IMPLICATIONS OF DENSITY DRIVEN CURRENTS FOR INTERACTION BETWEEN JELLYFISH (*AURELIA AURITA*) AND ZOOPLANKTON IN A DANISH FJORD

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SARSIA

The distribution of *Aurelia aurita* in a shallow fjord with a local population of numerous small jellyfish was influenced by density driven currents created by frequent salinity changes in the adjacent open sea. When new water of either higher or lower salinity entered the fjord this gave rise to changes in the jellyfish distribution. Likewise, the presence and distribution of zooplankton was influenced. Incoming copepods disappeared simultaneously with the invasion of the new water mass by the jellyfish. The time it took for *A. aurita* to enter a new water mass of higher or lower salinity was dependent on the salinity difference. Laboratory experiments indicated that the adaptation time for equilibrium buoyancy and normal swimming of the jellyfish was directly proportional to the salinity difference. Osmoconforming times of 2 to 4 h were found for salinity gradients of 2 to 4 psu typically found in the fjord. The population filtration impact exerted by *A. aurita* was usually able to keep the zooplankton biomass low (mean residence time of a zooplankton organism varied between 10 and 20 h). Similar dynamics governed by density driven currents may be expected in other shallow waters influenced by frequently changing salinities. Such knowledge about the dynamic interactions between hydrography and biology, explaining otherwise unaccountable large variations in phyto- and zooplankton biomasses may be of importance for a general basic understanding of the dynamics in coastal ecosystems.

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INTRODUCTION

In many coastal waters around the world scyphomedusan jellyfish, *Aurelia aurita*, can occasionally be rather abundant. *A. aurita* is a filter-feeder which mainly captures its prey on the tentacles lining the umbrella margin (COSTELLO & COLIN 1994). *A. aurita* may exert a considerable predatory impact on a broad spectrum of zooplankton species and fish larvae (LINDAHL & HERNROTH 1983; HERNROTH & GRÖNDAHL 1983 & 1985; GRÖNDAHL 1988; BÅMSTEDT 1990; SCHNEIDER & BEHRENDS 1994; BEHRENDS & SCHNEIDER 1995). The function of *A. aurita* as a local key organism may manifest itself causing great variations in the planktonic communities, both by reducing the impact of zooplankton grazing upon phytoplankton which may subsequently bloom, and by acting as a food competitor (e.g. fish larvae, MÖLLER 1980). The predatory impact exerted by jellyfish and its structuring effects on marine planktonic communities is uncertain. Although recently, a few attempts have been made to quantify these

effects (e.g. PAPATHANASSIOU & al. 1987; SCHNEIDER 1989; OLESEN & al. 1994; LUCAS & WILLIAMS 1994; RIISGÅRD & al. 1995).

Natural populations of *Aurelia aurita* are usually food limited (SCHNEIDER 1989; BÅMSTEDT 1990). In the shallow cove of Kertinge Nor, Denmark, the maximum diameter of the umbrella is usually only a few centimetres. High abundances of such small jellyfish (up to several hundred per m^3 of water) control the zooplankton biomass (OLESEN & al. 1994, RIISGÅRD & al. 1995). The energy required for respiration and growth of *A. aurita* has recently been studied by FRANDSEN & RIISGÅRD (1997) in order to evaluate its trophical role. An energy budget was calculated to identify both the lowest prey concentration resulting in maximum growth and the prey biomass necessary for maintaining the respiratory demand at zero growth. In the light of this, observed zooplankton biomasses may now be used to assess the energy balance of *A. aurita* in the field.
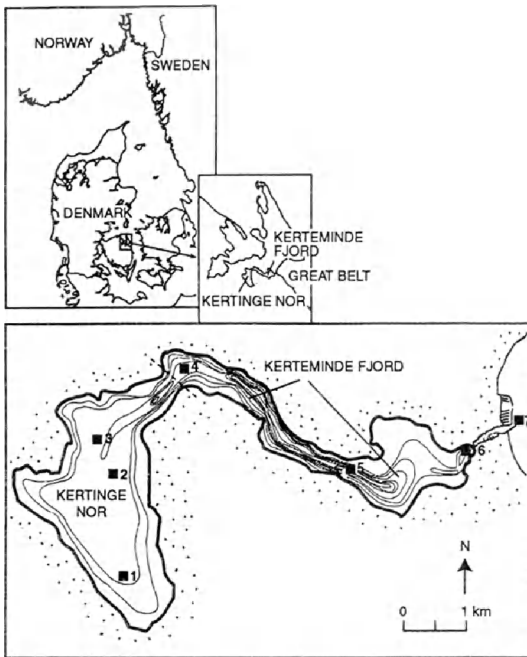
Fig. 1. Location of the 7 sampling stations in Kerteminde Fjord/Kertinge Nor on the island of Fyn, Denmark (55°26'N, 10°37'E). The fjord system consists of the two geomorphologically different subareas: the narrow and relatively deep (4-8 m) Kerteminde Fjord nearest to the Great Belt, and the innermost shallow cove known as Kertinge Nor with a mean depth of 2.5 m. Isobaths in m are also shown.

