Chapter 16
Odense Fjord and Kerteminde Fjord/Kertinge Nor

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16.1 Introduction

Odense Fjord (Table 16.1) is a shallow Danish fjord affected by freshwater and nutrient discharges from a large catchment area (1,060 km^2) dominated by agriculture. In contrast, the nearby Kerteminde Fjord/Kertinge Nor (Table 16.1) is a shallow fjord system with a small catchment area (36 km^2) and consequently small freshwater discharges, and where the water exchange and nutrient dynamics are greatly affected by density-driven currents caused by frequently changing salinities in the Great Belt. In both fjord systems, filter-feeding macro-invertebrates play a significant role in the biological structure as will become apparent from the two case studies detailed in this chapter.

16.2 Case Study: Odense Fjord

16.2.1 Basic Characteristics

The total area of Odense Fjord is 63 km^2. The outer fjord has a surface area of 49.3 km^2 and a mean depth of 2.7 m, and the inner fjord has a surface area of 10.7 km^2 and a mean depth of 0.8 m (Fig. 16.1). The water exchange between Odense Fjord and the open sea (Northern Belt Sea) takes place through a narrow opening in the northern part of the outer fjord. The tidal amplitude is about 0.5 m, changing approximately every 6 h. Hydrodynamic modelling has shown an annual average residence time for Odense River water of 17 days in the fjord as a whole, and of 9 days in the inner fjord (Fyn County 2003); Rasmussen and Josefson (2002) estimated a residence time of 11 days for Odense Fjord [see Chaps. 3 (Schiewer), 9 (Gasiūnaitė; et al.) and 12 (Telesh et al.), this volume]. The salinity in the shallow inner fjord varies between 10 and 15 psu during the year, being lowest in winter/spring where riverine runoff is highest. In the surface water of the outer fjord and outside the fjord the salinity varies from 16 to 20 and 16 to 23 psu, respectively

U. Schiewer (ed.), *Ecology of Baltic Coastal Waters. Ecological Studies 197.*

Table 16.1 Main characteristics of Odense Fjord and Kerteminde Fjord (*KF*)–Kertinge Nor (*KN*). *dw* Dry weight, *ww* wet weight, *Chl a* chlorophyll *a*, *DIN* dissolved inorganic nitrogen, *DIP* dissolved inorganic phosphorus, *POC* particulate organic carbon, *DOC* dissolved organic carbon, *PON* particulate organic nitrogen, *POP* particulate organic phosphorus, *POM* particulate organic matter

	Odense Fjord	Kerteminde Fjord/Kertinge Nor
a. **Climate and hydrology**		
Air temperature (°C)	8.2 (1961–1990)	8.2 (1961–1990)
Water temperature (°C)	0–22	0–22
Ice covering (days a^{-1})	< 7	< 7
Annual global radiation (kWh m^{-2})	ca. 1,000	ca. 1,000
Average precipitation (mm a^{-1})	768 (1961–1990)	768 (1961–1990)
Mean freshwater inflow ($10^6 m^3 a^{-1}$)	322 (mean 1989–2003)	13.6 (mean 1989–2003)
Mean inflow ($10^6 m^3 a^{-1}$)	No data	No data
Mean total outflow ($10^6 m^3 a^{-1}$)	322 (mean 1989–2003)	13.6 (mean 1989–2003)
Residence time (days)	9–17	ca. 90
Water exchange rate (a^{-1})	No data	No data
b. **Morphometry and sediments**		
Area (km^2)	62	8.5
Volume ($10^6 m^3$)	136	17
Mean depth (m)	2.25	2
Maximum depth (m)	12	8
Catchment area (km^2)	1,095	36
Area/catchment relation	0.055	0.236
Organic matter content (% dw)	<1–16	<1–16
Sediment respiration (dark O_2 flux) (mmol $O_2 m^{-2} day^{-1}$)	12–90 (inner), 5–170 (outer); min–max, 1999–2002	No data
Daily microphytobenthic production (gross) (mmol $O_2 m^{-2} day^{-1}$)	1–77 (inner), 0–98 (outer); min–max, 1999–2002	No data
Daily DIN-flux (mmol N $m^{-2} day^{-1}$)^{a,b}	−5.7–2.6 (inner), −3.9–9.7 (outer); min–max, 1999–2002	Gross annual flux = 173 t (1992)

Daily phosphate flux (mmol P m^{-2} day^{-1})[b]	−0.18–0.43 (inner), −0.05–0.44 (outer); min–max, 1999–2002	Gross annual flux = 16 t (1992)
Denitrification rate (mmol N m^{-2} day^{-1})	0.3–2.9/1.5 (inner), 0.1–1.0/0.4 (outer); min–max/mean 1995	Annual denitrification = 26 t (1992)
Sediment distribution	Inner: mostly sandy	Sandy (0–1 m), sand/silt (1–2 m), silty (below 2 m)
	Outer: sandy (0–2 m), sand/silt (2–4 m), silty (below 4 m)	
c. Pelagic biological components		
Secchi depth (m)	3.1 (deeper part); range of summer means, 1989–2004	KF: no data, KN: too shallow
Bacteria (10^6 ml^{-1})	No data	1–2
Phytoplankton biomass (µg Chl *a* l^{-1})	3.9–15.5 (inner), 4–10.1 (outer); range of summer means, 1998–2003	3–32; range of summer means, 1984–2003
Phytoplankton biomass (summer mean) (µg C l^{-1})	75–213; range of summer means, 1998–2003	No data
Phytoplankton biomass (spring and autumn maxima) (µg C l^{-1})	138–688 (spring), 55–458 (autumn); range, 1998–2003	No data
Dominating phytoplankton species	*Skeletonema costatum*, *Proboscis alata*, *Prorocentrum minimum*, *Euglenophyceae*, (quantitative dominance by diatoms, >50%)	No data; but sporadic blooms of *Prorocentrum minimum*, *Chrysochromulina parkae*
Flagellates		
Biomass (µg C l^{-1})	0.4 (summer mean), 9.1 (max)	No data
Dominating species	*Parvicorbula socialis*; 2002 data	No data
Ciliates		
Biomass (µg C l^{-1})	27 (summer mean), 343 (max)	No data
Dominating species	*Strombidium* spp., *Balanion* spp.; 2002 data	No data
Mesozooplankton		
Biomass (µg C l^{-1})	66 (summer mean), 172 (max)	No data
Dominating species	*Acartia tonsa* (copepod), *Spironidae* spp.; 2002 data	No data

(continued)

Table 16.1 (continued)

	Odense Fjord	Kerteminde Fjord/Kertinge Nor
Fish		
Recorded species	*Salmo trutta*, *Anguilla anguilla*, *Platichthys flesus*, *Belone belone*, *Gadus morhua*, *Gobius niger*, *Pomatoschistus minutus*, *Zoarces viviparus*, *Syngnathus typhle*, *Psetta maxima*, *Crenimugil labrosus*, *Salmo salar*, *Clupea harengus*, *Trachurus trachurus*, *Limanda limanda*, *Pleuronectes platessa*, *Pungitius pungitius*, *Gasterosteus aculeatus*, *Scomber scombrus*, *Ctenolabrus rupestris*, *Merlanguis merlangus*, *Ammodytes tobianis*, *Taurulus bubalis*, *Pomatochistus microps*, *Spinachia spinachia*, *Pholis gunnilus*, *Gobiosculis flavescens*	*Clupea harengus*, *Salmo trutta*, *Syngnathus typhle*, *Solea solea*, *Platichtys fleses*, *Merlangius merlangus*, *Sprattus sprattus*, *Gasterosteus aculeatus*, *Pungitius pungitus*, *Myoxocephalus scorpius*, *Perca fluviatilis*, *Anguilla anguilla*, *Hyperoplus lanceolatus*, *Zoarces viviparus*, *Pomatoschistus microps*, *Gobis niger*
Seston (mg l^{-1})	No data	No data
POC (µmol l^{-1})	16.4–181; min–max, 2002–2003	No data
DOC	No data	No data
PON (µmol l^{-1})	1.7–17.4; min–max, 2002–2003	No data
POP (µmol l^{-1})	0.21–2.5; min–max, 2002–2003	No data
C/N in POM	6.6–12.5; min–max, 2002–2003	No data
Annual primary production (g C m^{-2} a^{-1})	19–59 (inner), 118–143 (outer); range, 1981–2003	58–359; range, 1980–2003
Primary production (mg C m^{-2} day^{-1})	110–405 (inner), 600–1,810 (outer); range of summer means, 1978–2003	3–32; range of summer means, 1984–2003
Bacterial production (µg C l^{-1} h^{-1})	No data	No data
Mesozooplankton production (g C m^{-2} a^{-1})	No data	No data
Fish catches (t a^{-1})	No data	No data
d. **Benthic biological components**		
Macrophytes		

