

Population dynamics, growth and predation impact of the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa*, and *Aequorea vitrina* in Limfjorden (Denmark)

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ABSTRACT: The population dynamics, growth and predation impact of the common jellyfish *Aurelia aurita* and 2 hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina*, were studied in Limfjorden (Denmark), with the main focus on an inner branch of the fjord (Skive Fjord) from 2003 through 2005. We evaluated the degree to which the jellyfish realise their growth potential in Skive Fjord, and 2 other sites in Limfjorden (Nissum Bredning and Løgstør Bredning). We also evaluated whether the jellyfish were controlling the zooplankton, or if the biomass of zooplankton was controlling the growth of the jellyfish, by comparing prey concentrations in the sea with laboratory estimations of the minimum concentrations of prey needed for sustaining maximum growth of the jellyfish. In all 3 yr, *A. aurita* ephyrae and hydromedusae were present during spring, and in 2003 *A. aurita* was present through the entire study period (February to August). In April 2004, all jellyfish disappeared, but in August 2004 *A. vitrina* became abundant. In both 2004 and 2005, disappearance and reappearance of jellyfish coincided with sudden changes in the salinity caused by incoming water from the North Sea. By applying energy budgets from laboratory experiments, we calculated that the jellyfish realised their growth potential until August in 2003, after which negative growth was observed. In 2003, *A. aurita* in Skive Fjord had the potential to control the zooplankton from mid-May to August (half-life times between 0.8 and 6.2 d). In this period, almost no zooplankton or fish larvae were present. Release of phytoplankton from zooplankton grazing-control due to the predation pressure (on zooplankton) from *A. aurelia* resulted in a pronounced phytoplankton bloom (with up to $60 \mu\text{g l}^{-1}$ chl *a* in 2003) triggered by the release of nutrients from the sediment during a period of oxygen depletion in the near-bottom water. *A. vitrina* had no effect on the zooplankton population, but probably preyed on ctenophores. We conclude that in some years *A. aurita* may be very abundant in Limfjorden and might exert a considerable predatory impact on zooplankton and fish larvae during the summer. The abundance, species composition and population dynamics of jellyfish in Limfjorden may, at irregular time intervals, be strongly influenced by dramatic, but apparently rather unusual hydrographic events, and hydraulic processes may explain otherwise unaccountably large variations in the plankton (including jellyfish).

KEY WORDS: Predation impact · Control of growth · Plankton dynamics · *Aurelia aurita* · *Sarsia tubulosa* · *Aequorea vitrina*

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INTRODUCTION

Over the last 2 decades, the role of gelatinous predators in marine food-web and population dynamics has attracted growing scientific interest all over the world.

When jellyfish occur in large numbers, their predation impact may be so pronounced that they control the population sizes of prey organisms (Båmstedt 1990, Schneider & Behrends 1994, Behrends & Schneider 1995, Olesen 1995, Purcell 1997, Hansson et al. 2005).

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Thus, the common jellyfish *Aurelia aurita* was able to control the meso-zooplankton in Limfjorden, Denmark during the summer of 2003 (Hansson et al. 2005). When jellyfish are controlling the zooplankton, they may strongly compete with fish larvae and zooplanktivorous fish for food by eating the same prey items (Purcell & Grover 1990). Both scyphozoan and hydrozoan jellyfish can feed on fish larvae. *A. aurita* was found to have a pronounced predation impact on the herring population in Kiel Bight, Germany (Möller 1984), and the hydromedusa *Aequorea* sp. caused high mortality on herring larvae in Kullet Bay, British Columbia (Purcell & Grover 1990). It has been suggested that in the North Sea jellyfish have a negative impact on survival and recruitment of herring, probably by both direct predation and competition for food (Lynam et al. 2005).

Jellyfish seem well adapted to utilise favourable food opportunities, such as patches of zooplankton, and they can quickly increase predation and growth rates, causing rapid changes in the whole food-web structure (Båmstedt 1990). Nevertheless, jellyfish are often neglected in ecological studies, and little is known of their role in the energy flow of marine ecosystems.

The present study deals with population dynamics, growth and predation impact of *Aurelia aurita* and 2 hydromedusae *Sarsia tubulosa* and *Aequorea vitrina* (mainly in Skive Fjord, an inner branch of Limfjorden, Denmark) during the years 2003 to 2005. In this fjord, *S. tubulosa* is usually present in the plankton during early spring together with other hydromedusae and *A. aurita* ephyrae (Blanner 1982, Hansson et al. 2005). During summer, medusae of *A. aurita* may make up the largest part of the plankton (Hansson et al. 2005). However, during August and September 2004, *A. vitrina* became very abundant, and concomitantly with this unusual event, the common jellyfish disappeared (Møller & Riisgård 2007, this volume).

In a companion paper we examined the effects of temperature, medusa size, prey concentration and prey species on feeding and growth of species of jellyfish, and we constructed carbon budgets based on data from laboratory experiments in which feeding, growth and respiration were measured simultaneously (Møller & Riisgård 2007). In the present work we use these findings to evaluate the degree to which *Aurelia aurita*, *Sarsia tubulosa* and *Aequorea vitrina* realise their growth potential in Limfjorden, and we evaluate whether these jellyfish may control the zooplankton community in this fjord, or conversely, whether the biomass of zooplankton may control the growth of the jellyfish. This was done by comparing natural prey concentrations in Limfjorden with previously determined minimum concentrations of prey needed for sustaining maximum growth of the jellyfish.

MATERIALS AND METHODS

Study area. The field work was conducted in the strongly eutrophicated Limfjorden, Denmark, a shallow fjord-system that is open to both the North Sea (32 to 34 psu) and to the Kattegat (19 to 25 psu). Limfjorden covers an area of 1500 km² and has an average depth of 4.9 m (Fig. 1). The average salinity in the central part is 25 psu, and at the bottom it is usually a few psu higher than at the surface. During summer, a thermocline stabilizes this stratification, which can only be broken by strong winds. Large areas in the inner parts of the fjord (among these Skive Fjord) suffer each summer from oxygen depletion in the bottom waters, and this often results in release of toxic hydrogen sulphide from the sediments, causing mass mortality of the benthic fauna (Jørgensen 1980, Riisgård & Poulsen 1981, Hoffmann & Dolmer 2000).

Jellyfish population dynamics. In 2003, field sampling was carried out, in collaboration with the Danish Institute for Fisheries Research (Hansson et al. 2005), during 5 cruises at 12 stations around the western and middle part of Limfjorden. Collection of jellyfish for determination of size and abundance was the main objective, supplemented with sampling of fish eggs and larvae.

Oblique hauls were made through the water column to get the average abundance of jellyfish. A 500 µm mesh Bongo net (0.29 m² mouth area) was used for sampling hydromedusae and ephyra larvae, while a 2 mm plankton net (1.77 m² mouth area) was used for large medusae. Fish eggs and larvae were caught by Bongo net hauls towed obliquely between near sea bed and surface, and the samples were preserved in formalin for subsequent counting and measurement in the laboratory. The larger medusae were counted on ship, and their umbrella diameters were measured. During the first 4 cruises (24 to 27 February, 8 to

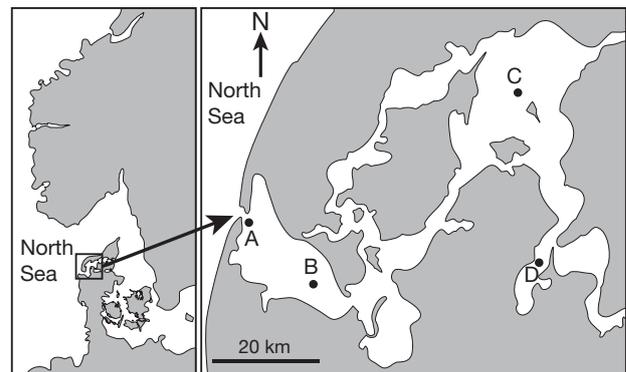


Fig. 1. Jellyfish sampling locations (A–D) in Limfjorden, Denmark. A: Thyborøn Kanal 56° 42' N–8° 14' E; B: Nissum Bredning 56° 36' N–8° 27' E; C: Løgstør Bredning 56° 59' N–9° 03' E; D: Skive Fjord 56° 39' N–9° 07' E

11 April, 20 to 24 May, 1 to 4 July) samples were taken of both types of jellyfish, fish eggs and larvae at all stations, but on the last cruise (26 to 27 August) only large scyphozoan jellyfish were collected (for further details, see Hansson et al. 2005).