In the present work we deal with the interaction between jellyfish and zooplankton in Kertinge Nor and Kerteminde Fjord. In this fjord system, density driven currents caused by salinity variations in the outside open sea (JÜRGENSEN 1995; RIISGÅRD & al. 1996a, b) often create a dynamic situation with new incoming seawater of varying salinity to which the jellyfish must adapt before they subsequently filter the water for small zooplankton organisms. We attempt to describe the different hydrodynamic and biological parameters which may at times have extensive consequences for the distribution (vertical/horizontal) and growth of the population of jellyfish in Kertinge Nor.

MATERIAL AND METHODS

Investigation area and cruises

In the period March to October 1995, 53 cruises were carried out to visit 7 fixed sampling stations in the shallow fjord system Kerteminde Fjord/Kertinge Nor located in the northern part of Fyn, Denmark (Fig. 1).

At its entrance to the open sea (Great Belt) Kerteminde Fjord has a sill over which water exchange is governed by the diurnal tide of about ± 20 cm. The mechanism of density driven circulation in the fjord system has previously been described by RIISGÅRD & al. (1996a). It is caused by varying salinity in the Great Belt where outflow of water from the Baltic Sea gives salinities down to 10 psu whereas inflow of North Sea water to the Baltic Sea gives salinities up to 27 psu. When light (low salinity) water is forced into the fjord propagating as a surface layer a counter-clockwise circulation is created (see sketch A supporting Table 1). On the other hand, when dense (high salinity) water is flushed over the sill by tidal forcing it flows down below the fjord water (see sketch B, Table 1) and gives rise to a clockwise density driven circulation. In periods of stable salinity the fjord system may be stratified in calm periods or well mixed in windy periods (see sketch C and D, Table 1). In the present work all hydrographical situations have been referred to as either A, B, C, or D. At the end of each cruise the hydrographical situation was laid down by making an isopleth diagram using the recently obtained salinity data. This procedure allowed a decision to be taken about a possible cruise the following day.

Every fourteenth day a 'standard cruise' was completed. At each station salinity was measured, and water samples for chlorophyll measurement were taken. Wind speed and direction were measured at St. 3. In addition, zooplankton and jellyfish were regularly collected in connection with the 'standard cruises'. If the hydrographic situation was found to be particularly interesting the frequency of such intensified 'extended cruises' involving hydrography, jellyfish, zooplankton and chlorophyll *a* was increased, in certain periods up to one cruise per day.

Chlorophyll a *and salinity*

At each station (except St. 6) surface and near-bottom water samples (5 l) were taken by means of a 'Limnos' water sampler for measurement of chlorophyll *a*. Further, salinity was measured at 0.5 m depth intervals by means of either a hand instrument (WTW Microprocessor Conductivity Meter LF 196) or, less frequently, with a CTD-probe (Aquamatic). Due to the strong current and vertical mixing at St. 6 salinity was only measured in a single water sample taken from the boat. The water samples for the chlorophyll *a* measurement were filtered (Whatman GF/C, 0.3 bar) and chlorophyll was extracted in 10 ml 96 % ethanol and placed in the dark for 24 h. The chlorophyll *a* (chl *a*) content was then measured according to ARVOLA (1981): i.e. measuring the absorption (Abs) at 750 and 665 nm on a Perkin-Elmer 554 spectrophotometer and subsequently using the formula: chl *a* (μl l^{-1}) = 10^3(Abs665 – Abs750)v/(83V) where v = millilitres of ethanol and V = litres of filtered seawater.

The mean salinity in the fjord system was estimated after each cruise. This was done by splitting up the area of the fjord system (5.48 km^2) into 36 subunits. The amount of salt (kg) contained in each subunit was estimated as the sum of water volume for each 0.5 m (i.e. cross sectional area × 0.5 m^3) times the measured salinity (kg m^{-3}). The mean salinity (kg m^{-3}) in the whole fjord system was then estimated as the sum of kilogram salt in all subunits divided by the total water volume of the fjord system (16 × 10^6 m^3).

