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Research article

High abundance of the jellyfish *Aurelia aurita* excludes the invasive ctenophore *Mnemiopsis leidyi* to establish in a shallow cove (Kertinge Nor, Denmark)

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Abstract

The population dynamics of the invasive ctenophore *Mnemiopsis leidyi*, which showed mass occurrence in Kerteminde Fjord (Denmark) for the first time in 2007, and the indigenous common jellyfish, *Aurelia aurita*, was followed in the fjord system Kerteminde Fjord/Kertinge Nor during late 2008 and 2009. The population density of *A. aurita* was always highest in Kertinge Nor while the density of *M. leidyi* was always highest in Kerteminde Fjord, indicating recruitment of the ctenophore from the adjacent sea (Great Belt). In the shallow cove of Kertinge Nor, the first *A. aurita* ephyrae appeared in March, by the end of May the medusae had obtained their maximum umbrella diameter of only 30 mm due to food limitation, and the estimated half-life of zooplankton was very low, <1 day from May to September 2009. The high predation impact explains why the holopelagic ctenophore, which presumably survives the winter in the adjacent open sea, is likely to be outcompeted in Kertinge Nor where the polyp stage of *A. aurita* every spring ensures a very large population of very small medusae. The population density of jellyfish, in Kertinge Nor, during the summer period is dependent on the extend of flush-out due to density-driven water exchange. A survey of data obtained every year in August since 1991 indicates that the unusually high population density (36 ± 34 ind. m^{-3}) and the small umbrella diameter (56 ± 5 mm) of *A. aurita* have remained unchanged during the last 20 years, and further, that a relatively high population density of jellyfish in certain years is correlated with a relatively small mean umbrella diameter.

Key words: *Aurelia*, competition, gelatinous plankton, *Mnemiopsis*, predation impact, zooplankton, specific growth rate, half-life of zooplankton

Introduction

The common jellyfish *Aurelia aurita* (Linnaeus, 1758) is periodically very abundant in many coastal waters where it exerts a considerable predatory impact on zooplankton and fish larvae (Båmstedt 1990; Schneider and Behrends 1994; Behrends and Schneider 1995; Purcell and Decker 2005; Hansson et al. 2005; Møller and Riisgård 2007a, b). Natural populations of *A. aurita* are usually food limited. An example is found in the shallow cove of Kertinge Nor in the southern part of Kerteminde Fjord (Denmark). Here, the maximum diameter of the umbrella is usually only a few centimeters (compared to about 30 cm in most other waters) owing to an extremely high abundance of small jellyfish causing shortage of prey and thus restricting their own growth (Olesen et al. 1994; Olesen 1995; Riisgård et al. 1995; Frandsen and Riisgård 1997; Nielsen et al. 1997; Riisgård et al. 2008). Further, Nielsen et al. (1997) found that the local population of jellyfish in Kertinge Nor is highly influenced by the density-driven circulation created by frequent salinity changes in the adjacent Great Belt.

In 2006 the invasive ctenophore *Mnemiopsis leidyi* A. Agassiz was observed in coastal waters, both to the north and south of Denmark (Hansson 2006; Faasse and Bayha 2006; Boersma et al. 2007; Javidpour et al. 2006), and soon after Tendal et al. (2007) reported that it had spread into all Danish waters, and large concentrations were recorded in Limfjorden (Riisgård et al. 2007).

The *Mnemiopsis leidyi* ctenophores observed for the first time in Kerteminde Fjord in the early spring of 2007 came from the Great Belt. However, the concentration in the Great Belt remained very low, between 0.4 and 3.4 individuals per 100 m^3 in the period 18 April to 18 June 2007, although the mean body length increased from 1.1 ± 0.4 to 4.6 ± 1.3 cm (Tendal et al. 2007). Unfortunately, the abundance of the ctenophore was not systematically followed and quantified before the onset of the present study that addresses the relationships of the invader with native *Aurelia aurita*.

The main aim of the present investigation was to study if a suggested high predation impact exerted by a large number of small *Aurelia aurita* in Kertinge Nor would be able to exclude the new invasive ctenophore to establish in this shallow cove.

Materials and methods

Study site: Kerteminde Fjord/Kertinge Nor

The fjord-system consisting of Kerteminde Fjord and Kertinge Nor covers an area of 8.5 km^2 and has a mean water depth of approximately 2 m and a maximum depth of 8 m (Figure 1). The fjord has a sill at its mouth to the open sea (Great Belt). Discharge over the sill is forced by a diurnal tide with an average amplitude of approximately 20 cm. The catchment area to Kerteminde Fjord and Kertinge Nor is limited (36 km^2), and therefore the freshwater input is negligible with respect to the water exchange of the fjord system. Water exchange in the fjord system is governed by density-driven circulation. The salinity in the Great Belt outside the fjord varies as a result of changing flow situations (Jürgensen 1995; Møller 1996; Riisgård et al. 2008). Outflow of water from the Baltic Sea gives salinities down to less than 10 psu whereas inflow to the Baltic Sea from the North Sea gives salinities up to 27 psu in the upper layer of the Great Belt. Because saline water is denser than fresh water the salinity variations cause longitudinal density variations from the inner part of the fjord system to the mouth, and this creates density-driven circulation. When dense water is flushed over the sill by tidal forcing, it flows below the fjord water and gives rise to a circulation system within the entire fjord system. When, on the other hand, lighter water is forced into the fjord the circulation is in the opposite direction. On an annual time scale the two circulation directions have equal probability. Because of the dynamics of the exchange processes, the term ‘residence time’ is somewhat dubious in this fjord system. An approximate time-scale for residence time of water in the central areas of the system lies between 1 week and a few months, with an average of approximately 6 weeks. In Kertinge Nor which is characterized by low current velocities and moderate tides, the alternating tidal current does not give rise to a net transport of water whereas the density-driven circulation can potentially flush the entire water mass within 10 days (Jürgensen 1995).