Biomass (g m^{-2})		
Number of species		
Dominating species	*Ulva lactuca*, *Chaetomorpha linum*, *Cladophora* sp., *Ectocarpus siliculosus, Fucus vesiculosus, Fucus serratus, Zostera marina, Ruppia maritima, Ceramium virgatum*	*Zostera marina, Potamogeton pectinaus, Zannichellia palustris, Ruppia* sp., *Chaetomorpha linum, Cladophora sericea, Fucus vesiculosus*
Macrozoobenthos		
Biomass (g m^{-2})		
Number of species		
Dominating species	*Nereis diversicolor*, *Corophium volutator*, *Mya arenaria*, *Cerastoderma glaucum*, *Mytilus edlis*, *Macoma balthica*, *Scrobicularia plana*, *Ensis* sp.	*Ciona intestinalis*, *Nereis diversicolor*, *Corophium volutator*, *Mytilus edulis*
e. Water chemistry, trophic status and pollution		
Salinity (psu)	10–15 (inner part), 16–23 (outer part)	14–22 (min 10, max 27)
pH	No data	No data
Oxygen saturation (%)	70–>100; (25–>100 in deeper part)	60–>100; (occasional local O_2-depletion with H_2S emission)
Total nitrogen (µmol l^{-1})	Inner: 85–650 (winter), 43–115 (summer); range of seasonal means, 1979–2003 Outer: 43–250 (winter), 23–64 (summer); range of seasonal means, 1979–2003	29–105; range of winter means, 1987–2003
DIN (µmol l^{-1})	Inner: 36–610 (winter), 4.3–36 (summer); range of seasonal means, 1979–2003 Outer: 30–235 (winter), 2.1–29 (summer); range of seasonal means, 1979–2003	11–80; range of winter means, 1987–2003
Total phosphorus (µmol l^{-1})	Inner: 2.1–15 (winter), 3.2–32 (summer); range of seasonal means, 1979–2003	0.6–2.6; range of winter means, 1987–2003

(continued)

Table 16.1 (continued)

	Odense Fjord	Kerteminde Fjord/Kertinge Nor
	Outer: 1.1–7.3 (winter), 1.6–13 (summer); range of seasonal means, 1979–2003	
DIP (µmol l^{-1})	Inner: 1.1–10, 1.8–26 (summer); range of seasonal means, 1979–2003	0.2–1.8; range of winter means, 1987–2003
	Outer: 0.6–5.3 (winter), 0.8–10 (summer); range of seasonal means, 1979–2003	
Annual nitrogen input (t a^{-1})	2,433 (mean 1989–2003)	109 (mean 1989–2003)
Annual phosphorus input (t a^{-1})	80.6 (mean 1989–2003)	2.0 (mean 1989–2003)
Limitation of PP and period	P, Si in spring (short), N in spring-summer (long)	P, Si in spring (short), N in spring-summer (long)
Main pollutants	N, P	N, P
Trophic level	Eu- to hypertrophic	Eutrophic

[a] DIN: nitrate+nitrite+ammonia

[b] Positive values: release, negative values: uptake

(Fig. 16.2). The monthly mean water temperature in the fjord varies between approximately 3 and 19°C (Fig. 16.2).

Resuspension events are frequent in the shallow wind-, wave- and tidally-impacted inner Odense Fjord. Together with a large number of bioturbating polychaetes (especially *Nereis diversicolor*) in the sediment, this causes a relatively homogeneous muddy/silty sand (2–3.5% loss on ignition) in the upper 10 cm or more of the inner fjord sediment. Fine material is trapped in the deep excavated fairway and the connected deeper channels in the outer fjord, and the sediment consists primarily of muddy silt (up to ca. 15% loss on ignition). Most of the outer Odense Fjord is shallow, however, and the sediment is primarily sandy (0.5–2% loss on ignition) and often heterogeneous due to presence of shells, stones and gravel. In a tidal flat in the eastern part of the outer fjord, innumerable faecal piles due to lugworms (*Arenicola marina)* are visible when the flat is laid bare. Riisgård and Banta (1998) found that the lugworm heavily reworked a sediment volume corresponding to the upper 12 cm of the sediment each year.

16.2.2 Nutrient Loads

The catchments area of Odense Fjord is 1,060 km^2 (about one-third of the island of Fyn), and the anthropogenic load of nutrients to Odense Fjord, which enter the fjord mainly via Odense River (Fig. 16.1), is high and originates from the agricultural land that comprises about 80% of the catchment area. Thus, in 2000, Odense Fjord received 2,332 t nitrogen (N) and 54 t phosphorus (P). This is equivalent to a total annual loading of 2.8 mol N m^{-2} and 0.029 mol P m^{-2} of fjord. The high nutrient load significantly affects the ecosystem, and Odense Fjord is characterised as eutrophicated (Fyn County 2003).

National and local initiatives to reduce the high loads began in the second half of the 1980s (Fig. 16.2). The phosphorous load has been reduced about six-fold since then, mainly as a result of reduced inputs from point sources (municipal and industrial waste water), which were the phosphorous sources clearly dominating at that time. The nitrogen load originates mainly from agriculture (i.e. diffuse sources), and therefore is correlated with variations in the freshwater run-off. Through measures against nitrogen losses in the agricultural sector, the N-load has been reduced by about one-third in the same period, after correcting for variations in the freshwater discharge (Fyn County 2003).

16.2.3 Nutrients in Water and Sediment

Year-to-year variations in N and P load to Odense Fjord determine the variations in the annual mean of total-N and total-P concentrations in the fjord (Fig. 16.2, left column). The concentration of dissolved inorganic nitrogen (DIN) is generally higher in the winter period (almost exclusively nitrate) due to the high run-off and

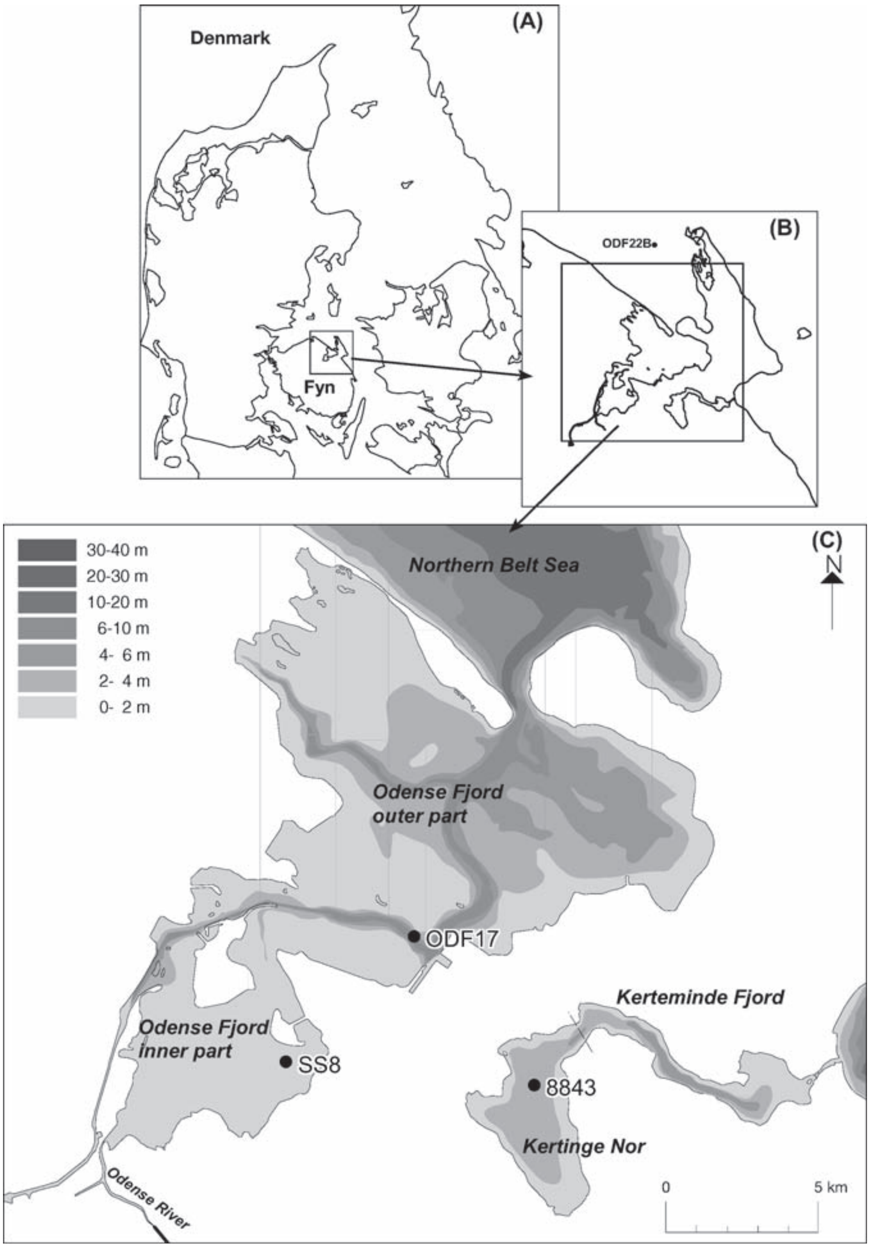

Fig. 16.1 **A** Map of Denmark. **B** Map of the north-eastern part of Fyn with station ODF22B in the Northern Belt Sea. **C** Odense Fjord with stations SS8 and ODF17, and Kerteminde Fjord/Kertinge Nor with station 8843