Aurelia aurita

Jellyfish, *Aurelia aurita*, were collected by means of a squared netbag (0.5×0.5 m 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 at a speed of 2 knots at a fixed depth of either 0.55 or 1.55 m water (depth = distance from surface to centre of net), was measured with a 'Hydrobios' flowmeter. The collected jellyfish were counted and the abundance (T_D, ind. m^{-3}) determined. Further, the umbrella diameter was measured in a number of jellyfish (usually >100) to calculate the mean diameter for the population. The umbrella inter-rhopalia diameter was measured to the nearest mm by placing the jellyfish with the dorsal site down over a mm-scale. The umbrella diameter (D, mm) was converted to body dry weight (W, mg) using the equation: $W = 0.00173D^{2.82}$ (OLSEN & al. 1994). The biomass (B, mg C l^{-1}) of *A. aurita* was estimated according to: $B = W \times T_D \times k$, where $k = 0.070$ mg C (mg W)$^{-1}$ for D < 20 mm, and $k = 0.051$ mg C (mg W)$^{-1}$ for $20 < D < 50$ mm (SCHNEIDER 1988).

Zooplankton

During 23 of the 53 cruises carried out from March to October 1995 zooplankton samples from each station (except St. 6) were taken by means of a 'Limnos' water sampler. Ten litres of water from the surface and bottom, respectively, were filtered (20 μm mesh) and the restrained organisms fixed in a Lugol solution for subsequent analysis. The biovolume (wet weight) of the different groups of zooplankton species were estimated, either from measured dimensions using simple geometrical shapes or by means of allometric formula. The biomass (B, μg C) was estimated from the wet weight (Wet wt): Dry wt = Wet wt $\times$ 0.13 and B = Dry wt $\times$ 0.37 (McCAULEY 1984;

Table 1. *Aurelia aurita*. Mean abundance (± SD) of jellyfish in 'old' and 'new' water in Kerteminde Fjord and Kertinge Nor split up into four different hydrographical situations: A, B, C, & D. Number of measurements indicated in brackets.
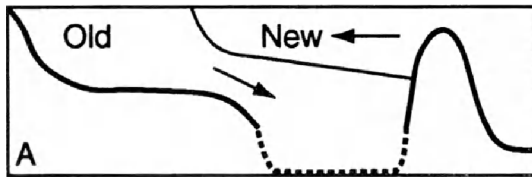
Date 1995	Old water ind. m^{-3}	New water ind. m^{-3}	Old/New
26 April	12.5 ± 11.4 (5)	6.9 ± 6.5 (2)	1.8
6 June	19.9 ± 6.7 (4)	13.9 ± 0.0 (1)	1.4
14 June	18.5 ± 11.9 (7)	9.5 ± 9.4 (2)	1.9
18 June	25.1 ± 18.9 (5)	9.3 ± 5.5 (2)	2.7
22 September	9.7 ± 5.8 (6)	2.3 ± 2.0 (2)	4.2
Average			2.4 ± 1.1
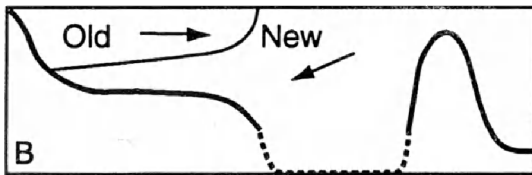
Date 1995	Old water ind. m^{-3}	New water ind. m^{-3}	Old/New
30 September	0.8 ± 0.3 (5)	0.2 ± 0.3 (4)	
1 October	1.9 ± 1.6 (8)	$\simeq$ (1)	
26 October	1.5 ± 2.1 (7)	$\simeq$ (1)	
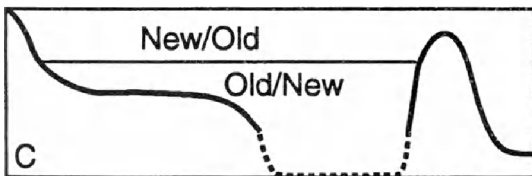
Date 1995	Old water ind. m^{-3}	New water ind. m^{-3}	Old/New
4 May (low salinity in)	98.5 ± 78.6 (3)	26.9 ± 36.4 (3)	3.7
3 October (high salinity in)	23.0 ± 45.6 (5)	7.5 ± 10.0 (3)	3.0
12 October (high salinity in)	16.1 ± 20.2 (7)	0.6 ± 0.6 (2)	27.3
Average (high salinity in)			15.2 ± 17.2

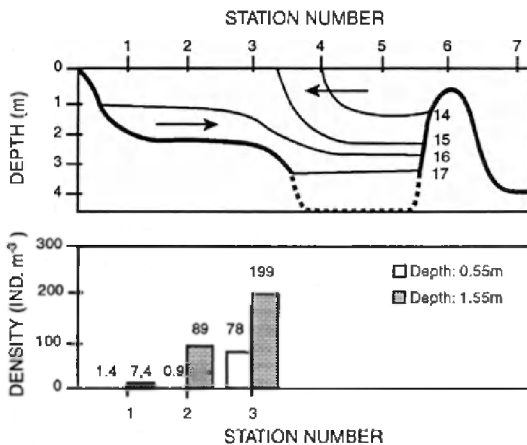| Date 1995	Old water ind. m^{-3}	New water ind. m^{-3}	Old/New
22 August	74.3 ± 30.5 (2)	17.0 ± 13.6 (6)	4.4
29 August	13.7 ± 15.8 (4)	10.1 ± 2.1 (3)	1.4
Average			2.9 ± 2.1

