophore species from the warmer south-western North Sea [34-36]. The present study supports the hypothesis that the North Sea in cold winters serves as a refuge from where *M. leidyi* reinvades Limfjorden, which may function as an incubator for *M. leidyi*, subsequently dispersing into the Kattegat and adjacent waters [10,11]. A number of observations support this hypothesis; thus, first observations of *M. leidyi* outside Limfjorden in 2014 were in Mariager Fjord (8 October, own observation), Kerteminde Fjord (3 October 2014, own observation), Kertinge Nor (7 November 2014, own observation) and the western Baltic Sea near Bornholm (21 November, Marie Stoor-Paulsen). The recent observations of *B. ovata* being a new species in Danish waters [11,37] has not yet caused measurable changes in the number and distribution of *M. leidyi*, and the biological and environmental factors controlling its sporadic occurrence are still poorly understood.

Interplay between biological and environmental factors: our present understanding

Recently, [3] gave an overview of the environmental status of the heavily eutrophicated Limfjorden, including the historical development of nutrient overloading and subsequent oxygen depletion in near-bottom water, and further how the bottom dwelling fish species decreased while the number of jellyfish and ctenophores increased. A case study of Skive Fjord [7] demonstrated the links between primary production, oxygen deficiency, nutrients and jellyfish. Each summer, Skive Fjord suffers from oxygen depletion in the near-bottom water and this causes large amounts of nutrients (phosphate and ammonia) to be released from the anoxic sediment, which subsequently stimulates a phytoplankton bloom, followed by an increase in zooplankton biomass [7] (Figure 2). The same phenomenon was observed in the present study, not only in Skive Fjord but also in Løgstør Bredning, where the chlorophyll *a* concentrations became very high during periods with oxygen depletion (Figures 4 and 5) followed by a bloom of *Noctiluca scintillans* succeeded by an increase in copepod biomass (Figure 7). [7] combined available data on jellyfish with data on dissolved oxygen, nutrients, chlorophyll

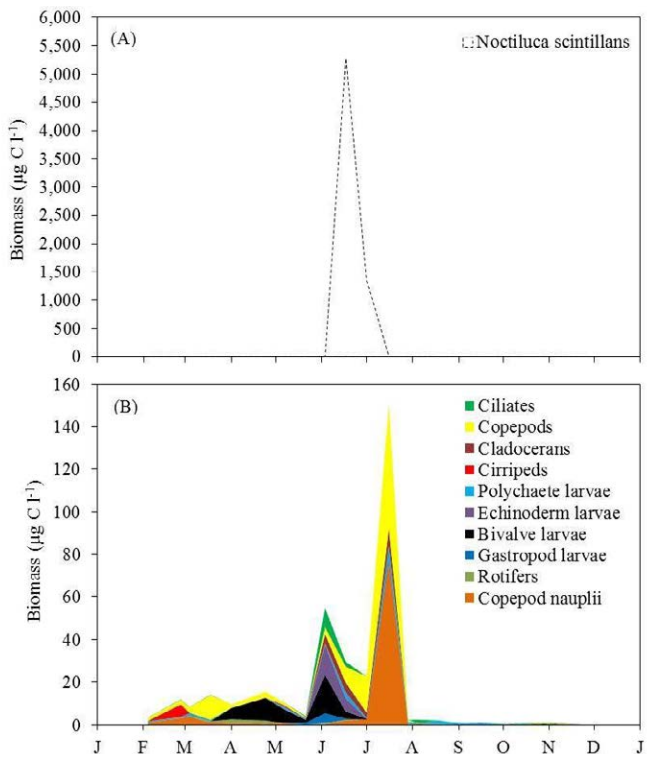


Figure 7: Løgstør Bredning (Figure 1, location 3). (A) June and July 2014 bloom-biomass of the dinoflagellate *Noctiluca scintillans*, (B) zooplankton biomass presented as the contribution of each zooplankton group of total biomass over time.

a, zooplankton, and other data from various studies conducted in Skive Fjord during the period 1996 to 2005 and found that especially severe cases of oxygen depletion apparently take place in years with mass occurrence of jellyfish. Due to their high predatory impact on the zooplankton community, blooming algae are not efficiently grazed on, but settle to the bottom and decay, thus leading to more severe hypoxia.