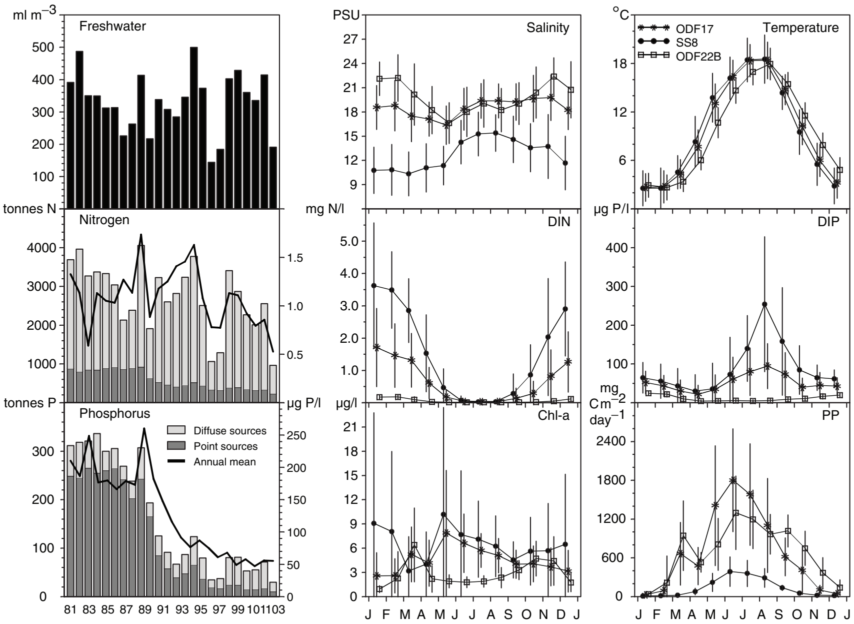

Fig. 16.2 *Left panels* Freshwater, nitrogen and phosphorus run-off to Odense Fjord and annual means of total nitrogen (*TN*) and total phosphorus (*TP*) at a mid-fjord station (ODF17) in Odense Fjord, 1980–2003. The nitrogen and phosphorus run-off are source-apportioned into point sources (mainly industrial and municipal waste water) and diffuse sources (mainly run-off from agricultural land). *Central and right panels* Temperature, salinity (psu), dissolved inorganic nitrogen (*DIN*), dissolved inorganic phosphate (*DIP*), chlorophyll-*a* (*Chl a*) and depth-integrated primary production (*PP*) in the inner fjord (SS8, 0.8 m depth), mid fjord (ODF17, 9 m) and in the bordering open sea (ODF22B, 17 m); data are monthly means ± SD (1989–2003) in surface water, except primary production (1998–2003)

little or no nutrient uptake by algae (Fig. 16.2). The low residence time of the water in the fjord, the large freshwater input, and the dynamic water exchange with the bordering sea create strong estuarine nutrient gradients in the fjord. Winter DIN concentrations are highest, at about 3,500 µg N l^{-1} in the inner fjord, decreasing to about 1,700 µg N l^{-1} in the outer fjord, and to about 130 µg N l^{-1} in the open sea (see Chap. 13 by Pitkänen et al., this volume). During summer, DIN is depleted both inside and outside Odense Fjord, but clearly for the shortest period in the nutrient-impacted inner fjord. Less pronounced winter gradients occur for dissolved inorganic phosphorus (DIP), from about 60 down to 20 µg P l^{-1} (Fig. 16.2). After a period of P-depletion in spring, the seasonal DIP peak occurs during June to October, reaching a maximum of about 250 µg P l^{-1} in the inner fjord and about 100 µg P l^{-1} in the outer fjord (Fig. 16.2). The increased phosphorous concentrations during summer are attributable mainly to the release of phosphorous bound to the oxidised iron pool when reducing conditions predominate during summer.

During the growth season, nutrient concentrations in Odense Fjord are potentially limiting for the phytoplankton (see Chap. 3 by Schiewer, this volume). The fjord is characterised by having more or less separated periods of potential P limitation (spring) and N limitation (summer) and no, or only very rare, potential silicate limitation (Fyn County 2003). This is based on concentration levels; experimental evidence (bioassays) confirms the N limitation during summer, whereas the limitation in spring is less clear but may be in the form of co-limitation by phosphate and silicate (M.H. Jensen et al., manuscript in preparation).

Nutrient and oxygen fluxes across the sediment surface (hence, internal nutrient loading and microphytobenthic photosynthesis) have been intensively studied in recent years by Fyn County. Benthic diatoms are present in almost the whole fjord, and could account for almost the same primary production as the pelagic primary producers on an annual basis (Fossing et al. 2005). In spring, microphytobenthic primary production (MPP) may contribute up to 75% of the total primary production (MPP + phytoplanktonic primary production, PPP) when increasing light conditions and nutrients from both the nutrient-rich water (Fig. 16.2) as well as the sediment below stimulate the growth of microphytobenthos. During the benthic diatom peak in spring, all nutrient fluxes – ammonium, nitrate, phosphate and silicate – are directed towards the sediment on a diurnal basis. However, during summer an increasing phytoplanktonic biomass absorbs most of the light entering the water column, causing MPP to decline so that by autumn PPP may contribute up to 80% of the total primary production (Fossing et al. 2005). In the growth season, the efflux of nutrients (N and P) can account for a minor part (roughly 10–15%) of the nutrient demand of the pelagic primary producers (Fossing et al. 2005). In terms of net primary productivity, however, the Odense Fjord sediment is heterotrophic on an annual basis (see Chap. 5 by Radziejewska and Schernewski, this volume).

Odense Fjord, especially the inner fjord, acts as a nitrogen sink in terms of the large amounts of nitrate that are loaded into the fjord from land during winter and spring, and because of microphytobenthic activity (temporary sink) and denitrification (permanent sink); the large number of bioturbating nereid polychaetes in the inner fjord clearly stimulates the latter, as is known from many studies (e.g. Kristensen et al. 1991). During summer, when mineralisation is high and macrozoobenthic grazing on diatoms is intensive and sediment oxygen availability therefore low, the nutrient fluxes are directed towards the water column; nitrogen occurs primarily in the form of mineralised ammonia but also as nitrate due to nitrification. Phosphate flux (evident as the summer peak in Fig. 16.2) occurs due of the gradual exhaustion of the oxidised iron pool.

Mass balance calculations using dynamic, deterministic modelling for the 1997–2003 period show that the annual nitrogen retention varies between 15 and 51% (mean 25%) of the nitrogen loaded into the fjord from land (Fyn County 2004); this is due primarily to denitrification as permanent burial is considered to be negligible. Phosphorus retention, however, is mostly negative (varying from balance, +4%, to −123%; mean −39%), i.e. more phosphorus is transported out of the fjord than is entering the fjord from land (Fyn County 2004); this is evidently due to the summer release from the sediment (Fig. 16.2) and can be ascribed to previously (pre-1990s) accumulated phosphorus pools. Both the highest nitrogen retention and highest negative phosphorus retention were found in the years with lowest rainfall

(1997 and 2003), and hence the lowest freshwater discharge. This is because the longer residence time of water in these years favours denitrification when nitrate concentrations are high in winter and spring, but also favours the exhaustion of the oxidised iron pool and the subsequent phosphorus release during summer due to lower oxygen availability.

16.2.4 Phytoplankton

The levels of chlorophyll-*a* (Chl *a*) are highest in the inner Odense Fjord and, as expected, decrease along the estuarine nutrient gradient (Fig. 16.2). Typically for fjords, the highest biomass is found during early summer, whereas a more traditional pattern is found in the open sea outside the fjords with biomass peaks in early spring and autumn (the very high winter chlorophyll peak in the shallow inner fjord is an "artefact", originating from macrophytes detritus and resuspended material). A more pronounced seasonal pattern is found for area-based primary production, the rates being lowest in the inner fjord due to the shallow depth (Fig. 16.2). The annual means of Chl *a* and primary production were about 16 and 20% lower in 2003 compared to 2002 (data not shown), due to the 2- to 3-times lower run-off and nutrient loads to the fjord in 2003 compared to 2002 (Fig. 16.2). This is a clear indication of the impact of the nutrient load on production patterns in Odense Fjord.