Field investigations

From November 2008 to August 2009, 11 cruises were carried out to visit 6 fixed sampling stations in Kerteminde Fjord/Kertinge Nor, northern part of Fyn, Denmark (Figure 1). At each station, 20 l of water collected by means of a 'Limnos' water sampler throughout the water column was filtered (80 µm) to obtain a representative sample of the zooplankton-species composition and biomass. Samples were preserved in Lugol’s solution and transported to the laboratory where they were examined with a stereo microscope. In addition, jellyfish were regularly collected at St. 1 in Kertinge Nor from March to late August 2009 in order to follow the density and growth of ephyrae and medusae. *Aurelia aurita* and *Mnemiopsis leidyi* were collected by means of a squared net bag (0.5×0.5m cross section and 1 m deep; mesh size = 1.0 mm) mounted on a 2 m long rod. The volume of water passing through the net, which was advanced with 2 knots at a fixed depth of either 0.5 or 1.5 m water (depth = distance from surface to centre of net), was measured with a flow meter (Hydrobios Digital Flow Meter Model 438 110). The caught jellyfish were counted and the abundance (ind. m^{-3}) determined. Furthermore, the *A. aurita* umbrella diameter was measured in a number (usually >50) to calculate the mean diameter of the population; the ephyra umbrella inter-rhopalia diameter was measured to the nearest mm with a Vernier calipers. The mean size of *M. leidyi* was determined by measuring the distance between mouth and the opposite pole (oral-aboral length) to the nearest mm on 50 individuals with a Vernier calipers.

Jellyfish in Kertinge Nor in 1991-2009

Ending the sewage outfall to the Kertinge Nor/Kerteminde Fjord system by the end of 1989 meant that land-based nutrient loads fell markedly (Riisgård et al. 2008). Thus, annual land-based discharges of nitrogen (N) and phosphorus (P) were reduced by 43% and 92%, respectively, as compared to mean values for

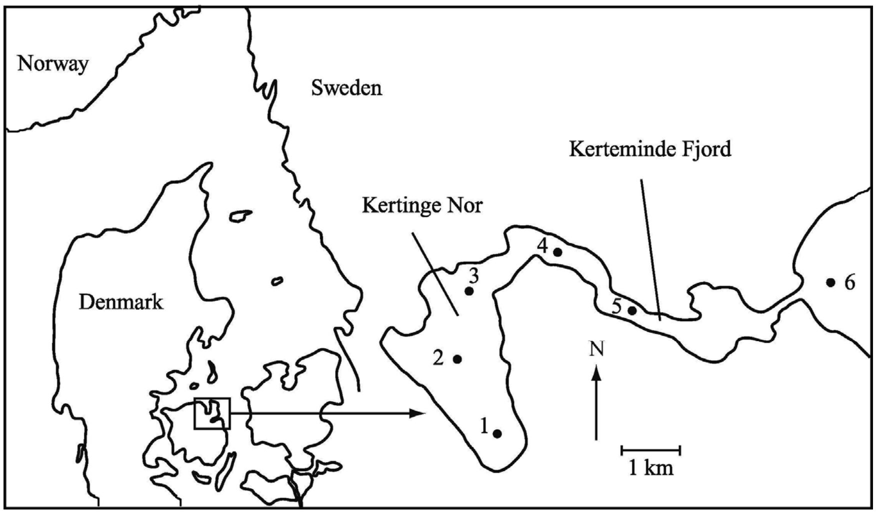

Figure 1. Map of the fjord system Kerteminde Fjord/Kertinge Nor, 6 locations studied are shown.