Fig. 2. An example of the 'hydrographical situation A' (cf. sketch supporting Table 1) and its consequence for the distribution of *Aurelia aurita* at Stns 1, 2 & 3 in Kertinge Nor. The upper figure shows a sketch with isohalines (wind 2-4 m s^{-1} from northwest) which outlines the hydrographical situation in the fjord system on 4 May 1995: less saline (i.e. lower density) water is forced into the fjord as a surface layer creating a counter-clockwise density driven circulation. On the lower figure the abundance of *A. aurita* in two water depths (0.55 and 1.55 m) is illustrated by means of columns supplied with the exact abundance (ind. m^{-3}) for Stns 1, 2 & 3.

COHEN & LOUGH 1981; JESPERSEN & OLSEN 1982). However, for rotifers we applied: Dry wt = Wet wt × 0.1 and B = Dry wt × 0.45 (HANSEN & al. 1992).

Filtration rate of jellyfish

The filtration rate of *Aurelia aurita* was measured as the volume of water cleared of brine shrimp nauplii, *Artemia* sp., per unit time. Prey organisms were added (100 individuals) to 5 aquaria with a known volume (V = 10 l) of filtered (0.7 μm) seawater containing one jellyfish. The reduction in the number of prey organisms as a function of time was followed by removing a jellyfish at 30, 60, 90 and 120 min and subsequently filtering (100 μm) the water so that the restrained prey organisms could be counted under a stereo-microscope. The filtration rate (F) was determined from the exponential reduction in prey organism concentration using the formula: F = (V/t)ln(C$_0$/C$_t$), where C$_0$ and C$_t$ are the prey concentrations at time 0 and time t, respectively. The filtration rate was measured in two size groups of jellyfish with umbrella diameters of 68 ± 2 and 74 ± 2 mm, respectively. The experiments were performed at 15 °C with seawater collected in Kertinge Nor at the time of collection of experimental jellyfish. The measured filtration rates were used to supplement (with larger jellyfish) and recalculate the data of OLESEN (1995) so that the filtration rate as a function of both umbrella diameter (D) and of body dry weight (W) could be expressed according to F = aD^2 and F = aW^b. The theoretical mean residence time (before being captured by *A. aurita*) of
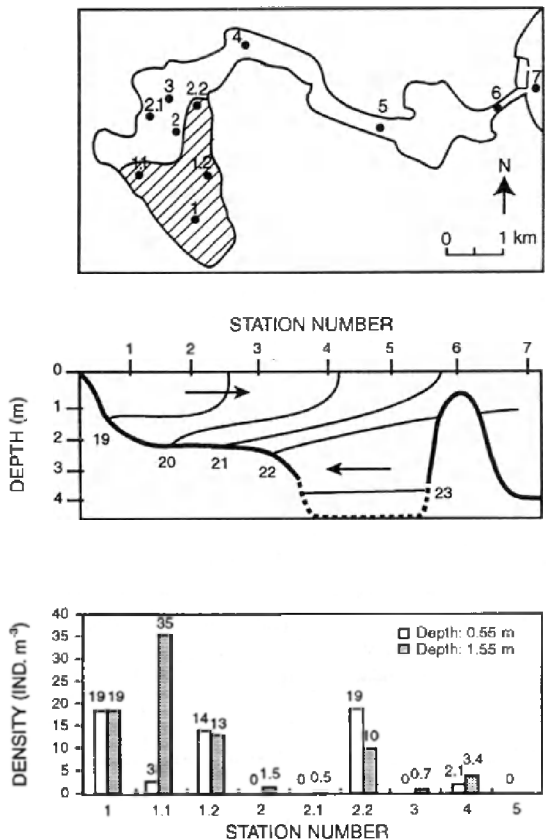

Fig. 3. An example of the 'hydrographical situation B' (cf. sketch supporting Table 1) and its consequence for the distribution of *Aurelia aurita* in the fjord system. The upper figure shows the investigation area with an expanded number of stations, and the hatched area represents the presence of *A. aurita* in Kertinge Nor. The middle figure shows a sketch with isohalines (wind 18 m s^{-1} from southwest) which outlines the hydrographical situation on 8 October 1995: more saline (i.e. denser) water is forced into the fjord at the bottom creating a clockwise density driven circulation. The lower figure shows the distribution of the *A. aurita* in the fjord system. The abundance of jellyfish in two water depths (0.55 and 1.55 m) is shown as columns provided with numbers for the exact population abundance (ind. m^{-3}) at each station.

a small zooplankton organism in a given volume of water in the fjord system was calculated as: t$_{1/2}$ = (1/F$_{pop}$)ln2, where F$_{pop}$ = F × T$_D$ = total filtration rate of jellyfish population in one m^3 of water.