The phytoplankton community in Odense Fjord is dominated by diatoms [see Chaps. 3 (Schiewer), 7 (Kruk-Dowgiałło and Szaniawska), 10 (Kotta et al.) and 12 (Telesh et al.), this volume]. On an annual scale, 50–75 % of the phytoplankton carbon biomass and most blooms are due to diatoms, which is typical of eutrophicated fjords. Bloom-forming (e.g. $>200\,\mu g\ C\ l^{-1}$) species are e.g. *Skeletonema costatum*, *Proboscis alata* and potentially toxic species belonging to the *Pseudonitzschia* group complexes. The second largest group in terms of carbon biomass are normally nanoflagellates. However, blooms of dinoflagellates (e.g. *Prorocentrum minimum*) or more opportunistic species belonging to *Euglenophyceae* occasionally occur. Zooplankton has not been monitored regularly in Odense Fjord, but a study conducted by Fyn County in 2002 suggests that the most important grazers on phytoplankton [see Chaps. 3 (Schiewer), 5 (Radziejewska and Schernewski), 8 (Chubarenko and Margoński) and 12 (Telesh et al.), this volume] are calanoid copepods (e.g. *Acartia tonsa*) and heterotrophic ciliates (e.g. *Strombidium* spp., *Balanion* spp.). However, the biomass level of pelagic phytoplankton in Odense Fjord is relatively low, despite the high nutrient loads and high concentrations in the fjord. Furthermore, the seasonal development of the phytoplankton biomass is very dynamic, with rapidly shifting concentrations of Chl *a*. Besides the dynamic water exchange, a high biomass of zoobenthic filter-feeders, which may efficiently filter the phytoplankton from the water column, especially when the water is efficiently mixed by the wind (Riisgård et al. 2004), is a major factor responsible for the shifting concentrations of Chl *a* (see below). Thus, there is no clear (statistical) trend in Chl *a* in the fjord over a longer time scale despite the fact that the nutrient load reductions (Fig. 16.2) have caused an increasing number of days where nutrients are potentially limiting for pelagic phytoplankton production (Fyn County 2003).

16.2.5 Macrophytes

In the shallow Odense Fjord, with its abundant filter-feeding zoobenthos, the biomass of phytoplankton is determined by nutrients and grazing forces. Because grazing forces apparently prevail, this means that high nutrient loads result in only a limited response by phytoplankton biomass. Instead, a surplus of nutrients may increase the biomass of ephemeral macroalgae, such as the sea lettuce *Ulva lactuca* and horsehair seaweed *Chaetomorpha linum*, which are abundant in Odense Fjord during the summer [see Chaps. 3 (Schiewer; Schlei) and 4 (Schiewer; Salzhaff), this volume]. A surplus of nutrients is generally known to change the balance among autothrophic components from dominance of perennial algae and sea grasses toward dominance of ephemeral algae (Borum 1996; Schramm 1996; Nienhuis 1996; Pedersen and Borum 1997).

In the 1980s, *Ulva lactuca* especially, but also *Chaetomorpha linum*, appeared in large quantities in Odense Fjord. *U. lactuca* appeared in the inner part of the fjord with extremely high biomasses [about 1 kg dry weight (dw) m^{-2}] and with an annual production of about 1,000 t carbon, or twice the annual phytoplankton production in the same area. In the outer part of the fjord, filamentous algae, primarily *Cladophora* sp. and *Ectocarpus siliculosus*, appeared in quantities of 150–300 g dw m^{-2} in the 1980s (Fyn County 1991). The very high sea lettuce biomass caused large fluctuations in oxygen conditions and pH in the water, both on a daily basis and over longer periods during the summer. When the sea lettuce biomass decomposed, this was frequently accompanied by oxygen deficit and the release of hydrogen sulphide (HS^-) (Fyn County 1991), even in very shallow water. Oxygen deficiency and the presence of HS^-, together with the shading and physical disturbance from ephemeral algae, is known to reduce the viability of rooted macrophytes (Bonsdorff et al. 1997; Holmer and Bondgaard 2001; Plus et al. 2003; Greve et al. 2004). Accordingly, rooted macrophytes were almost absent from the inner part of the fjord in the 1980s (Fyn County 2003). Since then, especially the phosphorus and the summer nitrogen loads (and accordingly, the nutrient concentrations in the water column) have decreased (Fig. 16.2), coinciding with a decrease in the abundance of ephemeral macroalgae in the fjord. In particular, the biomass and coverage of sea lettuce have been markedly reduced in the inner Odense Fjord, and the biomass of filamentous algae in the outer fjord has been reduced to a low level, i.e. below 20 g dw m^{-2} (Fyn County 2004), while the abundance of perennial macroalgae such as bladder wrack (*Fucus vesiculosus*) and of rooted macrophytes such as eelgrass (*Zostera marina*) and widgeon grass (*Ruppia maritima*) have increased (Fyn County 1991, 2003). The macrophyte community in the fjord is still very unstable, and still exhibits large inter-annual variation in coverage. Eelgrass has virtually disappeared in the northwestern part of the outer Odense Fjord. Whereas in the mid-1990s there were dense stands, the overall eelgrass coverage there is now at an all-time low, at less than 7% of suitable bottom area (Fyn County 2003).

Historical data show a reduction of eelgrass-depth limit in the outer Odense Fjord from 6.7 m (Ostenfeld 1908) to 2.5 m during the past ca. 100 years, which is most likely linked to the general deterioration of the light climate in the fjord caused by eutrophication, in parallel to the general development observed in Danish and European shallow coastal waters (Schramm 1996; Nienhuis 1996; Nielsen et al. 2002). The decreasing sea lettuce biomass has provided more stable oxygen conditions in the inner Odense Fjord, and oxygen deficit and release of HS^- are now rare or absent in this area. In a study of the ability of sedimentary metal oxides to buffer against release of HS^- in an Odense Fjord muddy sand (Kristensen et al. 2003), it was found that oxygen depletion could last for at least a month before sulphide was released into the water, during which time about 25% of the total pools of manganese and iron disappeared.

The outer Odense Fjord still experiences occasional oxygen deficit, primarily as a result of a density-driven circulation caused by the intrusion of hypoxic bottom water from the area outside the fjord via the excavated fairway.

16.2.6 Benthic Filter-Feeders and Grazing Impact

Odense Fjord is characterised by a large biomass of filter feeding polychaetes (*Nereis diversicolor*), clams (*Mya arenaria*) and cockles (*Cerastoderma glaucum*), which together make up about 70% of the total animal biomass (Fyn County 2001b). Other species of bivalves in Odense Fjord are *Mytilus edulis*, *Macoma balthica*, *Scrobicularia plana*, and *Ensis* sp. (see Chap. 3 by Schiewer, this volume; Schlei).

The density of the facultative filter-feeder *Nereis diversicolor* (cf. Riisgård 1991; Riisgård and Kamermans 2001) especially is unusually high in the inner part of Odense Fjord, and therefore it has been assumed that *N. diversicolor* along with *Mya arenaria* and *Cerastoderma glaucum* play an essential role in the regulation of the biomass of phytoplankton in the inner part of the fjord. A recent study conducted by Riisgård et al. (2004) has thrown light on the grazing impact of the filter-feeding zoobenthos in Odense Fjord. Thus, the filtration rate of each population (F_{tot}) of *N. diversicolor*, *M. arenaria* and *C. glaucum* was related to the total water volume (V_{tot}) in the different areas of Odense Fjord and expressed as 'the grazing impact':

$$Q = V_{tot}/F_{tot} \tag{1}$$

which is related to the half-life time for phytoplankton by:

$$t_{1/2} = Q \text{ x In } 2 \tag{2}$$

representing the time to reduce the concentration by a factor of 2 in the water column above the filter-feeding populations, assuming efficient vertical mixing.

Nereis diversicolor was distributed evenly in the inner part of Odense Fjord, and the estimated area-specific population filtration rates (F_{pop}) of *N. diversicolor* are shown in Fig. 16.3. The mean value in the inner part was found to be $F_{pop} = 2.74 \pm 1.80\,m^3\,m^{-2}\,day^{-1}$. Further, it was found that $Q = 0.29$ days, and $t_{1/2} = 0.2$ days. In other words, *N. diversicolor* is able to filter a volume of water equivalent to the whole water mass in the inner part of the fjord about three times per day, and – under conditions of efficient vertical mixing – the worm may reduce the phytoplankton biomass by 50% within less than 5 h, assuming 100% retention. *Mya arenaria* was found on most stations in the inner part of the fjord, with higher densities in a belt running north–south along a channel extending from the Odense River and out through the fjord. *Cerastoderma glaucum* was found on 50% of the stations in the inner part of Odense Fjord, with highest densities along the channel extending northwards from the outlet of Odense River (Fig. 16.3). The total potential grazing impact of these three filter-feeding species combined, using $F_{tot} = \Sigma F_{pop}$, was estimated to be $Q = 0.17$ days, and $t_{1/2} = 0.12$ days, or less than 3 h.