1976-1989. Since 1990, the nutrient loads have been due almost solely to diffuse sources, and the significant load reductions, down to 110 t N and 1.2 t P (mean 1990–2003), made the fjord system suitable for studying the effects of nutrient reduction on its recovery from eutrophication (Riisgård et al. 2008). In 1990 a large number of very small *Aurelia aurita* dominated the water column in Kertinge Nor, and therefore a study of the ecological importance of jellyfish became part of a 3-year environmental research project started in 1990 in order to follow the recovery of the ecosystem after the stoppage of sewage outfall. It was subsequently found that during the summers of 1991 and 1992, the water processing capacity of the many (up to 250-300 ind. m^{-3} in April to June) small 4 to 6 cm umbrella diameter *A. aurita* was very high. Thus, with a maximum rate attained in early September, the jellyfish population could daily process a water volume corresponding to approximately 10 to 15 times the whole water volume of Kertinge Nor (Olesen et al. 1994). No systematic monitoring of jellyfish in Kertinge Nor has been made in the intervening years. However, by means of data from a number of student field courses (run by HUR) over the years, and data from several master thesis studies (supervised by HUR), it has nevertheless been possible to obtain an overall picture of the jellyfish development in Kertinge Nor in an 18 years period, from 1991 to 2009. In all the studies, jellyfish were collected at St. 1 and St. 2, pooled, counted and measured by means of the same method used in the present work, and 50 individuals, out of at least 200 quantitatively collected jellyfish to assess the population density, were measured in order to estimate the mean umbrella diameter.

Clearance rates and half-life

Mnemiopsis leidyi. The following equation was used to estimate the individual clearance rate (Cl_{ind}, l d^{-1}) of ctenophores from the body volume (V, ml) (Riisgård et al. 2007, based on Decker et al. 2004):

$$Cl_{ind} = 2.64V \quad \text{Eq. (1).}$$

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

$$Cl_{ind} = 0.0073d^{2.1} \quad \text{Eq. (2).}$$

The volume-specific 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:

$$Cl_{pop} = Cl_{ind} \times D/1000 \quad \text{Eq. (3).}$$

The time it takes for a population of jellyfish to reduce the concentration of zooplankton (copepods) by 50 % (half-life; e.g. Riisgård et al. 1995, Hansson et al. 2005) was estimated as:

$$t_{1/2} = \ln 2/Cl_{pop} \quad \text{Eq. (4).}$$

For estimating the joint predation impact of the two jellyfish populations, with population clearance rates of Cl_{pop1} and Cl_{pop2}, respectively, the total half-life of zooplankton was estimated as:

$$tot\text{-}t_{1/2} = \ln 2/(Cl_{pop1} + Cl_{pop2}) \quad \text{Eq. (5).}$$

Biometric conversions

The inter-radial length or umbrella diameter (D, mm) of *Aurelia aurita* was converted to body dry weight (DW, mg) using the following equations (Møller and Riisgård 2007b):
A. aurita ephyrae:

$$DW = 1.9 \times 10^{-3} \times D^{2.998} \quad \text{Eq. (6)}$$

A. aurita medusae:

$$DW = 4 \times 10^{-3} \times D^{2.7} \quad \text{Eq. (7)}$$

Laboratory growth experiments

Growth experiments with *Aurelia aurita* ephyrae and medusae, and *Mnemiopsis leidyi* adults were conducted in 70 l tanks with filtered (80 µm) seawater, using 4-8 specimens of same size in each experiment. Ample amounts of freshly caught zooplankton were offered to *A. aurita* medusae and *M. leidyi* two times every day, whereas *A. aurita* ephyrae were offered a concentration of about 100 ind. l^{-1} of newly hatched *Artemia salina* fed with *Rhodomonas* sp. All jellyfish were every day measured to the nearest mm and put back in the experimental tank where they usually obtained normal swimming behaviour in less than 2 min.

Results

Jellyfish in the fjord system

The population densities of *Aurelia aurita* and *Mnemiopsis leidyi* in Kerteminde Fjord and Kertinge Nor are shown in Figure 2. It is seen that the density of *A. aurita* was always highest in Kertinge Nor while the density of *M. leidyi* was always highest in Kerteminde Fjord. During November 2008 the density of *M. leidyi* reached a maximum of about 590 ind. m^{-3} in Kerteminde Fjord. After this peak the density of *M. leidyi* declined, while the first ephyrae of *A. aurita* were observed. *M. leidyi* never established a demonstrable population in Kertinge Nor. The highest density (about 300 ind. m^{-3}) of *A. aurita* in Kertinge Nor was observed in June 2009, and after this peak, the density of *A. aurita* gradually decreased. The abundance of *A. aurita* in Kerteminde Fjord began to decline in late summer 2009 while the first individuals of *M. leidyi* were observed (Figure 2).

The estimated half-life of zooplankton organisms in Kerteminde Fjord was less than 7 days in late November 2008 due to very high densities (about 590 ctenophores m^{-3}) of small (3 to 5 mm) *M. leidyi* (Figure 2). The rest of the winter 2008 and spring 2009 the estimated half-life of zooplankton was high (i.e. negligible jellyfish predation impact) in both Kertinge Nor and Kerteminde Fjord due to very low concentrations or no *M. leidyi* in Kerteminde Fjord, and only few and small medusae and ephyrae with low clearance capacity in Kertinge Nor until March. But from April 2009 until the end of the field surveys in August 2009 the half-life of zooplankton in Kertinge Nor was high, between 0.7 and 5.4 days due to very high population densities of small (about 30 mm) *A. aurita* (Figure 2). But in August 2009 the half-life had increased to 5.4 days probably because the density of medusae had decreased in Kertinge Nor (Figures 2 and 3). Predation impact on the zooplankton in Kerteminde Fjord was until August 2009 solely exerted by *A. aurita*, but later on when the abundance of *M. leidyi* increased, the combined half-life subsequently decreased to only $tot\text{-}t_{1/2} = 0.9$ days (Figure 2).