In order to get information more detailed than that obtained in 2003, a sampling programme for 2004 and 2005 was conducted in Skive Fjord (Fig. 1) in cooperation with the Limfjord County Authorities (Limfjord-samterne). Skive Fjord is one of the locations in the Danish national monitoring program (Svendsen & Norup 2005), and as part of the weekly sampling programme, jellyfish were collected from February to October in 2004 and 2005. A plankton net (0.20 m² mouth area) with a mesh size of 500 µm was used for collecting hydromedusae. The samples were preserved in Lugol's solution and sent to the laboratory to be identified, measured and counted. In 2004, the 500 µm mesh net was used from February to June, and a 2 mm mesh net was used from June to October for collecting larger medusae. In 2005, the 500 µm and 2 mm nets were used from February to September, and from September to October, respectively. One and 3 hauls were made with the 2 mm net on each sampling day in 2004 and 2005, respectively, whereas 4 and 3 hauls per day were made with the 500 µm net in 2004 and 2005, respectively. The abundances of dominating hydromedusae and *Aurelia aurita* were estimated, and medusa height (*Sarsia tubulosa*) or diameter (*Aurelia aurita* and *Aequorea vitrina*) were measured on all individuals in every haul, and in no case were fewer than 10 ind. measured.

The following data from Skive Fjord for 2003 to 2005 were obtained from the Limfjord County Authorities' monitoring program: temperature, oxygen, nutrients, primary production, chl *a*, and zooplankton composition and concentration (including fish eggs and larvae). Zooplankton data were likewise obtained for Nissum Bredning and Løgstør Bredning in 2003 (for sampling details, see Andersen et al. 2004).

Bioenergetics. For *Aurelia aurita*, *Sarsia tubulosa* and *Aequorea vitrina*, specific growth rates (μ , d⁻¹) in the field were calculated as: $\mu = \ln(W_{C,t}/W_{C,0})/t$, where $W_{C,t}$ and $W_{C,0}$ = mean individual carbon content on Day 0 and Day *t*, respectively. μ was calculated for individuals collected on 2 sampling dates 1 wk apart, but only if the salinity profiles measured on the 2 sampling dates were similar, indicating that the individuals were sampled from the same water mass, and thus the same population.

The theoretical half-life time of prey organisms was calculated as $t_{1/2} = \ln 2/Q$, where $Q = F \times N$ = clearance rate of jellyfish population m⁻³ water, where F = individual clearance and N = density of jellyfish m⁻³, assuming F to be constant, regardless of prey concen-

tration. F (l d⁻¹) was calculated for a medusa of a given body mass (W , mg dry wt) at a given temperature from the following relations (Møller & Riisgård 2007): *Aurelia aurita* preying on copepods (*Acartia tonsa*): $F = 0.76W^{0.73}$ ($D = 5$ to 65 mm); *Aequorea vitrina* preying on copepods (*Acartia tonsa*): $F = 0.1W^{0.91}$ ($D = 6$ to 50 mm). For both medusa species, temperature correction was made using: $F = 1.17e^{0.18T}$, where T = temperature (°C). For *Pleurobrachia pileus* preying on copepods, we used the following expression: $F = 0.01D^{3.22}$, where D = body diameter (Gibbons & Painting 1992). We assumed that the relations between individual sizes and clearance rates used in the present study were also valid for medusae larger than those used in the clearance experiments.

Maximum specific growth rates, μ_{\max} , were calculated for a given medusa size at a given temperature (Møller & Riisgård 2007). For *Aurelia aurita* ephyrae and *Sarsia tubulosa*, maximum specific growth rates of 0.24 and 0.32 d⁻¹ (15°C) were used, while calculations from $\mu_{\max} = 0.34W_0^{-0.28}$ ($W_0 = 90$ to 1900 mg) were used for *A. aurita* medusae and $\mu_{\max} = 0.17W_0^{-0.34}$ ($W_0 = 2$ to 50 mg) for *Aequorea vitrina*, where W_0 = dry weight on Day 0. Temperature corrections were made from the following relations: $\mu = 0.0081e^{0.18T}$ (ephyrae and *Sarsia tubulosa*), and $\mu = 0.0032e^{0.14T}$ for *A. aurita* medusae and *A. vitrina*, respectively, where T is the average temperature between Day 0 and Day *t* (Møller & Riisgård 2007).

Conversion factors. The following equations were used to estimate body dry weight (W , mg) from umbrella diameter (D , mm) for *Aurelia aurita*: ephyrae: $W = 1.913 \times 10^{-3}D^{2.998}$ (Båmstedt et al. 1999); medusae (≥ 20 mm): $W = 0.004D^{2.7}$ (Møller & Riisgård 2007); and for *Aequorea vitrina*: $W = 0.03D^{2.3}$ (Møller & Riisgård 2007). For *Sarsia tubulosa*, the bell height (H , mm) was converted to carbon content (W_C , µg C): $W_C = 0.443H^{3.10}$ (Daan 1986). 1 mg dry wt (ephyra) = 3.66 µg C; 1 mg dry wt (medusae) = 50 µg C (Schneider 1988).

RESULTS

Jellyfish dynamics

The abundances of the dominating hydromedusae and *Aurelia aurita* in Skive Fjord in 2004 are shown in Fig. 2. From mid February to April, *Sarsia tubulosa* and *A. aurita* ephyrae were the most abundant species with densities of up to 2.5 and 5 ind. m⁻³, respectively. There was a marked change in the abundance of jellyfish in the period between 29 March and 5 April. From 5 April to 23 August, the abundance was low with only *Obelia* spp. appearing in quantifiable amounts. During

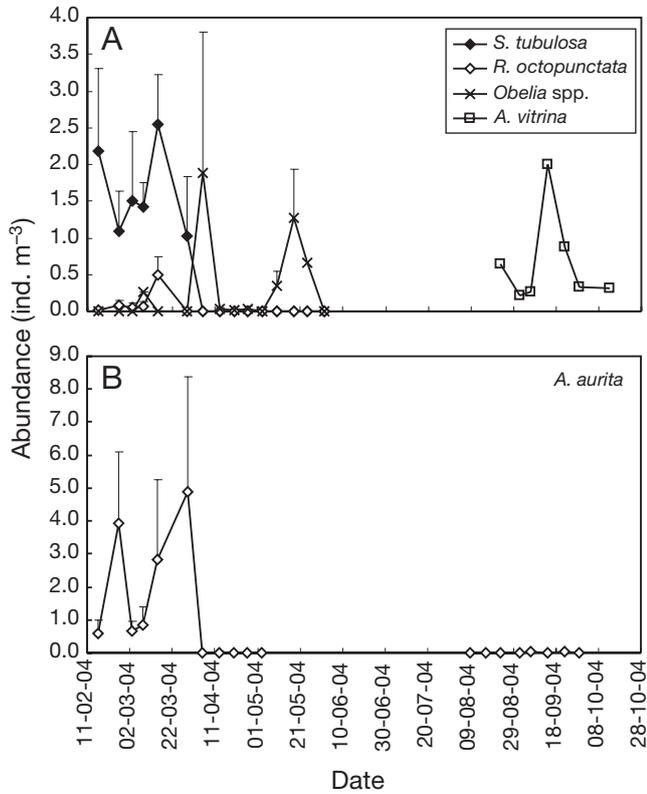


Fig. 2. Abundance (mean + SD) of (A) dominant hydro-medusae (*Sarsia tubulosa*, *Rathkea octopunctata*, *Obelia* spp., *Aequorea vitrina*) and (B) *Aurelia aurita* in Skive Fjord in 2004 (dates are dd-mm-yy)

summer, no sampling was made for small hydro-medusae. From 23 August to mid October, the hydro-medusa *Aequorea vitrina*, which had not been recorded previously in Limfjorden, became very abundant (up to 2 ind. m⁻³). Also, *A. aurita* reappeared. The drastic changes in jellyfish abundances in spring coincided with conspicuous changes in the salinity profile (Fig. 3A). Clearly, new highly saline and denser seawater gradually forced the older, less dense water masses out of Skive Fjord. Likewise in August, new highly saline water forced out the older more brackish water in Skive Fjord, and this time, the old 21.8 psu surface water (9 August) was completely replaced with 27 psu seawater in mid September, when no stratification was observed (Fig. 3B) and *A. vitrina* was seen for the first time. This indicates that *A. vitrina* was introduced into the Limfjord with highly saline North Sea water entering the fjord system from the west through the Thyborøn Kanal, assisted by exceptionally strong westerly winds.