Mass occurrence of *Mnemiopsis leidyi* was first observed in Limfjorden in 2007, but it probably arrived the previous year [38]. This invasive holoplanktonic ctenophore exerted further predation pressure in addition to the indigenous scyphomedusa *Aurelia aurita*, which frequently caused the zooplankton organisms to become virtually absent, as also observed with some time-lag after the arrival of *M. leidyi* (Figure 7 and Table 1) in the present study. [39] made an integrated ecosystem assessment for Limfjorden over the period from 1984 to 2008 and showed that from 1990 to 1995, the structure shifted from dominance by demersal fish species to that of pelagic fish species (sprat, herring, sticklebacks) and jellyfish. Nutrients (N, P) have been and are still considered as a major bottom-up forcing factor in the system. Since the early 1900s and up to the mid-1980s there was a six-fold increase in nutrients which caused recurrent events of oxygen depletion, but although the loadings have decreased by 33 % (N) and 67 % (P) due to a water action plan decided by the Danish Parliament in 1987 which has so far not resulted in any noticeable improvement in ecosystem state [39,40].

According to [41], the first severe case of oxygen depletion in Limfjorden in 2014 took place in mid-June, including the stratified Skive Fjord (Figure 6C), other inner and central parts and central north-western parts (Thisted Bredning, Dragstrup Vig, Figure 1) where dead fish were observed on the beaches. By the end of June strong westerly winds resulted in mixing of the water column and improved oxygen conditions, but from the beginning of July the water column became stratified resulting in further oxygen depletion soon after. Thus, by the end of July 2014, about 30 % of the total bottom waters in Limfjorden were depleted of oxygen with subsequent release of toxic hydrogen sulphide from the anoxic sediment [13]. In Skive Fjord, off-shore winds in late July and early August pushed the surface water away from the shore, which caused upwelling of near-bottom water containing high concentrations of hydrogen sulphide. Subsequent oxidation made the new surface water white-colored due to precipitation of free sulphur [41]. No systematic studies of the effects of oxygen-depletion on fish, phyto- and zoobenthos have been conducted by the environmental authorities in 2014, and likewise possible effects on jellyfish and ctenophores remain unknown. However, due to the presence of high population densities of *Mnemiopsis leidyi* in Skive Fjord in late August and September (Table 1), it may be suggested that this ctenophore is rather resistant to poor environmental conditions as also emphasized by [22,42] who observed that *M. leidyi* is more tolerant to hypoxia than their prey and competing zooplanktivorous fishes.

From both the present study and earlier accounts [11], it appears that the species composition of jellyfish and ctenophores, their population dynamics and predation impact in Limfjorden is highly unpredictable, depending on the complex interplay between recruitment, life cycles, and hydrographic conditions. Every year since 2007, *M. leidyi* has reinvaded Limfjorden from the North Sea via Thyborøn Kanal with water partly originating from the English Channel [43], the Belgian part of the North Sea [44], and the western Dutch Wadden Sea where it is present the whole year round [35] and recent modelling [46] supports this interpretation. *M. leidyi* has frequently exerted a significant predation impact on the zooplankton biomass in Limfjorden during late summer, but in October and November 2012 it was another ctenophore, *Pleurobrachia pileus*, that controlled the zooplankton in Løgstør Bredning, with $t_{1/2}$ = 1.5 and 2.8 d in October and November, respectively, while only very few *M. leidyi* were observed [11]. However in most years since 2007, *M. leidyi* has thrived extremely well during late summers in Limfjorden, from where the ctenophore with its rapid reproduction may further spread into Kattegat and the inner Danish waters, perhaps even to the western Baltic Sea [47].

In the present study, it was observed that *Beroe gracilis* feed on small (<20 mm) *Mnemiopsis leidyi* (Figure 3) which confirms recent observations by [35,48]. Apparently, *B. gracilis* follows *M. leidyi* from the southern North Sea from where also *Pleurobrachia pileus* comes, but hitherto, *B. gracilis* has been considered a specialized predator on *P. pileus* and new to the inner Danish waters [37]. This phenomenon may be another consequence of the now established self-sustaining populations of *M. leidyi* in the English Channel and southern North Sea coasts.

Herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) are pelagic fish species in Limfjorden and have to date been used for both human consumption and industrial processing for fish meal and oil, but because these fish feed on zooplankton, they may, in certain areas and periods, compete with large numbers of ctenophores and/or jellyfish [11]. The herrings enter Limfjorden from both the North Sea and the Kattegat in late autumn and early winter to spawn in the spring, and the adults leave again in early summer while the juveniles stay (Erik Hoffmann, pers. comm.), but no studies have so far attempted to determine the degree of interspecific competition for zooplankton. The short estimated half-lives of zooplankton caused by *M. leidyi* in August 2014 in Løgstør Bredning and Skive Fjord (Table 1) and the conspicuous reduction of the zooplankton biomass (Figure 7) suggest very poor feeding conditions for juvenile herrings in Limfjorden.

The present study has been focused on the complex interplay between biological and environmental factors that control the jellyfish and ctenophore populations in Limfjorden, and hopefully, the many still unsolved questions may stimulate future research with focus on e.g. how gelatinous predation of zooplankton may reinforce anoxia and further habitat degradation in eutrophicated waters.

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