Kerteminde Fjord is closely connected with the adjacent Great Belt and water is forced in and out by the diurnal tide. On the other hand, the alternating tidal current does not give rise to any direct transport of water in Kertinge Nor. Thus, density-driven water exchange, caused by changing salinities in the Great Belt, is the only mechanism for exchange of jellyfish between Kerteminde Fjord and the open sea with relatively low densities of *Aurelia aurita* and relatively high densities of *Mnemiopsis leidyi* in recent years. The interplay between incoming water with zooplankton from the Great Belt pumped into Kerteminde Fjord with the tide, and the subsequent density-driven water exchange between the outer Kerteminde Fjord and the inner Kertinge Nor is clearly reflected in the density and composition of zooplankton (Figure 2). Nevertheless, Kerteminde Fjord and Kertinge Nor may be considered as two rather separate systems. Thus in contrast to Kerteminde Fjord, no holoplanktonic calanoid copepods are found in Kertinge Nor. This is due to a large number of

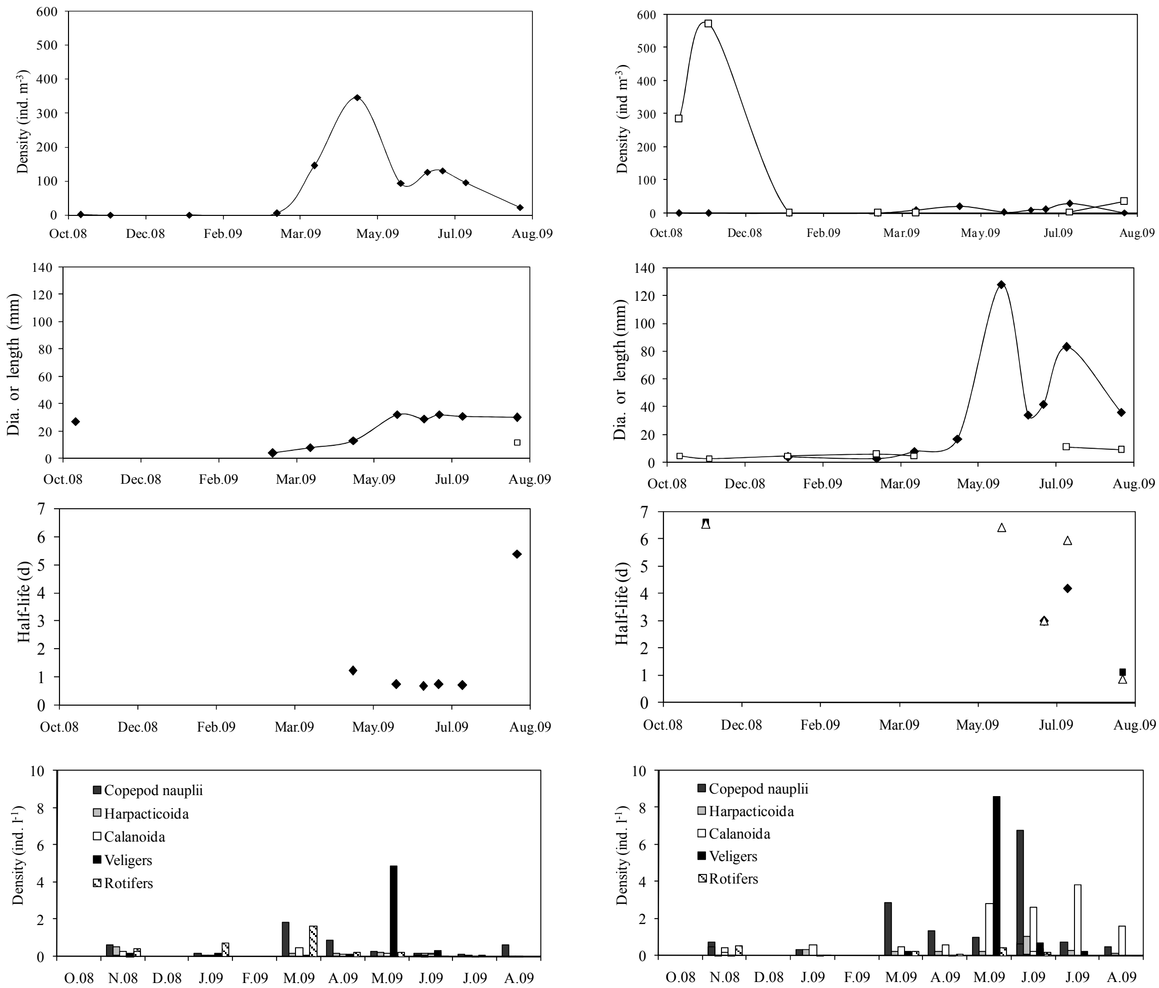

Figure 2. Kertinge Nor (left panel) and Kerteminde Fjord (right panel). Mean density and size of *Aurelia aurita* (♦) and *Mnemiopsis leidyi* (□) are shown along with the estimated half-life of zooplankton (copepods) and recorded densities of zooplankton. The presented results are based on data from 11 cruises, and 3 hauls with the jellyfish net at 2 depths on every location (Stations 1, 2, and 3 in Kertinge Nor; Sts. 4, 5, and 6 in Kerteminde Fjord, see Figure 1). In the case of Kerteminde Fjord, the combined half-life (*tot-*$t_{1/2}$) of the two species is indicated (Δ), because both *M. leidyi* and *A. aurita* in certain periods contributed a significant predation impact on the zooplankton.