However, a dense population of the amphipod *Corophium volutator* may further help to exert a pronounced grazing impact. *C. volutator* lives in a U-shaped semicircular tube in the sediment in shallow water. Like *Nereis diversicolor*, *C. volutator* has two feeding modes: (1) surface deposit feeding, and (2) filter feeding (cf. review by Riisgård and Kamermans 2001). During the latter, particles larger than about 7 µm are retained. The ability of *C. volutator* to filter suspended particles from the ambient water has recently been studied by Møller and Riisgård (2006), who made experimental measurements of water pumping and particle retention efficiency and used the data obtained to assess the potential grazing impact and the area-specific population filtration rate (F_{pop}), of a dense population (up to about 18,000 ind. m^{-2} in August) of this burrowing amphipod in the inner part of Odense Fjord. The potential grazing impact values of F_{pop} were 1 and $20.6\,m^3\,m^{-2}\,day^{-1}$ in January and July, respectively, and the estimated grazing impact varied between Q = 20 and 1 h, whereas the potential half-time varied between 14.5 and 0.7 h. These values indicated that *C. volutator* is able to filter a volume of water equivalent to the whole column about 25 times per day, and – under conditions of efficient vertical mixing – the amphipod may reduce the phytoplankton biomass by 50% within less than 0.7 h in June and July. However, it must be strongly emphasised that the estimated grazing impacts are potentials that may be realised only if a decisive prerequisite is fulfilled, namely that the filter-feeding animals on the bottom are exposed to the whole water column by effective vertical mixing of the water.

In the shallow inner part of Odense Fjord with a mean depth of only 0.8 m, the water may often be well mixed by wind action, but so far no systematic studies focusing on this aspect have been performed. On the other hand, it has previously been clearly demonstrated that, on calm days a phytoplankton-depleted near-bottom layer only 5–10 cm thick is established above a dense population of *N. diversicolor* (Vedel et al. 1994; Riisgård et al. 1996c; Vedel 1998). The thickness of this algal depleted layer is determined by the ability of the worms sitting in

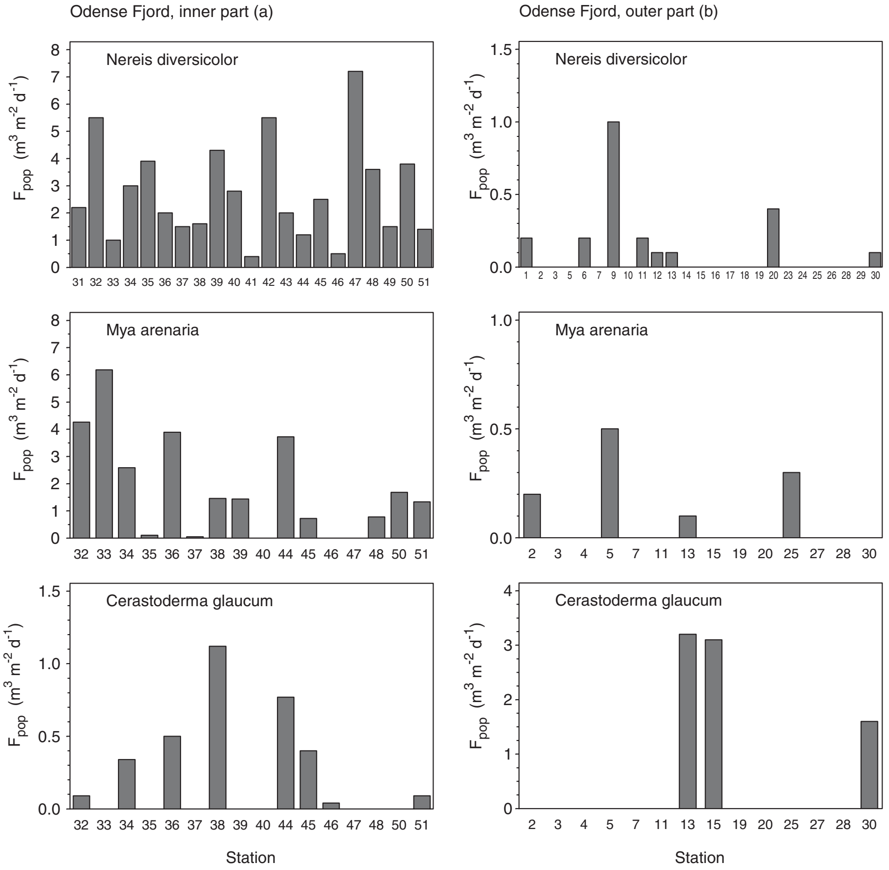

Fig. 16.3 Area-specific population filtration rates (F_{pop}) estimated for *Nereis diversicolor*, *Mya arenaria* and *Cerastoderma glaucum* in Odense Fjord. *Left panels* Inner part (stations 31 to 51); *right panels* outer part of fjord (stations 1–30). From Riisgård et al. (2004)

their U-shaped burrows to 'biomix' the overlaying water by means of their inhalant and exhalant feeding currents (Larsen and Riisgård 1997). The short residence time for phytoplankton can be as little as 3 h (with a generation time of about 1 day for larger species and ca. 6 h for very small species), showing that the filter-feeding zoobenthos may, on especially windy days, control the phytoplankton biomass in the inner part of Odense Fjord. It may therefore be predicted that, depending on the actual wind speed, the biomass of phytoplankton measured as Chl *a* may fluctuate strongly. Figure 16.4 illustrates that this is actually seen to be the case in the inner part of Odense Fjord, whereas the variation in Chl *a* at 17 m water depth outside the fjord is much less conspicuous (apart from the phytoplankton spring bloom in March). When the wind is weak, an 'uncoupling' of the benthic filter-feeders in the shallow Odense Fjord is likely to occur, which may contribute to triggering a rapid algal bloom in the overlying water. This phenomenon may be the reason for the very noticeable peak of Chl *a* in May during a long preceding period with generally decreasing wind speed (Fig. 16.4). In contrast, in windy weather the benthic filter will again be coupled, soon resulting in clear water.

As a consequence of intense zoobenthic grazing, surplus nitrogen released as ammonium in urine may subsequently accumulate in the ambient water, in particular if a grazing-reduced phytoplankton biomass simultaneously leads to a reduced assimilation of ammonium (NH_4^+) in the algal cells. To examine the possibility of increased grazing impact due to wind mixing subsequently leading to reduced Chl *a* and elevated ammonium concentrations, the actual concentrations of these substances (measured routinely by Fyn County in Odense Fjord) have been plotted as a function of wind speed (Riisgård et al. 2004). The slopes of the regression lines support the suggested causal connection, although the correlations are not strong because the actual fate of ammonium and Chl *a* are also determined by other factors.

More extensive field studies in Odense Fjord, involving time series of simultaneous measurements of vertical profiles of Chl *a*, wind-mixing of the water column above benthic filter feeders, and water current speed and direction, are now been carried out by the Marine Biological Research Centre in order to further investigate the suggested causal connections. Field studies are supplemented

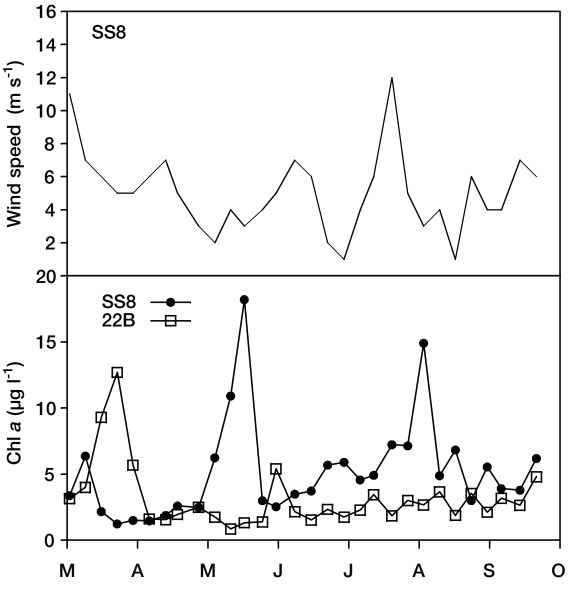

Fig. 16.4 *Upper panel* Variation in wind speed at station SS8 (water depth 0.8 m) in Odense Fjord from March to October 2000. *Lower panel* Variation in Chl *a* at station ODF22B (water depth 17 m) outside Odense Fjord compared to station SS8 (see Fig. 16.1). From Riisgård et al. (2004)

with underwater video observations of the filter-feeding zoobenthos. Preliminary results show that when the filter feeders are uncoupled, with an algal depleted near-bottom layer created soon after, this results in switching from a filter-feeding mode of nourishment to surface deposit feeding in *Nereis diversicolor* and *Corophium volutator* (Riisgård and Kamermans 2001; Møller and Riisgård 2006), whereas filter-feeding bivalves withdraw their siphons and close their valves (Riisgård et al. 2003).