In 2005 the hydromedusae, especially *Sarsia tubulosa*, and *Aurelia aurita* ephyrae, were abundant during early spring (Fig. 4). On 15 March both ephyrae, *S. tubulosa* and *Rathkea octopunctata* were abundant,

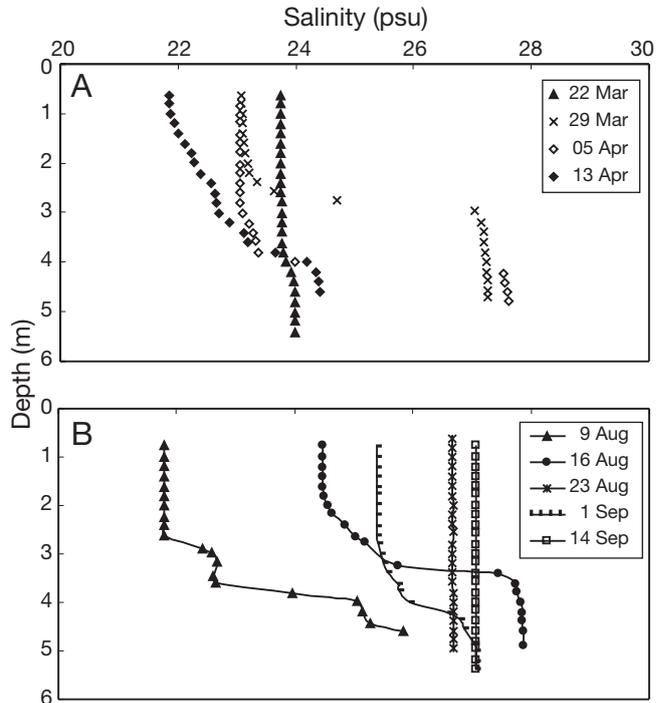


Fig. 3. Salinity profiles in (A) spring and (B) autumn in Skive Fjord in 2004

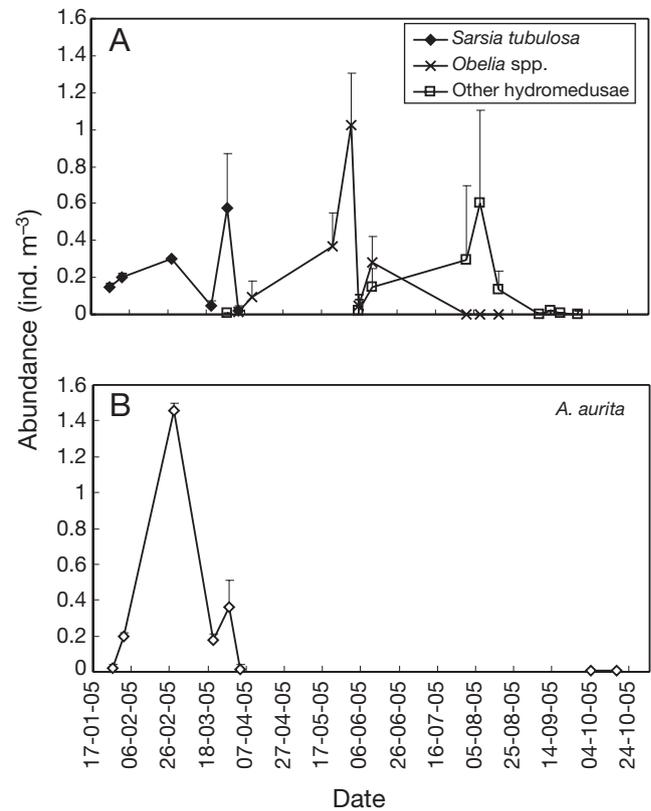


Fig. 4. Abundance (mean + SD) of (A) dominant hydro-medusae and (B) *Aurelia aurita* in Skive Fjord in 2005 (dates are dd-mm-yy)

but due to an algal bloom it was impossible to count the numbers in the samples. In general, the abundances were lower than in 2004 (maximum 0.4 ind. m⁻³ for *S. tubulosa* and 1.4 for ephyrae). During the 2 sampling dates, 4 April and 11 April, all jellyfish disappeared and, as in 2004, this occurred concurrently with pronounced changes in salinity. Since the 500 µm net was used during summer, hydromedusae were also recorded. During spring/summer *Obelia* spp. reappeared, and after June, other hydromedusae, especially *Sarsia gemmifera* and *Leuckartiara octona*, also occurred. In August a few large *A. aurita* and *Aequorea vitrina* occurred, but at very low densities, with maxima of 0.01 and 0.04 ind. m⁻³, respectively.

Monitoring of the abundance of ctenophores *Pleurobrachia* sp. was not a regular part of the programme. However, during the cruises on 23 August and 22 September, a marked change in abundance was noted. On 23 August the net filled up with *Pleurobrachia* sp., while only few were present on 22 September. In 2005, *Pleurobrachia* sp. was present in such high densities that it clogged the net from the beginning of August to the end of September. Ctenophores are difficult to preserve and they easily break, but intact individuals were counted in the preserved samples. The abundances of individuals of about 1 cm diameter was 0.5 to 1 ind. m⁻³ during August and September, but this number is an underestimate since many damaged individuals were seen in the samples, and they were not counted.

Growth and predation impact of jellyfish

The measured umbrella diameters and estimated actual specific growth rates (μ_{act}) for *Aurelia aurita* col-

lected at different localities in Limfjorden in 2003 are shown in Table 1. In general, the specific growth rate was relatively low in April (0.05 d⁻¹), maximum in May (0.15 to 0.17 d⁻¹), followed by a reduction in July (0.02 to 0.11 d⁻¹), and finally specific growth rate was negative in August (-0.03 to 0 d⁻¹).

The actual specific growth rates (μ_{act}) for *Aurelia aurita* in Skive Fjord, Nissum Bredning and Løgstør Bredning in 2003 are shown in Table 2, together with the estimated maximum specific growth rates (μ_{max}) (calculated on basis of laboratory experiments), and the estimated half-life times ($t_{1/2}$) of copepods (*Acartia tonsa*). Since μ_{act} conformed to μ_{max} in most cases, we conclude that the growth potential of the jellyfish was usually realised until August, when the actual growth became lower than the estimated growth (production). In Skive Fjord, the half-life times were low during summer, viz. 6.2, 3.2 and 0.8 d in May, July and August, respectively. In Nissum Bredning, the $t_{1/2}$ -value was relatively low (12.1 d) around the beginning of July, but during the rest of the summer, the half-life times were higher than 30 d. In Løgstør Bredning, $t_{1/2}$ -values were 26 d at the end of May, after which the half-life times became relatively low, viz. 6.1 and 11.1 d in July and August, respectively.

In Table 3 the actual specific growth rates for *Aurelia aurita* ephyrae and *Sarsia tubulosa* are shown for spring 2004 and 2005. The specific growth rates varied between 0 and 0.12 for ephyrae and -0.07 and 0.16 for *S. tubulosa*. For comparison, the calculated maximum specific growth rate was about 0.05 d⁻¹ for both *A. aurita* ephyrae and *S. tubulosa*.

In August 2004, *Aurelia aurita* reoccurred and its specific growth rate was 0.05 d⁻¹, but after that there was a tendency towards negative growth (Table 4). Half-life times for copepods were >37 d.