small jellyfish exerting a high predation impact in Kertinge Nor. In addition locally produced meroplanktonic organisms only survive for a short period of time before they are removed by the jellies. On this background, the development, growth and population density of *A. aurita* in Kertinge Nor in 2009 has been more closely followed.

Case study (Kertinge Nor)

The development of *Aurelia aurita* ephyrae to medusae and change in density in Kertinge Nor, which was monitored at St. 1 from March to August 2009, is shown in Figure 4. It is seen that the first ephyrae appeared in March and disappeared again in May. Clearly, one well-defined year group of *A. aurita* was produced with a maximum of about 400 ind. m^{-3} in May 2009, followed by a general decrease in density during the period May-August, probably due to flush out of the cove by a water exchange caused by a decrease in salinity in the same period (Figure 3). Based on mean population density and umbrella diameter of *A. aurita*, the population volume-specific clearance rate (Cl_{pop}), and subsequently the half-life of the zooplankton ($t_{1/2}$) has been estimated and related to the concentration of zooplankton in Figure 6.

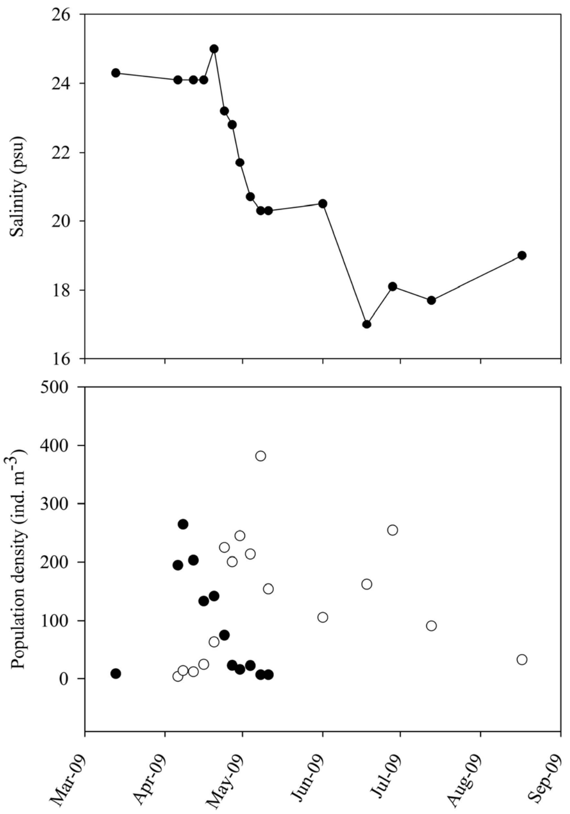

Figure 3. (Upper) Salinity measured at 0.5 m depth at Station 1 in Kertinge Nor (Figure 1) from March 2009 to September 2009. The general decrease in salinity indicates a steady exchange of water caused by density-driven circulation due to less saline water in the adjacent Great Belt. (Lower) Change in density of *Aurelia aurita* ephyrae (closed symbols) to medusae (open symbols) at St. 1 in Kertinge Nor (Figure 1) from March to August 2009.

Clearly, the predation impact was very high from early spring to late summer leading to a shortage of prey that was dominated by temporarily appearing meroplanktonic larvae of bivalves and polychaetes, and very few holoplanktonic copepods.

The mean diameter of *Aurelia aurita*, from the first appearance of ephyrae in March 2009 to September 2009, is shown in Figure 4B. The equation for an exponential regression line for the initial growth phase of small medusae in the period middle of April to beginning of May 2009, based on the data shown in Figure 5 is $DW = 0.009e^{0.126\times day}$ (r^2 = 0.842), which shows that the maximum initial weight specific growth rate was 12.6 % d^{-1}. Furthermore, from the feeding and growth experiments shown in Figure 6 it is seen that the maximum weight specific growth rate measured in the laboratory was 26.3 to 32.4% d^{-1} for *A. aurita* ephyrae, and 15.5 to 16.5% d^{-1} for the small (36 ± 1 mm) medusae. By comparing these rates with the somewhat lower actual specific growth rate of 12.6% d^{-1} in Kertinge Nor (Figure 5) it is apparent that *A. aurita* was able to partly exploit its growth potential in Kertinge Nor only for a short period of time. It may be concluded that the very high number of small *A. aurita* exerted such a high predation impact (half-life <1 d from May to September 2009) that the jellyfish population became food limited by the end of May (Figure 4). In comparison, the growth potential of *M. leidyi* was found to be somewhat lower, 22.8 and 12.5% d^{-1}, respecti-vely, in the two growth experiments performed in the laboratory (Figure 6E, F). This indicates that the ctenophore is neither a more effective filter-feeding predator nor more effective in utilizing the captured prey that the indigenous medusa.