16.2.7 Fish

In addition to Odense River, five streams flow into Odense Fjord, and several of these are important spawning and maturation sites for sea trout (*Salmo trutta*). During the last 25 years great efforts have been made to improve conditions for fish life, and fishing restrictions have been imposed. Recreational fishing of, primarily, eel (*Anguilla anguilla*) and flounder (*Platichthys flesus*) takes place by means of net, trap and fishing rod, but few professional fishermen operate in the fjord. Other species of fish in Odense Fjord are: *Belone belone* (garfish), *Gadus morhua* (cod), *Gobius niger* (black goby), *Pomatoschistus minutus* (spotted goby), *Zoarces viviparus* (viviparous blenny), *Syngnathus typhle* (greater pipefish), *Psetta maxima* (turbot), *Crenimugil labrosus* (thick-lipped grey mullet), *Salmo salar* (salmon), *Clupea harengus* (herring), *Trachurus trachurus* (horse mackerel), *Limanda limanda* (dab), *Pleuronectes platessa* (plaice), *Pungitius pungitius* (nine-spined stickleback), and *Gasterosteus aculeatus* (three-spined stickleback).

16.2.8 Impacts of Hazardous Substances

In Odense Fjord, hazardous substances occur in high and potentially toxic concentrations in the sediment, and for some compounds in such quantities that they may impact the flora and fauna in certain areas of the fjord (Fyn County 2004). This is true for compounds such as tributyltin (TBT) – for which concentrations in common mussels *Mytilus edulis* from Odense Fjord are 3–35 times higher than the ecotoxicological criteria endorsed by the Oslo-Paris Commission (OSPARCOM) – as well as for certain PAHs (polyaromatic hydrocarbons), PCBs (polychlorinated biphenyls) and others, but may also be true to a lesser extent for heavy metals such as copper, nickel and lead.

TBT may especially affect the biota in Odense Fjord. The Lindø Shipyard, located in the eastern part of the outer fjord, and traffic in the shipping lane are the major sources of TBT (Fyn County 2001a). Thus, Jensen et al. (2004) demonstrated a likely impact on *Ruppia maritima* in the inner Odense Fjord at ambient sediment concentrations of TBT. A conspicuously unfortunate effect of TBT is malformation of the genital systems in certain marine snails, e.g. the common periwinkle *Littorina littorea*, which seriously affects their ability to reproduce. In females, male sexual characteristics can develop (intersex), and in males, the penial glands are affected. Investigations have revealed that a large number of common periwinkles show such signs of being affected by TBT (Fyn County 2001a).

16.3 Case Study: Kerteminde Fjord/Kertinge Nor

16.3.1 Basic Characteristics

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 (Fig. 16.1). 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 tide gives rise to maximum discharges at the fjord entrance of 100–200 m^3 s^{-1}. The catchment areas to Kerteminde Fjord and Kertinge Nor are limited (1% of the island of Fyn), at 18.6 and 17.4 km^2, respectively, most of which is agricultural land and forests. The freshwater input of <0.05 m^3 s^{-1} is negligible with respect to the water exchange of the fjord system. The salinity in the central part of the system varies typically between 15 and 21 psu over the year, and the monthly mean temperature ranges between 2 and 18°C (Fig. 16.5).

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). Outflow of water from the Baltic Sea gives salinities down to less than 10 psu whereas inflow to the Baltic Sea gives salinities up to 27 psu in the upper layer of the Great Belt. Because saline water is more dense than fresh water the salinity variations cause longitudinal density variations from the inner part of the fjord system to the mouth, and density-driven vertical circulation occurs. When dense water is flushed over the sill by tidal forcing it will flow down below the fjord water and give rise to a density-driven 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 [see Chaps. 3 (Schiewer), 5 Radziejewska and Schernewski), 10 (Kotta et al.) and 12 (Telesh et al.), this volume], with an average of approximately 6 weeks (Jürgensen 1995). In Kertinge Nor – and similar localities characterised by low current velocities caused by density-driven currents and moderate tides – it should be emphasised that 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).

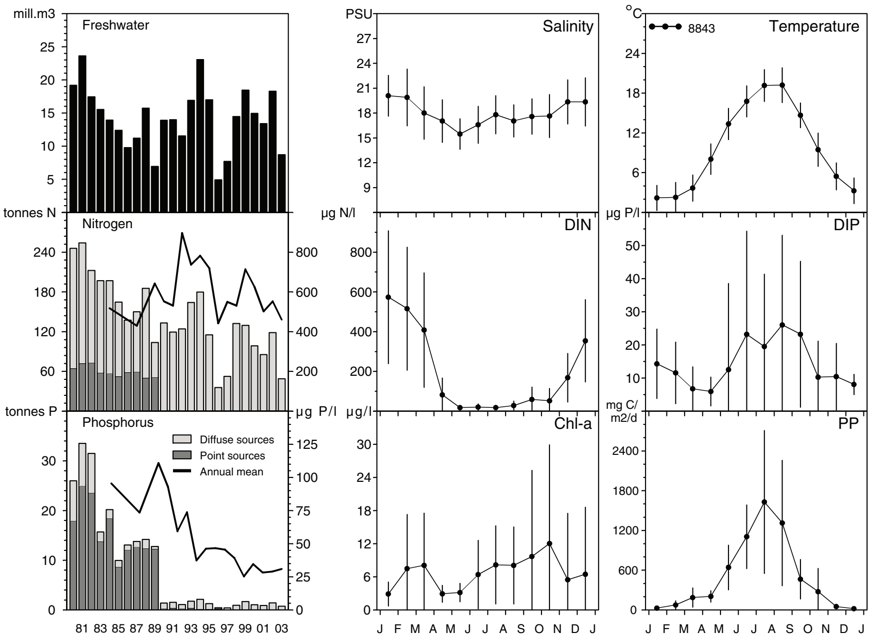

Fig. 16.5 *Left panels* Freshwater, nitrogen and phosphorus run-off to Kertinge Nor/Kerteminde Fjord and annual means of total nitrogen (*TN*) and phosphorous (*TP*) at station 8843 in the central part of Kertinge Nor, 1980–2003. The nitrogen and phosphorus run-off are source-apportioned into point sources (mainly industrial and municipal waste water) and diffuse sources (mainly run-off from agricultural land). *Central and right panels* Temperature, salinity (psu), dissolved inorganic nitrogen (DIN), dissolved inorganic phosphate (DIP), Chl-*a* and depth-integrated primary production (PP) at station 8843 (2.7 m); data are monthly means ± SD (1989–2003) in surface water, except primary production (1998–2003)

Sandy sediments dominate the Kerteminde Fjord/Kertinge Nor system (Miron and Kristensen 1993). The silt and clay fraction (mean particle diameter <63 µm) is usually under 7%, and percentages of particulate organic carbon (POC) are also low (<1.5%). Differences between localities are most conspicuous with respect to the pore water HS^- concentration, with the mussel-bed area near the mouth of Kerteminde Fjord having the highest HS^- concentrations.

16.3.2 Nutrients and Phytoplankton

The stoppage of the sewage outfall to the Kertinge Nor/Kerteminde Fjord system during the late 1980s meant that land-based nutrient loads fell markedly (Fig. 16.5). Thus, annual land-based discharges of nitrogen and phosphorus were reduced by 43% and 92%, respectively, as compared to mean values for 1976–1989 and 1990–

2003. Since 1990, the nutrient loads have been due almost solely to diffuse sources, which imply that they co-vary with the freshwater run-off (Fig. 16.5). 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, as the reduction obtained almost fulfilled the objectives of the first Danish Action Plan of the Aquatic Environment, the so-called APAE 1 from 1987 (Fyn County 2001a), of a 49% reduction in N and an 80% reduction in P.

The dramatic decrease in the P-load is clearly reflected in the annual means of phosphate in Kertinge Nor (Fig. 16.5). The decrease discernable for the N-load is less pronounced, and the actual annual load varies by more than 100% depending on the freshwater run off. The annual means of nitrogen in Kertinge Nor show large fluctuations and no temporal trend, but to some extent seem to follow the annual fluctuations in the N-load. This may reflect the fact that both the relative importance and the temporal changes in load are secondary. Thus, the inter-annual variations in N-load are still considerable, and the magnitude of the mean reduction is less than that of the P-reduction.