Table 1. *Aurelia aurita*. *D*: umbrella diameter (mean ± SD); μ_{act} : actual specific growth rate at various sampling stations in Limfjorden in 2003. (Data and stations are from Hansson et al. 2005, see their Fig. 1. No data were available for Thyborøn)

Station/Locality	<i>D</i> (mm)					μ_{act} (d ⁻¹)			
	24–27 February	8–11 April	20–24 May	1–4 July	26–27 August	8–11 April	20–24 May	1–4 July	26–27 August
A Thyborøn									
B Nissum Bredning	4.3 ± 0.8	8.0 ± 3.0		192 ± 20	141 ± 29	0.05		0.11	-0.02
C Venø			104 ± 44	219 ± 44				0.05	
D Nykøbing-Kås Bredning			127 ± 47						
E Visby Bredning				223 ± 33	129 ± 35				-0.03
F Thisted Bredning			125 ± 28	164 ± 34	106 ± 36			0.02	-0.02
G Løgstør Bredning	3.6 ± 3.9	7.7 ± 2.7	111 ± 20	147 ± 28	122 ± 34	0.05	0.17	0.02	-0.01
H Løgstør Kanal			107 ± 30	154 ± 31				0.03	
I Øst Livø Bredning				149 ± 30					
J Risgård Bredning			98 ± 31	132 ± 23	129 ± 28			0.02	0.00
K Skive Fjord		7.1 ± 2.7	65 ± 24	141 ± 22	136 ± 29		0.15	0.05	0.00
L Lovns Bredning			63 ± 25	142 ± 23	155 ± 37			0.06	0.00

Table 2. *Aurelia aurita*. Data from 3 localities in 2003 (Fig. 1): Skive Fjord (S), Nissum Bredning (N) and Løgstør Bredning (L). W_C : mean individual (\pm SD) carbon content of medusae; N : abundance; μ_{act} : actual specific growth rate; μ_{max} : estimated maximum specific growth rate; $t_{1/2}$: half-life time for *Acartia tonsa*. ∞ indicates $t_{1/2} > 30$ d

Date	Locality	Temp. (°C)	W_C (mg C)	N (ind. m ⁻³)	μ_{act} (d ⁻¹)	μ_{max} (d ⁻¹)	$t_{1/2}$ (d)
09 April 03	S	5	0.1 \pm 0.0	11			∞
20 May 03	S	12	15.7 \pm 1.1	3.7	0.15	0.15	6.2
01 July 03	S	18	126.4 \pm 0.8	0.6	0.05	0.07	3.2
26 August 03	S	18	115.6 \pm 2.1	2.4	0	0.07	0.8
09 April 03	N	6	0.1 \pm 0.0	0.04	0.05	0.04	∞
20 May 03	N	11		0			∞
01 July 03	N	17	293.0 \pm 0.7	0.08	0.11	0.18	12.1
26 August 03	N	18	127.0 \pm 1.8	0.01	-0.02	0.05	∞
09 April 03	L	6	0.1 \pm 0.0		0.05	0.04	
20 May 03	L	12	66.6 \pm 0.7	0.7	0.17	0.14	25.7
01 July 03	L	18	142.2 \pm 1.6	0.5	0.02	0.04	6.1
26 August 03	L	18	86.0 \pm 2.7	0.3	-0.09	0.07	11.1

Specific growth rates for *Aequorea vitrina* in Skive Fjord 2004 are listed in Table 5. During the period 23 August to 6 September, μ_{max} was about 0.04 d⁻¹. For comparison, the estimated maximum specific growth rate (for the observed sizes of animals at the temperature measured) was 0.02 to 0.05 d⁻¹, which indicates that the growth potential was realised. Half-life times calculated for copepods were >54 d. Due to changes in hydrography in the period 6 to 14 September (not shown), we were probably not sampling individuals from the same populations of *A. aurita* and *A. vitrina*, as can also be seen from the large variations in size and abundance of *A. vitrina* in this period.

Predation impact ($t_{1/2}$) of *Pleurobrachia* sp. was estimated to be approximately 25 d in August and September. However, the actual predation impact was certainly higher since the abundance of *Pleurobrachia* sp. was underestimated.

Table 3. *Aurelia aurita* and *Sarsia tubulosa*. Mean (\pm SD) individual biomass (W_C) and actual specific growth rate (μ_{act}) of *A. aurita* ephyrae and *S. tubulosa* in Skive Fjord during spring 2004 and 2005

Date	Temp. (°C)	W_C (μ g C)		μ_{act} (d ⁻¹)	
		Ephyrae	Sarsia	Ephyrae	Sarsia
16 February 04	1.6	1.3 \pm 0.0	0.3		
26 February 04	1.6	2.5 \pm 0.1	1.6	0.06	0.16
03 March 04	2.4	4.5 \pm 0.2	0.8	0.12	-0.07
08 March 04	1.7	4.5 \pm 0.2	0.8	0.00	0.00
15 March 04	2.7	4.5 \pm 0.5	3.3	0.00	0.14
29 March 04	5.2	10.8 \pm 0.1	7.6	0.08	0.06
02 February 05	2.5	0.5 \pm 0.0	0.2		0.06
28 February 05	-0.9	0	0.3		0.02
21 March 05	2.5	9.9 \pm 0.2	1.0	0.07	0.05
29 March 05	5.7	13.7 \pm 0.5	1.3	0.04	0.03

Plankton dynamics

Data on oxygen, nutrients, primary production, chl *a*, and zooplankton in Skive Fjord in 2003, 2004 and 2005 are shown in Fig. 5. Oxygen deficiency occurred every summer, causing nutrient (phosphate and ammonium) release from the sediment in August, and this subsequently triggered a peak in the primary production. In 2003, this event resulted in a phytoplankton bloom with extremely high chl *a* concentrations (up to 60 μ g l⁻¹) in the surface water. In both 2004 and 2005, the phytoplankton blooms were considerably smaller, at 20 and 10 μ g chl *a* l⁻¹, respectively. In all 3 yr, the meso-zooplankton responded to the phytoplankton bloom by increasing its biomass.

Fig. 6 shows the species composition of the most abundant meso-zooplankton species in Skive Fjord. The peak biomass of meso-zooplankton in mid August appearing in response to the phytoplankton bloom consisted mainly of nauplii (200 μ g C l⁻¹) in 2003,

Table 4. *Aurelia aurita* in Skive Fjord 2004. W_C : mean individual (\pm SD) carbon content of medusae; N : abundance; μ_{act} : actual specific growth rate

Date	Temp. (°C)	W_C (mg C)	N (ind. m ⁻³)	μ_{act} (d ⁻¹)
09 August 04	21.5		0.01	
23 August 04	17.7	702 \pm 5	0.01	0.05
01 September 04	17.2	546 \pm 4	0.02	-0.04
06 September 04	17.6	344 \pm 2	0.02	-0.09
14 September 04	16.5	334 \pm 1	0.01	0.00
22 September 04	14.3	189 \pm 27	0.04	-0.07
29 September 04	13.6	184 \pm 1	0.02	0.00

Table 5. *Aequorea vitrina* in Skive Fjord 2004. W : mean individual (\pm SD) dry weight of medusae; N : abundance; μ_{act} : actual specific growth rate

Date	W (mg)	N (ind. m ⁻³)	μ_{act} (d ⁻¹)
23 August 04	167 \pm 16	0.6	
01 September 04	259 \pm 27	0.2	0.05
06 September 04	283 \pm 40	0.3	0.02
14 September 04	98 \pm 25	2.0	
22 September 04	148 \pm 11	0.9	0.05
29 September 04	143 \pm 31	0.3	0.00
13 October 04	105 \pm 8	0.3	-0.02