Jellyfish in Kertinge Nor in 1991-2009

All available data on umbrella diameter and population densities of *Aurelia aurita* in the period 1991 to 2009 have been shown in Figures 7 and 8. The data show that despite the fact that the outlet of sewage to Kertinge Nor was stopped about 20 years ago this has so far neither influenced the unusually high population density nor the unusually small umbrella diameter of *A. aurita*. In accordance with this, the predation impact on the zooplankton has remained largely unchanged, and likewise the growth of the jellyfish is still strongly food limited.

Discussion

Earlier studies have shown that the maximum diameter of the umbrella of *Aurelia aurita* in Kertinge Nor is usually only a few centimeters and that high abundances of these small jellyfish (up to several hundred per cubic meter of water) control the zooplankton biomass (Olesen et al. 1994; Riisgård et al. 1995; Frandsen and Riisgård 1997; Nielsen et al. 1997). The present study indicates that neither the high number nor the small size of *A. aurita* may have changed during the last 15-20 years (Figure 2).

Nielsen et al. (1997) found that the local population of jellyfish is highly influenced when new water of either higher or lower salinity enters the fjord from the adjacent Great Belt. The time it takes for the jellyfish to enter a new water mass of higher or lower salinity was found to be

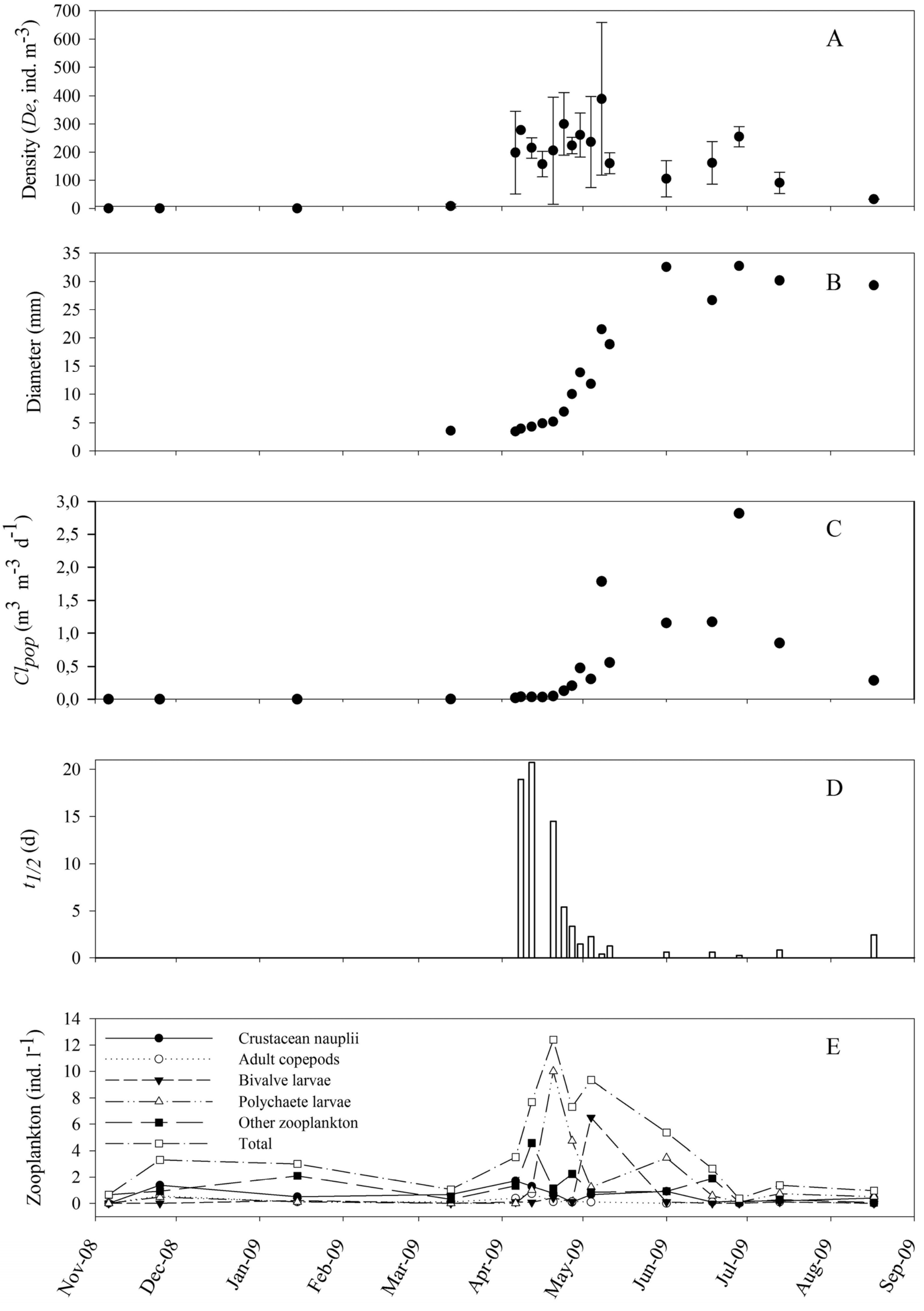

Figure 4. *Aurelia aurita* at St.1 in Kertinge Nor (Figure 1). (A) Mean (± SD; n = 3 hauls) population density in the period of November 2008 to August 2009. (B) Mean umbrella diameter. (C) Estimated population volume-specific clearance rate (Cl_{pop}). (D) Half-life of the zooplankton ($t_{1/2}$, ≤21 days). (E) Concentration of zooplankton.