The mean seasonal variation in inorganic nutrients in Kertinge Nor is shown in Fig. 16.5. The seasonal variation in inorganic nitrogen is typical, with high concentrations during winter (up to ca. 600 µg N l^{-1}), and a progressive depletion of the pool with low concentrations, often potentially limiting for the phytoplankton, during summer. The inorganic phosphate concentrations peak during summer at about 25 µg P l^{-1}, when release from the sediment is high due to depletion of the oxidised iron pool to which the phosphate is bound.

There are generally two biomass peaks of phytoplankton in Kertinge Nor, as reflected in the seasonal Chl *a* cycle (Fig. 16.5): one in spring and one in late summer/autumn (see Chap. 4 by Schiewer, this volume). The seasonal primary production pattern is typically more distinct, with a clear peak in mid-summer (Fig. 16.5). This peak is displaced in relation to the later biomass peak, presumably reflecting grazing patterns (see below). There are no systematic recordings of phytoplankton species in the Kerteminde Fjord/Kertinge Nor fjord system, but sporadic blooms of e.g. dinoflagellates such as *Prorocentrum minimum*, and Prymnephyceae such as *Chrysochromulina parkae*, have been observed after nutrient release events triggered by oxygen-depletion.

16.3.3 Biological Structure and Nutrient Dynamics in Kertinge Nor

The combination of exceptionally clear water, a varied vegetation of rooted macrophytes (*Zostera marina*, *Potamogeton pectinaus*, *Zannichellia palustris* and *Ruppia* sp.) and periodic thick mats of filamentous algae (primarily *Chaetomorpha linum* and *Cladophora sericea*) with biomasses of 50–100 g dw m^{-2} (Fyn County 1991), high densities of small jellyfish (*Aurelia aurita*), and a dense population of benthic ascidians (*Ciona intestinalis*) makes the cove Kertinge Nor interesting for studying the dynamics of the biological structure in an eutrophic ecosystem, in which nutrient fluxes and suspension-feeding organisms play a decisive role.

Plankton dynamics are at times governed by the interplay between filter feeders and hydrodynamics, especially density-driven currents. This is especially true in the Kertinge Nor/Kerteminde Fjord system (Riisgård et al. 1996a; Riisgård 1998). Attention must be paid to these phenomena in order to understand the dynamic behaviour of Danish fjords and coastal areas that are influenced by the water exchange between the Baltic Sea and the North Sea.

16.3.3.1 'Normal Years'

The biological structure of the Kertinge Nor ecosystem in a 'normal year' is summarised in Fig. 16.6. The water column is clear, allowing sufficient light penetration to the bottom where a significant benthic primary production of filamentous algae and eelgrass may be found (see Chap. 4 by Schiewer, this volume; Salzhaff). The algal mat is important for the control of nutrient flux from the sediment to the water column, and in the spring and summer period N and P concentrations often drop below potentially limiting levels for phytoplankton production (i.e. about 2 µm DIN and 0.2 µmol DIP) (Fyn County 2004). Below the algal mat, the sediment is black and sulphidic due to anoxic conditions and lack of living animals. A dense population of filter-feeding ascidians (*Ciona intestinalis*) keep the water clear, and a large number of small, maximum diameter 4–6 cm, umbrella jellyfish (*Aurelia aurita*), dominate the water column.

During summer, the water processing capacity of the many (up to ca. 250–300 ind. m^{-3} in April–June) small *Aurelia aurita* is very high, with a maximum rate attained in early September, where the jellyfish population can daily process a water volume corresponding to approximately 10–15 times the whole water volume of Kertinge Nor (Olesen et al. 1994). This indicates that *A. aurita* controls zooplankton in the cove during summer and autumn. Laboratory experiments have proved that the medusae are food-limited at in situ zooplankton concentrations. Moreover, *A. aurita* is presumably growing in excess of its food source, as zooplankton densities in the water column of Kertinge Nor during the day cannot explain the observed growth of *A. aurita*. It has been observed, however, that the density of harpacticoids in the water column at night can exceed the density during the day by a factor of 20, and night-swimming harpacticoids may therefore be an important food source for jellyfish in Kertinge Nor (Olesen et al. 1994; Olesen 1995; Nielsen et al. 1997).

The dense population of the filter-feeding *Ciona intestinalis* exerts a high grazing pressure on phytoplankton, which may partly explain the low observed phytoplankton biomass. In particular, during late summer and autumn, the *Ciona* population can reach densities of approximately 250 ind m^{-2}. During fall, the population of *C. intestinalis* usually has the potential capacity to filter the total water volume of Kertinge Nor 0.2–1.2 times daily, and the mean residence time of an algal cell in the water column in September may only be about 7 h (Petersen and Riisgård 1992). From previous data and observations, the 'normal' summer situation for the

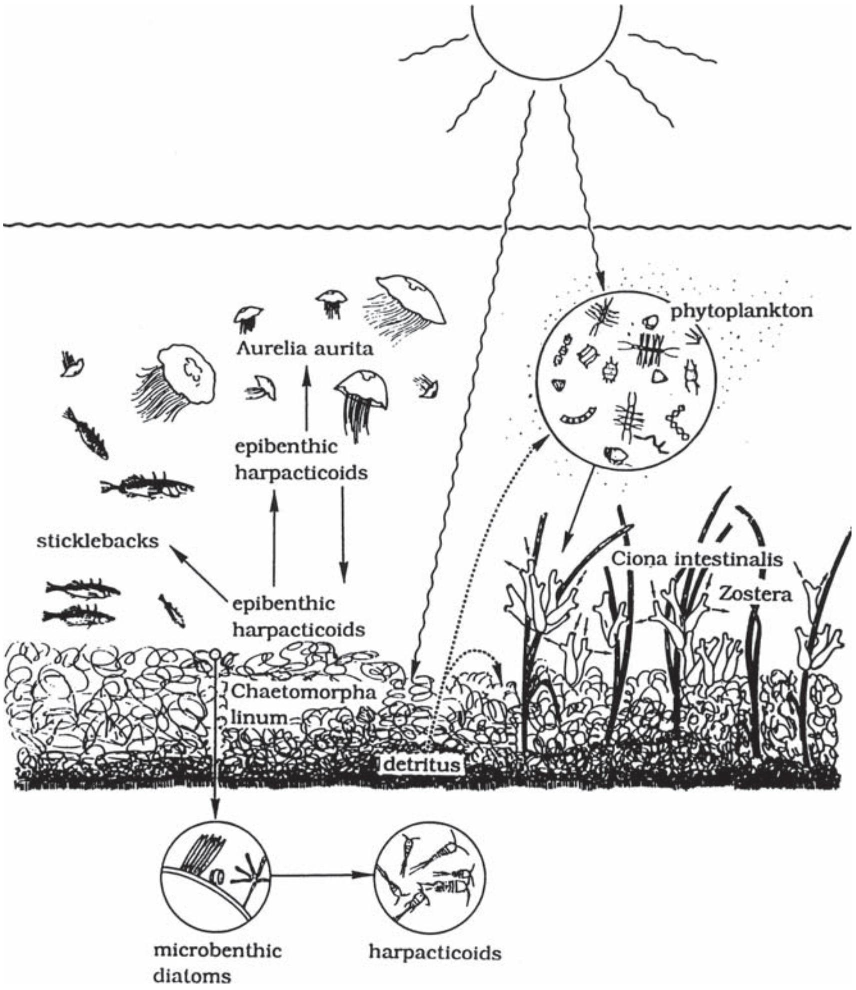

Fig. 16.6 Biological structure in 1991 ('normal year') in Kertinge Nor. Three food-chains were identified: (1) phytoplankton → ascidians (*Ciona intestinalis*); (2) epiphytic diatoms → epibenthic harpacticoids → jellyfish (*Aurelia aurita*) + sticklebacks; (3) macrophytes → detritus → decomposing microorganisms. From Riisgård et al. (1994b)

biological structure and dynamic of Kertinge Nor outlined above prevails, but the ecosystem is inherently unstable.

16.3.3.2 The 'Unusual Year': 1992

As explained above, the water column of Kertinge Nor is usually very clear, and Chl *a* concentrations are low throughout the growth season, but this situation can change dramatically as observed in 1992 where the 'normal' situation existed only until June.