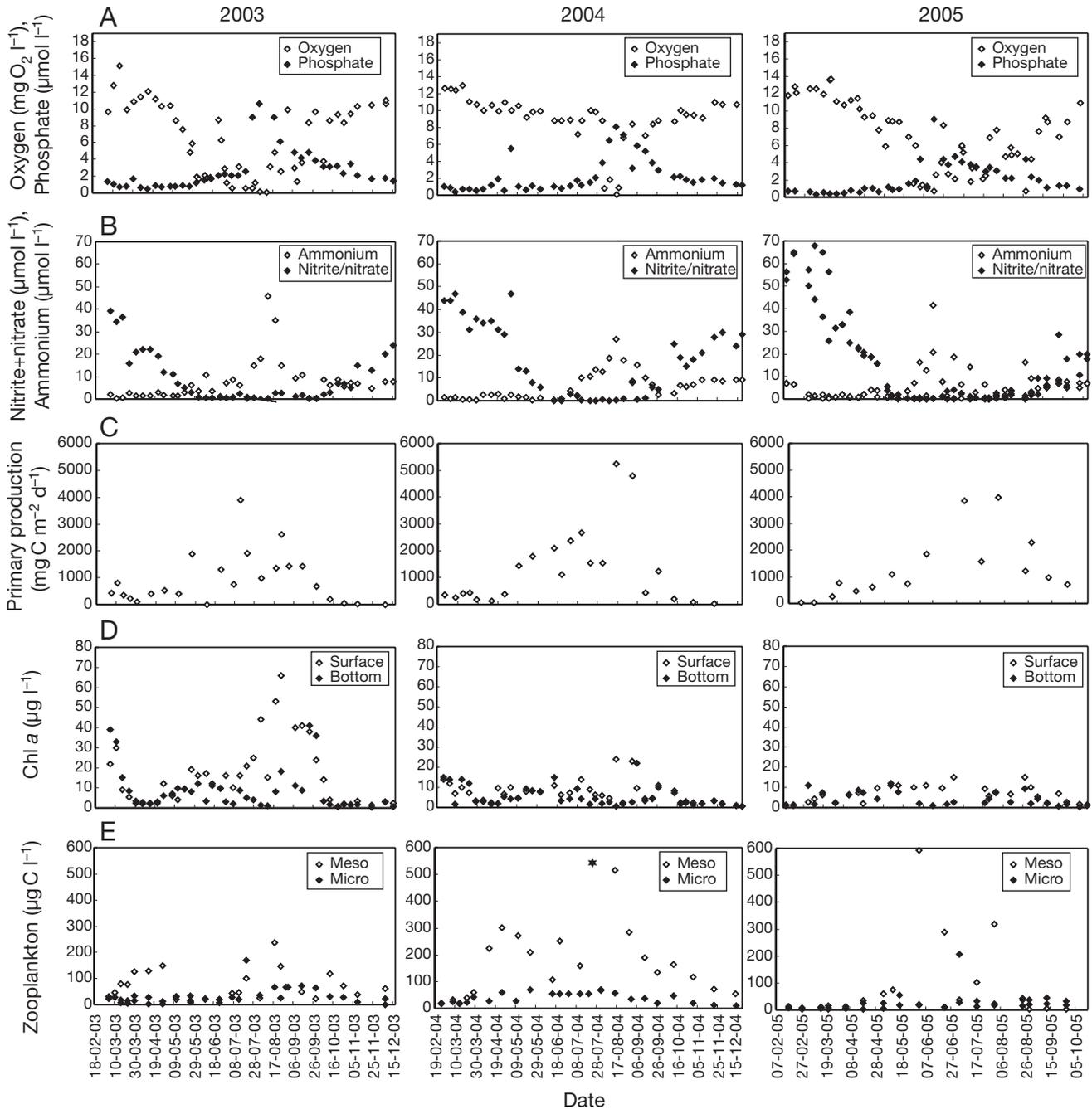


Fig. 5. Skive Fjord: Physico/chemical factors in 2003, 2004, and 2005. (A) Oxygen and phosphate concentration in bottom water; (B) ammonium and nitrate + nitrite concentration in bottom water; (C) primary production; (D) chl a concentration in surface and bottom water; (E) total biomass of micro- and meso-zooplankton, * indicates a total biomass of $1300 \mu\text{g C l}^{-1}$ (mainly polychaete larvae) (dates are dd-mm-yy)

mostly copepods and some nauplii ($500 \mu\text{g C l}^{-1}$) in 2004, and mostly nauplii and some copepods ($300 \mu\text{g C l}^{-1}$) in 2005. In 2003, almost no zooplankton was present from mid May to the beginning of July. During July, zooplankton (mainly copepods, up to $120 \mu\text{g C l}^{-1}$) was present. In 2004 zooplankton was present all summer (250 to $300 \mu\text{g C l}^{-1}$), mainly

copepods and cladocerans. But polychaete larvae were also very abundant, and peaked in late July at $1300 \mu\text{g C l}^{-1}$. In 2005, cladocerans were the dominant species from mid May to July, with concentrations up to $550 \mu\text{g C l}^{-1}$. The species composition during spring consisted mainly of copepods in 2003, while in 2004 and 2005 cirriped and polychaete larvae dominated.

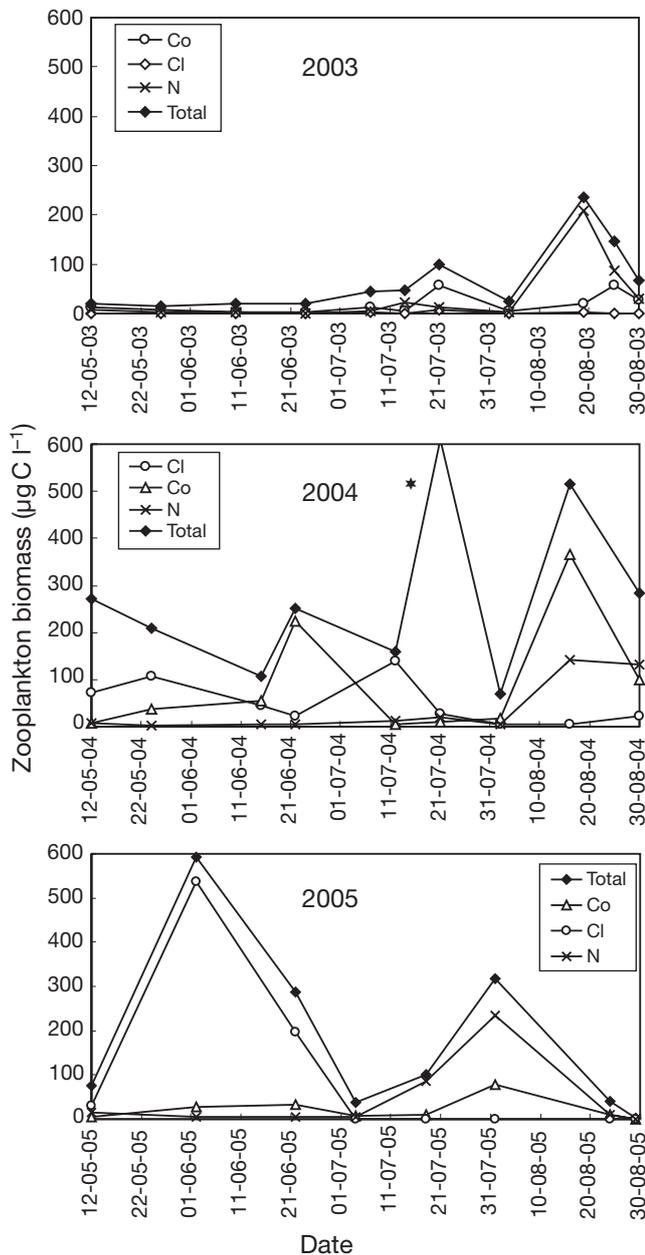


Fig. 6. Biomass and composition of dominant meso-zooplankton species in Skive Fjord in 2003, 2004, and 2005. N: copepod nauplii; Cl: cladocerans; Co: copepods. * in (2004) indicates peak with a total biomass of $1300 \mu\text{g C l}^{-1}$ (mainly polychaete larvae) (dates are dd-mm-yy)

In Nissum Bredning (Fig. 7A) a stable biomass of meso-zooplankton was recorded during summer (about $100 \mu\text{g C l}^{-1}$), consisting of both copepods, nauplii and cladocerans. The total meso-zooplankton biomass (mainly nauplii) increased to $200 \mu\text{g C l}^{-1}$ in August. In Løgstør Bredning (Fig. 7B) copepods, cladocerans and nauplii were present in late May (100 to $150 \mu\text{g C l}^{-1}$). Subsequently, the biomass of all species declined to almost zero in mid June. From July through