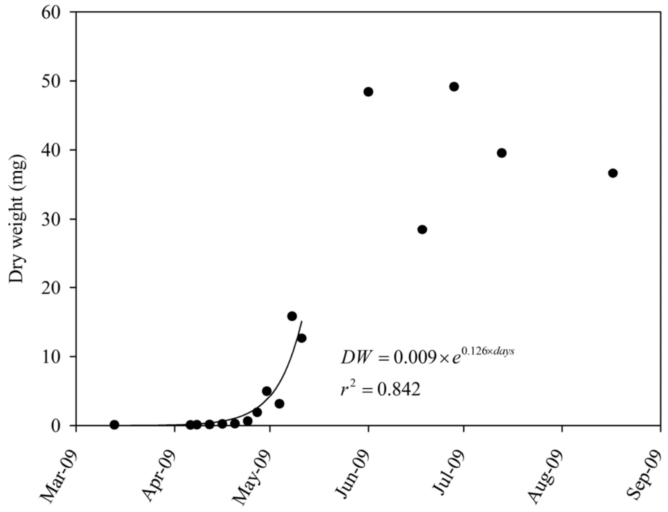

Figure 5. *Aurelia aurita* at St.1 in Kertinge Nor (Figure 1). Estimated dry weight of medusae, based on data from Figure 4B and Eq.(7). The exponential regression line and its equation for the initial population growth is shown. From the exponent it appears that the initial weight specific growth rate was $\mu = 12.6\%\ d^{-1}$.

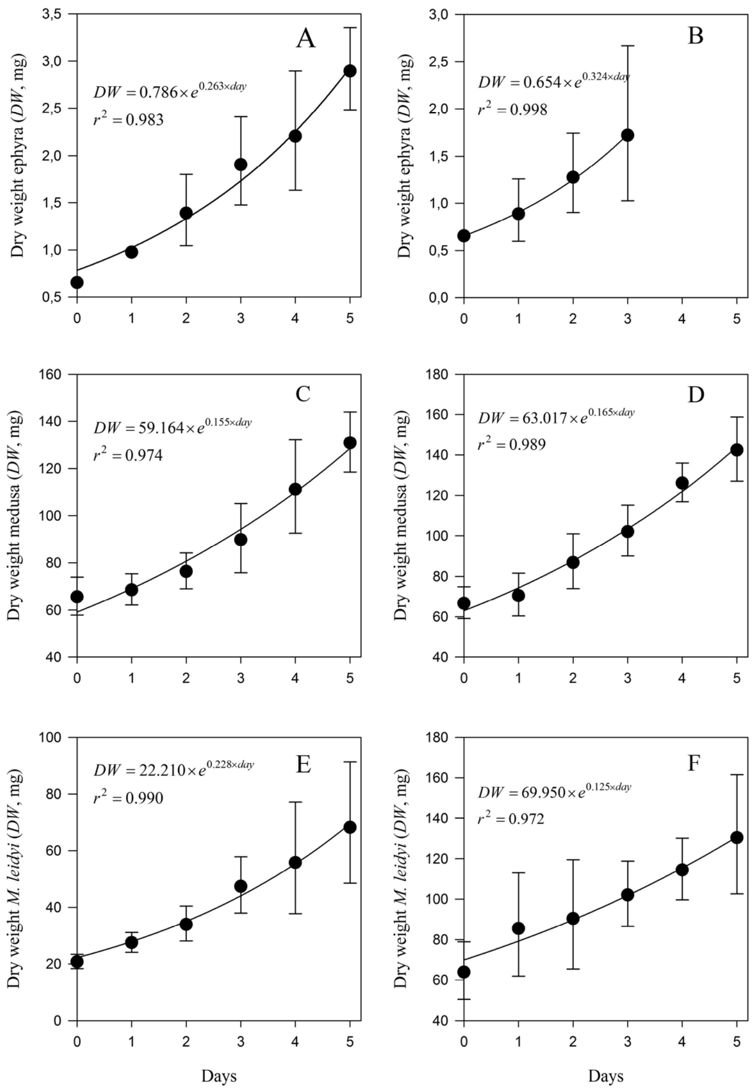

Figure 6. (A, B) Growth of *Aurelia aurita* ephyrae fed a high concentration of *Artemia salina*.
(C, D) *A. aurita* medusae (initial umbrella diameter = 36 ± 1 mm) fed on an excess amount of freshly caught natural zooplankton.
(E, F) Growth of *Mnemiopsis leidyi* adults offered an excess diet of natural zooplankton. The exponential regression lines and their equations are shown.