Adaptation of jellyfish to various salinities

Within 3 to 20 h of collection in Kertinge Nor the medusae of *Aurelia aurita* were transferred to aquaria with seawater (10 l, 15 °C) of various higher or lower salini-

ties. The introduced salinity difference (ΔS) relative to the salinity to which the medusae were adapted ranged from 0 to 10 psu. The various salinities were obtained by adding fresh tap water or sea salt to laboratory system seawater. Salinities were measured with a salinometer (WTW Microprocessor Conductivity Meter LF 196). The behaviour of the jellyfish was observed and the position and stroke frequency of the umbrella was recorded. This information was used to determine the adaptation time (A, h), i.e. the time elapsed from transfer of the jellyfish to a new salinity until their buoyancy and activities returned to normal.

RESULTS

Examples of hydrographical situations A and B (cf. sketches supporting Table 1), and the simultaneous occurrence of *Aurelia aurita* are given in Figs 2 and 3, respectively. In the first case (Fig. 2) it is apparent that the highest density of jellyfish was found in the near-bottom 'old' high salinity water at St. 3. In the second case (Fig. 3) the jellyfish were found at highest densities in the 'old' water in the southern and easterly part of Kertinge Nor.

The distribution of *Aurelia aurita* (given as an average density ratio = 'density of jellyfish in old original fjord system water/density of jellyfish in new water') for the whole investigation period, and for the 4 'standard' hydrographical situations A, B, C and D, are presented in Table 1. It appears that the density of jellyfish was always highest in the 'old' fjord water.

The relationship between jellyfish filtration rate (F, ml h^{-1} ind.$^{-1}$) and the square of the umbrella diameter (D, mm) was found to be: $F = 0.75D^2$ ($r^2 = 0.91$; n = 12; umbrella diameters from 3 to 74 mm), whereas filtration rate as a function of weight (W, mg body dry wt) was be to be: $F = 16.07W^{1.01}$ ($r^2 = 0.91$). Combining the individual filtration rate with jellyfish size distribution and density allows an estimate of the population filtration rate (F_{pop}) per m^3 water which may be used to calculate the mean residence time ($t_{1/2}$) for zooplankton in Kertinge Nor. Thus, in the period June to November 1995 it was found that $t_{1/2}$ varied between 10 and 20 h.

The mean zooplankton biomasses (μg C l^{-1}) in Kertinge Nor and Kerteminde Fjord in 1995 are shown in Table 2. The zooplankton biomass in Kertinge Nor was about 2.5 times as high as than the zooplankton biomass in Kerteminde Fjord. This was almost exclusively due to a higher concentration of rotifers in Kertinge Nor. Apparently, a short generation time of rotifers allows this group to survive in Kertinge Nor in spite of the considerable predation pressure exerted by *Aurelia aurita*.

The adaptation time of *Aurelia aurita* to a new salinity (i.e. adaptation to neutral buoyancy and normal swimming behaviour) is shown in Fig. 4. A doubling of
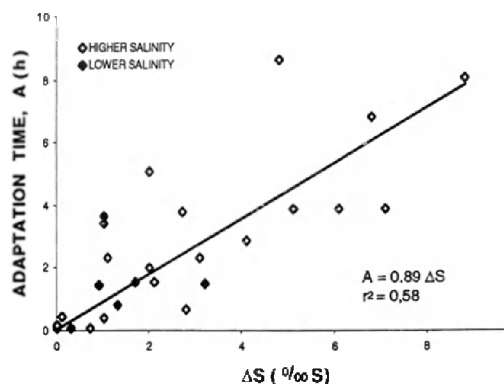

Fig. 4. *Aurelia aurita*. Adaptation time (A, h) of jellyfish (umbrella diameter = 40 ± 18 mm) transferred to seawater with altered salinity. ΔS indicates the difference between the salinity (psu) at the collection site and the salinity of the water in the experimental aquarium. Open symbols indicate a change in salinity to higher, and the closed symbols a change to lower salinity. The shown regression line is given by: A(h) = $0.89 \Delta S$(psu); $r^2 = 0.58$

salinity difference results in almost a doubling of the adaptation time.