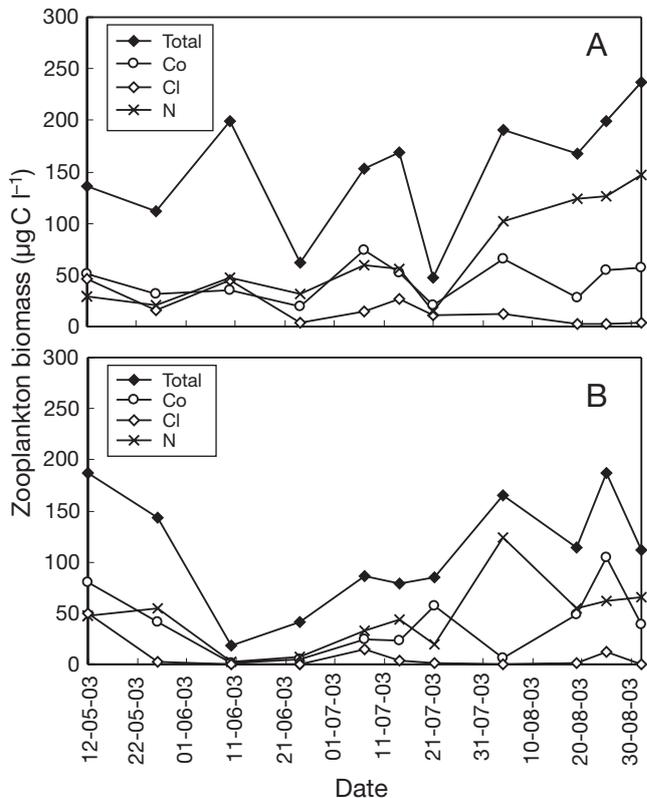


Fig. 7. Biomass and composition of dominant zooplankton species in (A) Nissum Bredning and (B) Løgstør Bredning in 2003. N: copepod nauplii; Cl: cladocerans; Co: copepods (dates are dd-mm-yy)

the rest of the summer, some adult copepods were present (up to $50 \mu\text{g C l}^{-1}$), but the total meso-zooplankton was dominated by nauplii (50 to $100 \mu\text{g C l}^{-1}$).

Fish eggs and larvae

In 2003, hauls were to estimate the number of fish eggs and larvae (Fig. 8). In Skive Fjord almost no eggs and larvae were found. The maximum concentrations recorded were 3 and 0.4 ind. m^{-3} eggs and larvae, respectively. The larvae present were herring *Clupea harengus* and gobies *Gobiidae* sp. More eggs and larvae were found in Løgstør Bredning (up to about 8 and 3 ind. m^{-3} , respectively, in the period mid March to mid June). The larvae present were primarily *C. harengus*, *Gobiidae* sp., gunnels *Pholis gunnellus*, short-spined sea scorpion *Myxocephalus scorpius* and sand eels *Hyperoplus* sp. The highest abundance and diversity were found in Nissum Bredning. In the period mid April to the end of June, up to 25 eggs m^{-3} were found. Larvae were present from mid April to the end of June, when the concentration reached a maximum of 9 larvae m^{-3} . In addition to the species above, sprat

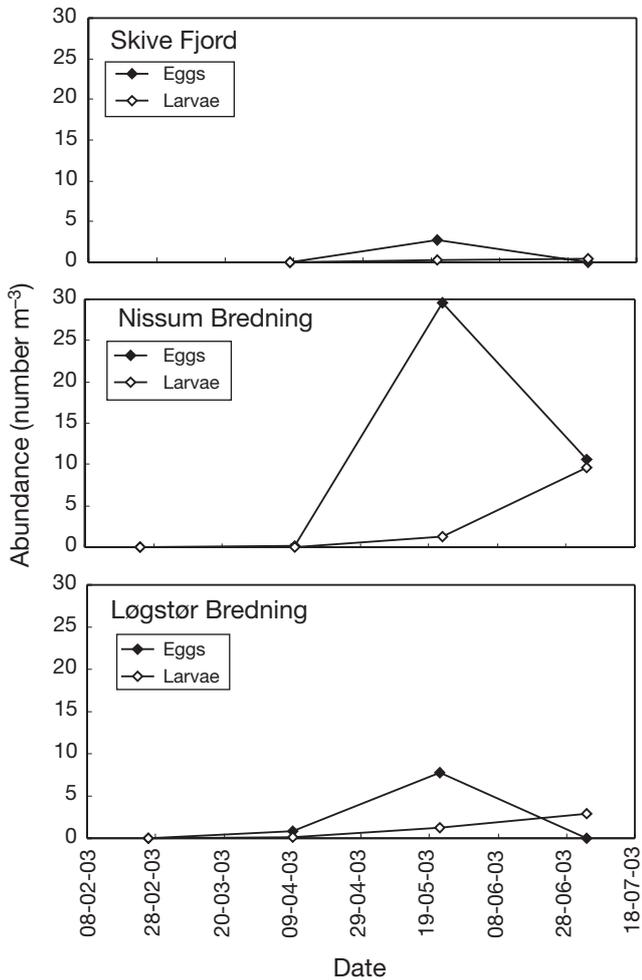


Fig. 8. Abundance of fish eggs and larvae in Skive Fjord (Fig. 1, location D), Nissum Bredning (location B), and Løgstør Bredning (location C) in 2003 (dates are dd-mm-yy)

Sprattus sprattus, flounder *Platichthys flesus*, pipefish *Syngnathidae*, and common sole *Solea solea* were among the dominant fish species in Skive Fjord.

In 2004 and 2005 there was no special sampling for eggs and larvae, but in all 3 yr the Limfjord County Authorities estimated their biomass ($\mu\text{g C l}^{-1}$) from weekly zooplankton sampling, giving a relative index of changes in biomass from year to year (Fig. 9). In 2003 no eggs were found, and larvae were present only at the beginning of July ($0.2 \mu\text{g C l}^{-1}$). In 2004, eggs were present from mid June to the end of July in concentrations up to $3 \mu\text{g C l}^{-1}$. Larvae were present from late June, reaching a maximum concentration of $3 \mu\text{g C l}^{-1}$ at the end of July. In 2005 eggs were present from early May ($1 \mu\text{g C l}^{-1}$), reaching a maximum of $7 \mu\text{g C l}^{-1}$ in early June, after which the concentration rapidly decreased to zero at the beginning of July. Larvae were present from early May, peaking in early June ($2 \mu\text{g C l}^{-1}$) and decreasing until the beginning of July.

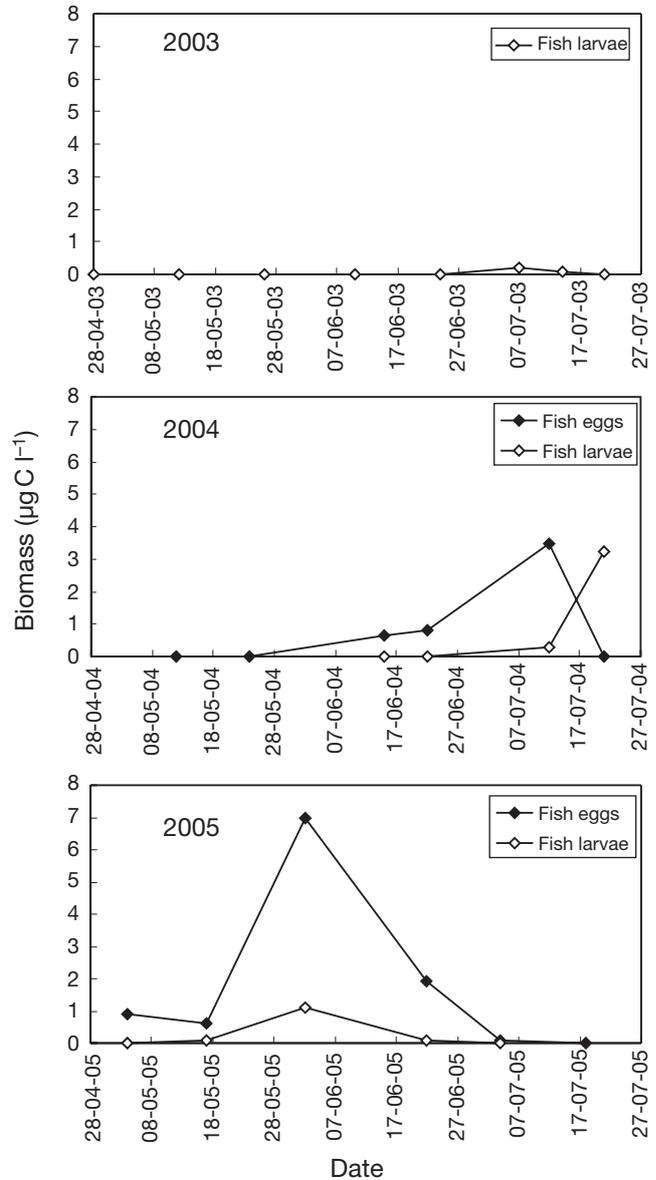


Fig. 9. Biomass of fish eggs and larvae in Skive Fjord in 2003, 2004, and 2005 (recorded in zooplankton samples collected by the Limfjord County Authorities) (dates are dd-mm-yy)