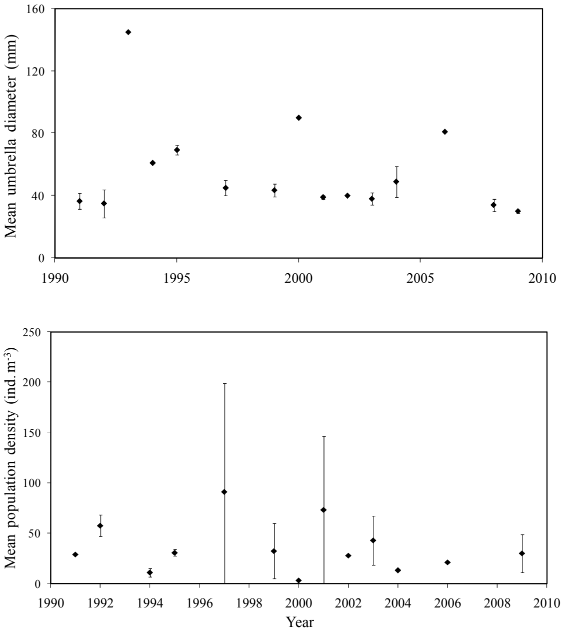

Figure 7. *Aurelia aurita*. (Upper) Mean (± S.D.) umbrella diameter of jellyfish in Kertinge Nor measured in August in the period 1991-2009. Overall mean umbrella diameter for the entire period 1991-2009 was found to be 56 ± 5 mm. (Lower) Mean (± S.D.) population density of jelly-fish in Kertinge Nor measured in August in the period 1991-2009. Overall mean population density in August for the entire period 1991-2009 was found to be 36 ± 34 ind. m^{-3}.

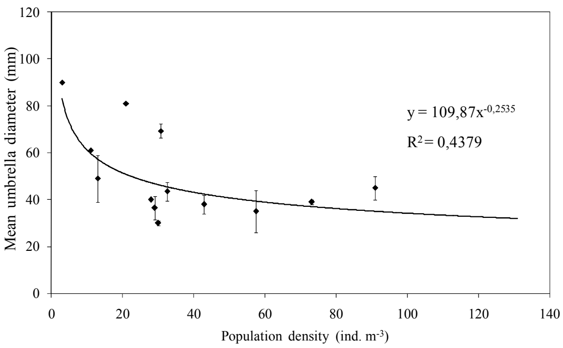

Figure 8. *Aurelia aurita*. Mean (± S.D.) umbrella diameter as a function of jellyfish population density in Kertinge Nor recorded in August in the period 1991-2009. The regression line for a power function is shown.

dependent on the degree of changes in salinity because the adaptation time for equilibrium buoyancy and normal swimming of the jellyfish is directly proportional to the salinity difference.

Further, Nielsen et al. (1997) found that the number and distribution of zooplankton was highly influenced by the presence of *A. aurita* in Kertinge Nor. The disappearance of incoming holoplanktonic copepods from the Great Belt occurred simultaneously with the conquest of the new water mass by the jellyfish. Thus, the occurrence of *A. aurita* in different hydrographical situations showed that the density of jellyfish was always highest in the "old" fjord water (Nielsen et al. 1997).

The present study shows that a high number of small *Aurelia aurita* in Kertinge Nor can exert such a high predation impact (half-life <1 d from May to September 2009) that it leads to shortage of prey, dominated by temporarily appearing meroplanktonic larvae of bivalves and polychaetes, and very few holoplanktonic copepods (from the Great Belt) (Figure 4). The high predation impact may also explain why the otherwise invasive *Mnemiopsis leidyi* so far has been unable to establish a conspicuous population in Kertinge Nor (Figure 2). It seems reasonable to conclude that the holopelagic *M. leidyi* cannot survive in the long term in the shallow Kertinge Nor where the polyp stage of *A. aurita* in the early spring produces a large number of ephyrae, and thus every year a large population of small medusae (Figure 3). Although density-driven water exchange may at times replace some of the 'old' water (with *A. aurita*) in Kertinge Nor with new water (with *M. leidyi*) from the outer part of Kerteminde Fjord and Great Belt, *M. leidyi* does not seem to be able to outcompete the local scyphomedusa and take over its dominating role as a pelagic filter-feeding key organism in Kertinge Nor.

Figure 8 shows that the umbrella diameter of *Aurelia aurita* apparently decreases with increasing population density. Therefore, it may be suggested that a certain reduction of the population density of jellyfish caused by the more or less pronounced density-driven water exchange and flush-out of jellyfish from the shallow cove, makes more food available to the remaining jellyfish. Subsequently the jellyfish therefore increase in size until the growth again becomes food limited. In this way, Kertinge Nor may act as a nursery for small *A. aurita* which are frequently flushed out into the Great Belt where they may grow big. On the other hand, larger jellyfish from the Great Belt may occasionally be transported into Kertinge Nor where they gradually obtain an intermediate size due to starvation and degrowth (personal observation).

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