Fig. 5 shows an example of a clockwise density driven circulation and demonstrates the dynamics in Kertinge Nor and Kerteminde Fjord. Prior to the 4 day period, the salinity in the Great Belt was about 25 psu due to a strong westerly wind, and high salinity water flowed into the fjord system causing stratification. On 29 and 30 September a density driven circulation was obvious, although a strong wind caused a vertical mixing of the

Table 2. Mean zooplankton biomasses (μg C l^{-1}) in Kertinge Nor and Kerteminde Fjord in the period March through October 1995. The mean biomasses are based on 23 samplings during the period, either with 3 top and 3 bottom samples (Kertinge Nor) or 2 top and 2 bottom samples (Kerteminde Fjord) collected at each station.

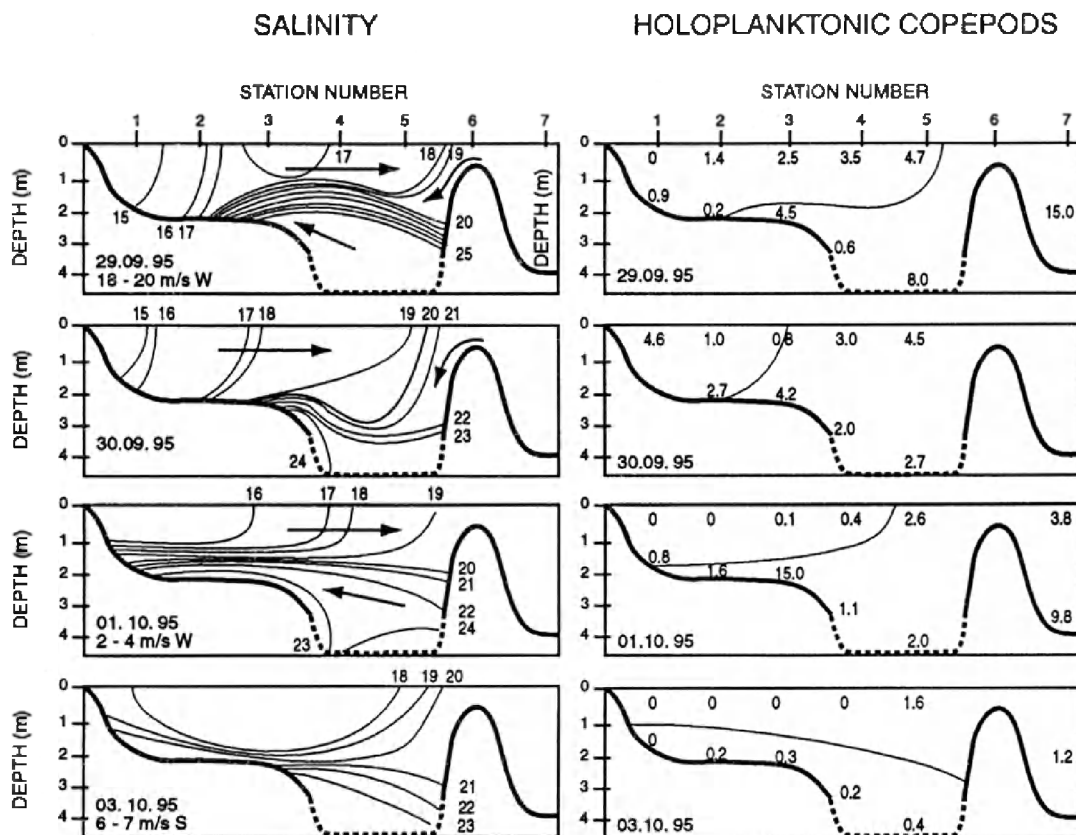|	Kertinge Nor	Kerteminde Fjord
Ciliates (> 20μm)	0.9	0.1
Harpacticoids	0.2	0.1
Holoplanktonic copepods	1.0	1.5
Nauplius larvae	2.0	2.6
Cladocerans	0.2	0.6
Rotifers	10.9	0.9
Polychaete larvae	0.6	0.5
Bivalve veligers	0	< 0.1
Gastropod veligers	0	< 0.1
Planula larvae	< 0.1	< 0.1
Others	0.1	0.2
Total	15.9	6.5

Fig. 5. Hydrographical situations (sketches on left side) and the biomasses (µg C l⁻¹) of holoplanktonic copepods (right side) on 4 days from 29 September to 3 October 1995. Wind speed and direction is indicated, and arrows show the direction of density driven water circulation in the fjord system.

water masses in the inner part of the fjord system. On the following days, the density driven circulation continued, and the system became more and more saline. On the last day in the period (3 October), the fjord system was stratified without strong circulation. The concentrations of holoplanktonic copepods at the various sampling stations during the 4 day period varied accordingly with variations in salinity and water circulation. On 29 September, the concentration of copepods was high (15 µg C l⁻¹) in the Great Belt, and decreased towards Kertinge Nor, indicating that the copepods in the fjord system were brought in by the incoming high salinity water. On the following days, the concentrations of copepods were generally higher in the 'new' water masses from the Great Belt than in the 'old' fjord water. On 3 October, when the fjord system was stratified and the water masses stagnant, the concentration of copepods in Kertinge Nor was nearly zero as a result of predation by *Aurelia aurita*.