DISCUSSION

Population dynamics

The dynamics of *Aurelia aurita* and hydromedusae at 12 localities in Limfjorden in 2003 were described by Hansson et al. (2005) who found that Skive Fjord was one of the sites with highest biomass of this species. Accordingly, we chose Skive Fjord for more intensive studies during the following 2 years. In the early spring of 2004 and 2005, *A. aurita* ephyrae and hydromedusae were present in Skive Fjord, but they all disappeared in April/May. However, in August 2004 a new

species, *Aequorea vitrina*, became abundant (Fig. 2). In addition to *A. vitrina*, which was also rather abundant in late summer 2005 (Fig. 4), the other species present in 2004 and 2005 were similar to those found in 2003, when *Sarsia tubulosa*, *Rathkea octopunctata* and *Obelia* sp. were dominant during spring (Hansson et al. 2005). In 2005, the small hydromedusae were also found during summer, with *Leuckartiara octona*, *S. gemmifera* and *Lizzia blondina* being the dominant species, although not in high concentrations. This corresponds to previous records by Blanner (1982).

Usually, the salinity in Limfjorden is slightly higher at the bottom than at the surface (Hansson et al. 2005), but this was not the case in either 2004 or 2005, when dramatic changes in the salinity levels and vertical profiles (Fig. 3) coincided with rapid disappearance and re-introduction of jellyfish. Thus, infrequent influxes of large volumes of highly saline seawater from the North Sea via Thyborøn Kanal may radically change hydrographic conditions and thereby strongly influence the distribution and abundance of jellyfish in Limfjorden. This phenomenon makes a straightforward interpretation of the data on population densities and actual specific growth rates of jellyfish from 2004 and 2005 somewhat difficult, and it underlines the necessity of including hydrodynamic factors for a satisfactory understanding of the population dynamics of jellyfish in this fjord (which is actually a sound, with an opening to the highly saline North Sea in west and another to the more brackish Kattegat in east). However, to deal with the above uncertainties in the present study, we calculated actual specific growth rates only in those cases when the salinity profiles measured on 2 sampling dates were similar, indicating that the jellyfish were sampled from the same population.

The influence of varying hydrodynamic conditions on the interaction between *Aurelia aurita* and zooplankton, and hence the phytoplankton, were studied in the Kertinge Nor (northern part of Fyn, Denmark) by Nielsen et al. (1997). The local population of jellyfish was highly influenced by density-driven circulation created by frequent salinity changes in the adjacent Great Belt. When new water entered the fjord (either higher or lower salinity), changes in the jellyfish distribution were apparent. The time it took for the jellyfish to enter a new water mass of higher or lower salinity was found to be dependent on the degree of changes in salinity. Further, the number and distribution of zooplankton was found to be highly influenced by the presence of jellyfish. The disappearance of incoming copepods from the Great Belt occurred concurrently with the burgeoning of the jellyfish population in the new water mass. Obviously, similar conditions with density-driven currents may be important for understanding the population dynamics of jellyfish

and their predation impact in Limfjorden, which, in addition to incoming North Sea water via Thyborøn Kanal, also receives a high input of freshwater from the surrounding, mainly agricultural, land area, resulting in a salinity gradient from west to east (Jørgensen 1980).

Growth and predation impact

Hansson et al. (2005) found that the predation of *Aurita aurita* ephyrae and the hydromedusae was of minor importance during spring 2003, and since their abundance was even lower in 2004 and 2005, this aspect has not been considered in the present study. Although not important in relation to predation potential, the present work provides information on growth and prey selection for *A. aurita* ephyrae and *Sarsia tubulosa*. In 2004 and 2005, specific growth rates were obtained for ephyrae and *S. tubulosa* during spring (Table 3). Maximum specific growth rates (0.05 d^{-1}) were achieved in certain periods, but the actual growth rate varied conspicuously, probably due to strobilation of new individuals. The main prey item for *S. tubulosa* is believed to be copepods (Daan 1986), but the species can also feed on copepod nauplii (Møller & Riisgård 2007) and cirriped larvae (Hansson & Kiørboe 2006). Ephyrae are known to prey and grow on a variety of prey types, including cirriped larvae (Møller & Riisgård 2007). The main prey item for both *A. aurita* ephyrae and *S. tubulosa* was probably cirriped larvae in both 2004 and 2005, since almost no other prey items were present in sufficiently high concentrations to account for the observed growth rates (Møller & Riisgård 2007).

In 2003, when *Aurelia aurita* was present during the entire study period (February to August), we measure the actual specific growth rate at 12 sampling localities throughout the year (Table 1). Because the growth pattern was similar at all sampling localities, it can be assumed that we sampled the same population from week to week. The trend with low growth rates during winter, higher rates during spring, then lower again during summer, and finally negative growth in August is a pattern that has been observed previously at several study sites, e.g. Kiel Bight (Möller 1980) and Vågsbøpollen, Norway (Ishii & Båmstedt 1998). By estimating specific growth rates from the data reported by Möller (1980), we calculated 0.05 d^{-1} for spring, 0.15 d^{-1} for early June, and 0.03 to 0.05 d^{-1} for summer, and then negative growth in September, i.e. a pattern comparable to that in Limfjorden (Table 1).

Patterns of growth and maximum bell diameter may, however, vary considerably among different *Aurelia aurita* populations (Lucas 2001). In more open areas,

the individuals often reach bell diameters of 20 to 30 cm (Møller 1980, Schneider & Behrends 1994). In some localities, however, natural populations of *A. aurita* can be severely food-limited. Thus, in the shallow cove of Kertinge Nor, the maximum diameter of the umbrella is usually only 3 to 4 cm, although high abundances of such small jellyfish (up to 300 ind. m⁻³) control the zooplankton biomass (Olesen et al. 1994, Riisgård et al. 1995, Frandsen & Riisgård 1997). A similar situation has been described for Horsea Lake, England (Lucas & Lawes 1998).

To evaluate whether the jellyfish in Limfjorden realised their growth potential, or whether they were food-limited in the study period, the actual specific growth rates in the field (μ_{act}) may be compared to the maximum specific growth rates obtained in controlled laboratory experiments (μ_{max}) (Møller & Riisgård 2007). As discussed by Møller & Riisgård (2007), the maximum specific growth rate decreases with increasing medusa size. In the present study, the relation used (estimated from data obtained by Ishii & Båmstedt 1998, and assumed in the present work to be valid also for larger individuals) was $\mu_{\text{max}} = 0.34 W^{-0.28}$. When correcting for the ambient temperature, we estimate that *Aurelia aurita* realised its growth potential in Limfjorden in 2003 from April until August, after which negative growth was observed. In 2004, data were only available in late summer, and the growth potential was realised in August, followed by negative growth.

It has been suggested that negative growth may be due to lack of food, infection by the parasite *Hyperia galba*, or genetic programming (Møller 1980). *H. galba* was found in up to 80% of the *A. aurita* population in July and August 2003, and this parasite could have caused the negative growth. However, by comparing the minimum concentration of a specific prey organism (C_{min}) needed to sustain maximum growth with the actual prey concentrations in the field, we can estimate whether the observed negative growth is likely to have been caused by lack of food. From laboratory experiments, Møller & Riisgård (2007) found that C_{min} was about 100 $\mu\text{g C l}^{-1}$ for *Aurelia aurita* preying on the copepod *Acartia tonsa*. Since the biomass of zooplankton in August was generally higher than 100 $\mu\text{g C l}^{-1}$, food was apparently available in superfluity. However, the zooplankton biomass consisted mainly of nauplii, and several studies indicate that the clearance of nauplii is considerably lower than that of copepods (Hansson et al. 2005, Hansson 2006), and because this will increase the estimated C_{min} , the actual prey concentration may not have been sufficiently high to sustain maximum growth.

When comparing data for Skive Fjord in 2003 with those for 2004 and 2005, the predation effect of jellyfish can be assessed during summer, since almost no

Aurelia aurita were present until August in 2004 and 2005. In the present study, half life times ($t_{1/2}$) have been calculated for *Acartia tonsa*, which was the prey organism used for constructing carbon budgets for jellyfish (Møller & Riisgård 2007). In 2003, *A. aurita* had a high potential ($t_{1/2} = 1$ to 6 d) for preying on *A. tonsa* from mid May to August in Skive Fjord (Table 2). According to Hansson et al. (2005) and Hansson (2006), clearance of cladocerans is even higher than for copepods, and almost none of the 2 prey organisms appeared in Limfjorden from the end of May to the beginning of July 2003. Both copepods and cladocerans were present in high concentrations during the summer of 2004, when no *A. aurita* were present, and in 2005 where cladocerans were present in concentrations up to 600 $\mu\text{g C l}^{-1}$ (Fig. 6). In Nissum Bredning, the half-life times (Table 2) were relatively high through most of the summer, during which the biomass of zooplankton (consisting mainly of copepods, nauplii and cladocerans; Fig 7A) was rather stable (about 100 $\mu\text{g C l}^{-1}$). In Løgstør Bredning, the half-life time was high ($t_{1/2} = 26$ d) in late May when copepods, cladocerans and nauplii were present in a combined total concentration of 100 to 150 $\mu\text{g C l}^{-1}$. Subsequently, the half-life times decreased to 6 to 11 d during the rest of the summer, coinciding with the absence of adult copepods and cladocerans during June. From July, adult copepods were present (up to 50 $\mu\text{g C l}^{-1}$), but the total zooplankton was dominated by nauplii (up to 100 $\mu\text{g C l}^{-1}$).

In the 3 years of the study, a large number of nauplii appeared in August in response to increased chl *a* concentrations caused by nutrient release from the bottom during events of severe oxygen depletion (Fig. 5). In 2003, however, the nauplii did not develop into adults, probably because *Aurelia aurita* exerted a very high predation pressure. In 2004, the nauplii developed to adult copepods, likely because the predation impact exerted by *A. aurita* was insufficient to control the zooplankton. In 2005, the ctenophore *Pleurobrachia* sp. was very abundant at the end of the summer, and presumably responsible for low copepod concentrations at that time.

Copepods and cladocerans are suggested to be some of the primary prey items of *Aurelia aurita*. Barz & Hirche (2005) found that cladocerans were the dominant food items in the gut of *A. aurita* during summer in the Bornholm Basin. In the Black Sea, Mutlu (2001) found that *A. aurita* preyed primarily on copepods and bivalve larvae, and to some extent on fish eggs and larvae, while Martinussen & Båmstedt (1995) found that bivalve larvae and cladocerans dominated the food of *A. aurita* in Raunefjorden, Norway.

The present study indicates that during summer *Aurelia aurita* may also prey heavily on prey types

other than meso-zooplankton. *A. aurita* realised its growth potential during the summer of 2003, although the zooplankton biomasses recorded at the 3 localities were not sufficiently high to sustain the actual observed growth. In Skive Fjord, almost no meso-zooplankton was present in June (Fig. 6). An explanation may be that *A. aurita* fed on prey organisms that we have not considered. Fish eggs and larvae may have supplemented the food for a short period, but they were not abundant enough to sustain the observed growth of *A. aurita*. A few studies have suggested that micro-zooplankton, e.g. ciliates may be prey items for *A. aurita* (Stoecker et al. 1987, Båmstedt 1990, Olesen 1995), but little is known about the role of ciliates in the diet of *A. aurita*.

The function of *Aurita aurita* as a local key organism may manifest itself not only as great variations in zooplankton, but also in the abundance of phytoplankton communities. Release of phytoplankton from zooplankton grazing control (due to top-down predation pressure by *A. aurelia* on zooplankton) may trigger, or reinforce phytoplankton blooms. Thus, in Skive Fjord, oxygen depletion triggered nutrient release from the sediment in each year of the project (in July to August), but in only 2003 (when the zooplankton was controlled by *A. aurita*) did this lead to a pronounced algal bloom (up to $60 \mu\text{g chl a l}^{-1}$). Thus, similar algal blooms were not observed in 2004 and 2005, when *A. aurita* was absent, and although the primary production was equally high (Fig. 5).

The hydromedusa *Aequorea vitrina* is a new species in Limfjorden, occurring in high abundances for the first time in August to September 2004. To our knowledge, no previous records exist on specific growth rates of *Aequorea* sp. in the field. Laboratory feeding experiments made by Møller & Riisgård (2007) indicate that *A. vitrina* was growing at maximum specific growth rates in Limfjorden during late August and early September (Table 5). Copepods and nauplii were the only zooplankton species present in this period, but from the estimated half-life times for copepods (>54 d), it is clear that *A. vitrina* had no predatory effect on the copepod biomass. However, as pointed out by Møller & Riisgård (2007), the predation impact by *A. vitrina* on soft-bodied prey may be several times higher than on zooplankton, thus indicating that this cnidarian population in Skive Fjord could have exerted control on soft-bodied prey, such as the ctenophore *Pleurobrachia* sp. Arai (1980) showed that *A. victoria* is able to grow on *Pleurobrachia* sp., however no data on predation rates exist. In Skive Fjord, *Pleurobrachia* sp. disappeared in the period when *A. vitrina* was growing (L. F. Møller unpubl. obs.), and therefore this ctenophore may have been the primary prey item.

Effect on fish larvae

Hansson et al. (2005) reported that *Aurelia aurita* may have had a severe impact on fish larvae in Limfjorden during late spring and summer 2003, and this statement is supported by the present study. Titelman & Hansson (2006) estimated clearance of cod larvae by *A. aurita*, and they reviewed the existing literature on predation on fish larvae. In general, it was found that the predation on fish larvae is higher than that on zooplankton, implying that *A. aurita* in Skive Fjord and Løgstør Bredning may have had the potential in 2003 to control the abundance of fish larvae from early May, but only during mid-summer in Nissum Bredning. Only few fish larvae of *Clupea* sp. and *Gobidae* sp. were present in Skive Fjord in 2004 (Fig. 8). By comparing Skive Fjord with Nissum Bredning and Løgstør Bredning, a negative relation between abundance of *A. aurita* and abundance of eggs and larvae is indicated (Fig. 8). Although the 3 yr data set for fish eggs and larvae in Skive Fjord may be underestimates (because no specific samplings for fish eggs and larvae were made) it is striking that almost no fish eggs and larvae were found in 2003 when *A. aurita* was abundant in the fjord, whereas higher concentrations were recorded in 2004 and 2005 when *A. aurita* was absent (Fig. 9).

CONCLUSION

In certain years, *Aurelia aurita* may be very abundant in Limfjorden, and during the summer period it may exert a considerable predatory impact on a broad spectrum of zooplankton species and fish larvae. The abundance, species composition and population dynamics of jellyfish in Limfjorden may be strongly influenced at times by dramatic, but apparently rather unusual hydrographic events, and hydraulic processes may explain otherwise unaccountably large variations in the plankton (including jellyfish) composition and biomass. The jellyfish predatory impact and its structuring effects on the planktonic communities in Limfjorden is not yet completely clear, but zooplankton (and fish larvae) and phytoplankton biomasses may be severely affected by mass occurrence of *A. aurita*, as observed in 2003 when *A. aurita* realised its growth potential, although the concentration of zooplankton recorded was not sufficiently high to sustain the observed growth, implying that *A. aurita* may also feed on prey types not considered in the present study.

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