Fig. 6 shows various data for Kertinge Nor in 1995: chlorophyll *a*, biomass of zooplankton, and population abundance, umbrella diameter and biomass of *Aurelia aurita*. The average abundance of jellyfish (April to November) was 16.6 ind. m⁻³, and the maximum umbrella diameter of 73 ± 13 mm was attained in July.

The mean salinity in the fjord system during March to October 1995 is shown on Fig. 7. It is seen that the salinity varied from 13.6 (Day 143; 23 May 1995) to 22.2 (Day 299; 26 October 1995). In the spring and autumn the salinity suddenly changed, indicating fast inflow of water from the Great Belt. The decrease in salinity in spring indicates inflow of low salinity water from the Great Belt which created an anti-clockwise density driven circulation in the fjord system (see sketch A supporting Table 1). In late September and October there was an inflow of high salinity water creating a clockwise circulation (see Fig. 5 and sketch B supporting Table 1). The relatively constant salinity during the
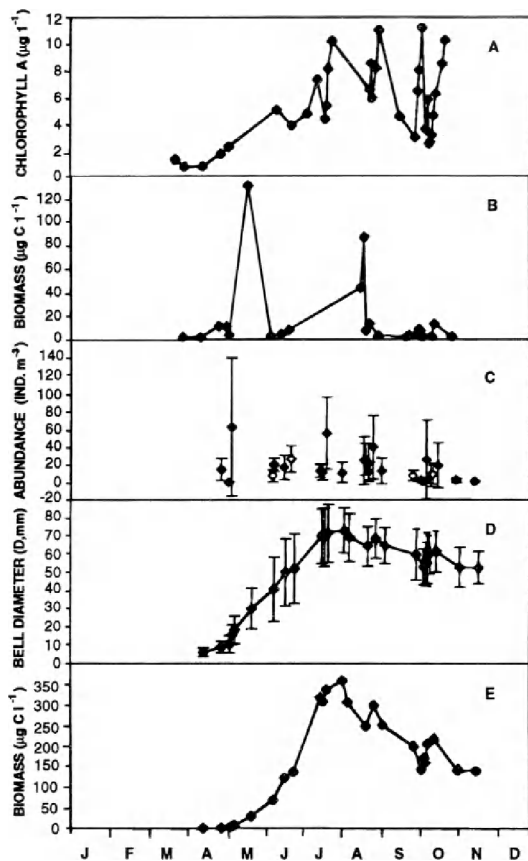
Fig. 6. Data for Kertinge Nor in 1995. (A) Chlorophyll *a*. (B) Biomass of zooplankton. (C) Mean population abundance (± SD) of *Aurelia aurita*; closed symbols indicate densities based on data from Stns 1, 2 & 3 and two depths (0.55 and 1.55 m); open symbols indicate abundances calculated from a population investigation with more stations. (D) Mean (± SD) umbrella diameter of *A. aurita*; the first 3 sets of data represent ephyra. (E) Biomass of *A. aurita*.
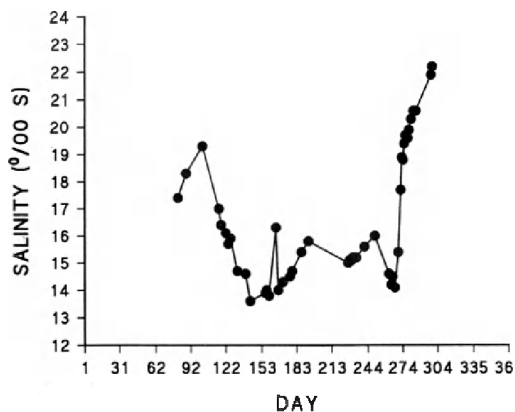

Fig. 7. Mean salinity in Kerteminde Fjord and Kertinge Nor from March to October 1995.

DISCUSSION

This study demonstrates that the distribution of *Aurelia aurita* in a shallow fjord-system, with a local self-maintained population of jellyfish in the innermost part (Kertinge Nor), is influenced by density driven currents created by frequent salinity changes in the adjacent open sea (Great Belt). When new water of either higher or lower salinity enters the fjord this may cause changes in the jellyfish distribution (Figs 2 & 3). Likewise, the presence and distribution of zooplankton in the fjord system is influenced by the density driven currents. Thus, incoming holoplanktonic copepods, characteristic of Great Belt water, disappear simultaneously with the jellyfish's conquering the new water mass (Fig. 5). The actual advection of *A. aurita* into and out of the system is unknown, but Fig. 6C shows that the abundance did not fall markedly during the summer of 1995.

The time it takes for *Aurelia aurita* to enter a new water mass of higher or lower salinity is dependent on the salinity difference. The ability of a halocline (or a thermocline, cf. HAMMER & al. 1994) to act as a density barrier which the jellyfish have difficulties crossing before they can start osmoconforming (MILLS & VOGT 1984; MILLS 1984) must be taken into consideration. In this study the adaptation time for equilibrium buoyancy and normal swimming of the jellyfish was found to be directly proportional to the salinity difference (Fig. 4). The laboratory experiments indicate osmoconforming times of 2 to 4 h for typical salinity gradients of 2 to 4 psu, but the time-lag before a new water mass was actually occupied by the jellyfish is presumably longer.

The filtration impact exerted on the zooplankton by the numerous *Aurelia aurita* in Kertinge Nor was usually able to keep the zooplankton biomass low (Table

summer months indicates that the water exchange was modest (i.e. no wash-out of jellyfish from the fjord system). Although the exact water exchange was not quantified in the present study the salinity curve depicted in Fig. 7 reasonably well describes the relative water exchange and thus the frequency and strength of density driven currents in the fjord system during 1995. Referring to Table 1 the incidence of the different hydrographic situations observed during the 53 cruises were: A = 20 %, B = 13 %, C = 18 %, and D = 49 %. In 1995 situation A and B with density driven water exchange mainly took place during spring and autumn, respectively.

2). A mean zooplankton biomass of 15.9 µg C l^{-1} (Table 2) could only support modest growth of the jellyfish. The mean umbrella diameter increased almost rectilinear in the period from 5 May to 17 July (Fig. 6D). From this relationship the increase in biomass and thus the specific growth rate could be estimated. It was found that the maximum specific growth rate of 12 % d^{-1} in early May decreased to 3 % d^{-1} in mid-July.

FRANDSEN & RIISGÅRD (1997) found that the zooplankton biomass required to maintain the respiratory demand of a 10 mm *Aurita aurita* is 13 µg C l^{-1}. This may be compared to 68 µg C l^{-1} for the maximum possible specific growth rate of 24 % d^{-1} (i.e. the growth capacity). Utilizing the growth equation and conversion factors used by FRANDSEN & RIISGÅRD (1997) it can be calculated that for the mean zooplankton biomass of 15.9 µg C l^{-1} found in Kertinge Nor the specific growth rate of a 10 and 70 mm jellyfish is 1 and 7 % d^{-1}, respectively. These theoretically estimated figures do not compare very well with the actual specific growth rates of 12 and 3 % d^{-1}, respectively; but nevertheless the different figures indicate that shortage of food can explain why the maximum umbrella size was only 73 ± 13 mm in late July 1995 (Fig. 6D), like preceding years (OLESEN & al. 1994; RIISGÅRD & al. 1995). The above anomalies may be due to the difference in b-exponents for the size dependent filtration and respiration equations as discussed by FRANDSEN & RIISGÅRD (1997). Also, the fact that the mean zooplankton biomass may not be exact makes further energetic considerations unprofitable.

The variations in chlorophyll *a* and zooplankton biomasses in Kertinge Nor (Fig. 6A & B) can not be explained simply. Frequent occurrences of density driven currents and intrusion of new water create a dynamic pelagic interaction between jellyfish, zooplankton and phytoplankton. On calm days incoming water may give rise to a stratification which considerably influences the benthic grazing impact exerted by a dense population of filter-feeding ascidians (*Ciona intestinalis*) which become dependent on near-bottom horizontal water currents. Such a situation with decoupling of the benthic grazing organisms may go on until the water column perhaps is mixed by strong wind action (RIISGÅRD & al. 1996a). This causality, partly determined by the meteorology, makes it impossible to interpret the actual variations in the phytoplankton biomass unless the major influential hydrographical and biological parameters are closely monitored during the preceding days/hours. See also RIISGÅRD & al. (1996b) for a discussion of plankton dynamics and biological structure in Kertinge Nor.

The present study has pointed out some of the most important parameters for understanding the dynamics in the biological structure of the pelagic in Kertinge Nor. However, a higher time-resolution for the different parameters may be necessary to give a true description of actual cases of e.g. short-time rotifer and phytoplankton variation, like those observed in 1995 (Fig. 6A & B) and 1994 (RIISGÅRD & al. 1996a: fig. 4). Similar dynamics governed by density driven currents may be expected in other shallow waters influenced by frequently changing salinities, such as the inner Danish waters. The significance of density driven currents awaits closer inspection, however it is clear that such knowledge may be of importance for marine monitoring programmes using phyto- and zooplankton biomasses as parameters for assessing the environmental condition. Unaccountable large variations in these parameters may possibly be explained by similar dynamic interactions between hydrography and biology as demonstrated in this study.

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