A high biomass of the filamentous macroalga *Chaetomorpha linum* was recorded on the bottom throughout the year (mats up to 40 cm thick during the summer). The filamentous algal production was limited by the availability of N, and the algal mat therefore controlled the release of inorganic N from the sediment (Christensen et al. 1994). This 'normal' situation existed for Kertinge Nor until June, but a long period of calm clear weather with high insolation began in the middle of May and persisted for about 2 months. This caused a high primary production of the filamentous algal mat, which led to the formation of large oxygen bubbles that caused parts of the whole algal mat to float up and away from the sediment to the water surface (Christensen et al. 1994). In this position the filamentous algal mat could no longer act as an absorbing filter for the nutrient flux from the underlying anoxic sediment and large amounts of nutrients were released to the water column. The phytoplankton population immediately responded to the elevated nutrient concentrations. Within a week, in areas where the algal mat was more or less separate from the sediment surface, the phytoplankton biomass increased 80 times due to photosynthetic activity (Christensen et al. 1994). During June 1992, the phytoplankton biomass increased almost exponentially, which reduced the light penetration depth into the water to only 30 cm. This massive shading effect caused a total collapse of the remaining benthic algal mats and, from August, *Chaetomorpha linum* disappeared from Kertinge Nor (Fig. 16.7). The growth of eelgrass also decreased (see Chap. 3 by Schiewer, this volume). This enabled a constant high flux of nutrients from the sediment, and extremely high Chl *a* concentrations were measured in October. During June 1992, the parent generation of *Ciona intestinalis* died off (due to its natural life cycle) and

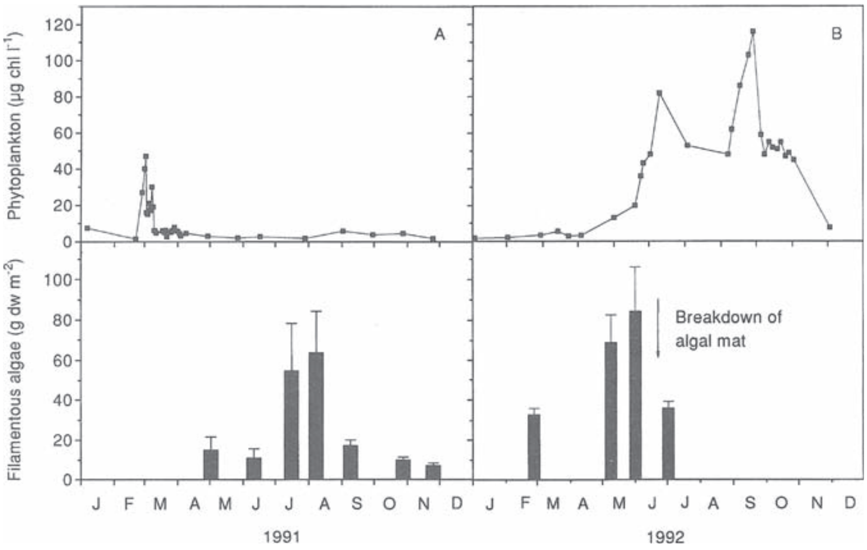

Fig. 16.7 Chlorophyll-*a* concentration and biomass of filamentous algae in Kertinge Nor during 1991 (**A**) and 1992 (**B**). From August and throughout the remaining part of 1992, filamentous algae were absent in Kertinge Nor. From Riisgård et al. (1995)

the filtration capacity of the ascidian population was low at the end of June to the beginning of July because only newly settled specimens were present. The decline in filtration capacity coincided with the increasing phytoplankton biomass. In July, algal cell concentrations exceeded optimum concentrations for filtration, and *C. intestinalis* became saturated and subsequently reduced its filtration rate to a minimum of its potential capacity (Petersen and Riisgård 1992). *C. intestinalis* did not, therefore, control phytoplankton during the summer and autumn of 1992 in Kertinge Nor. However, the marked change in primary producers had no significant influence on the jellyfish population, and the high predation rate prevented the meso-zooplankton from increasing in numbers in response to the increased phytoplankton biomass. Thus, even during extreme situations with Chl *a* concentrations of up to $120\,\mu g\ l^{-1}$, the *Aurelia aurita* population had an important controlling impact on the zooplankton density.

The pelagic biomass levels and the successions of plankton species were similar during the spring periods of 1991 and 1992, but developments were very different during the two summer and autumn periods (Fig. 16.7). In 1991, auto- and heterotrophic biomasses were low and dominated by diatoms and dinophyceans as well as ciliates, rotifers and epibenthic harpacticoids. In 1992 the biomass of phytoplankton was exceptionally high. At the beginning of that period the autotrophic biomass was dominated by the diatoms *Skeletonema costatum* and *Stephanodiscus hantzschii*. The diatom bloom was succeeded by a bloom of small Cyanobacteria that lasted until the end of November. The heterotrophic biomass was dominated by ciliates at the beginning of the period, but was later succeeded by heterotrophic dinoflagellates appearing in very high biomasses (Riisgård et al. 1996a).

16.3.3.3 Impact of Chaetomorpha linum Mats

Krause-Jensen et al. (1996) studied the productivity of dense mats of *Chaetomorpha linum* in Kertinge Nor in relation to the vertical gradients of light and nutrient availability created within the mats. This was done by incubating a 15 cm dense mat of *C. linum* in the laboratory at low and high surface irradiance, and simultaneously simulating the nutrient efflux from the anoxic sediment by pumping nutrients up through the mat. The algal activity resulted in steep vertical gradients in O_2 and NH_4^+ concentration profiles within the mats. In the light, O_2 production caused supersaturation in the surface layers, and algal assimilation significantly reduced the flux of nutrients to the water column. The depth gradients of decreasing light and increasing nutrient availability within the mat suggested light limitation in the bottom of the mat, and progressive N limitation towards the mat surface. Algal productivity declined with depth in the mats, reflecting a pronounced self-shading, and the depth of 1% surface irradiance was only 8 cm. Krause-Jensen et al. (1996) found that filamentous macroalgal mats can switch from being net productive to a status where consumption exceeds production, and it was concluded that reduced irradiance and high water temperature may trigger such shifts in a macroalgal-dominated ecosystem. In similar studies, McGlathery et al. (1997) found that the patterns of ammonium uptake within dense mats of actively growing *C. linum* can efficiently restrict benthic nutrient inputs to the overlying water and thus reduce nutrient availability to a level that may limit phytoplankton production.

16.3.3.4 Ecosystem Stability

It may be concluded that Kertinge Nor is an inherently unstable eutrophic ecosystem in which interactions between suspension-feeding organisms and mobilisation of nutrients from the sediment determine the dynamics of the biological structure. The instability of the system blurs the possible effects of the significant reduction in nutrient discharge to the fjord system by the end of 1989. Since 1992, mats of filamentous algae (*Chaetomorpha linum* and *Cladophora sericea*) have frequently been observed in Kertinge Nor, but not to the same extent as in 1992 (Fyn County 2004), while the number of both ascidians and jellyfish do not seem to have not changed since then. During summer periods with calm and warm weather, sporadic incidents of oxygen depletion and macroalgae up-floating and subsequent decay followed by nutrient release from the bottom and subsequent local algal blooms may still – at least for a certain period of time – change the ‘normal’ clear water into green water, as e.g. observed in 2001 (Fyn County 2002).

16.3.4 Implications of Density-Driven Currents for Predation Impact by Jellyfish

In Kertinge Nor, the maximum diameter of the umbrella of *Aurelia aurita* is usually only a few centimetres, although high abundances of such small jellyfish (up to several hundred per cubic metre of water) control the zooplankton biomass (Olesen et al. 1994; Riisgård et al. 1995; Frandsen and Riisgård 1997). The implications of density-driven currents for the interaction between *Aurelia aurita* and zooplankton, and thus the phytoplankton, were studied in the Kertinge Nor by Nielsen et al. (1997). It was found that the local population of jellyfish is highly influenced by the density-driven circulation created by the frequent salinity changes in the adjacent Great Belt. When new water of either higher or lower salinity enters the fjord, changes in the jellyfish distribution are apparent. The time it takes for the jellyfish to enter a new water mass of higher or lower salinity has been found to be dependent on the degree of changes in salinity. In laboratory experiments, Nielsen et al. (1997) found that the adaptation time for equilibrium buoyancy and normal swimming of the jellyfish is directly proportional to the salinity difference. Osmo-conforming times of 2–4 h were found for the salinity gradients of 2–4 psu typically measured in the fjord. Further, the number and distribution of zooplankton was found to be highly influenced by the presence of jellyfish. The disappearance of incoming holoplanktonic copepods from the Great Belt occurred simultaneously with the conquest of the new water mass by the jellyfish (Fig. 16.8). The filtering activity of the *A. aurita* population was able to keep the zooplankton biomass low (mean residence time of a zooplankton organism varied between 10 and 20 h), and negligible zooplankton grazing explains why the Chl *a* concentration can increase markedly during a few days of rapid growth when the benthic filter feeding *Ciona intestinalis* is uncoupled due to stratification (see Riisgård et al. 1996b, 1998). 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).

16.3.5 Density-Driven Currents and Grazing Impact of Filter-Feeding Benthos

The realisation of the benthic filter feeders grazing potential is highly dependent on currents and mixing of the overlying water. Grazing impact is enhanced by the turbulent mixing of the water mass due to wind-, wave- and current action, coupling the benthic filter feeders to the pelagic biomasses. However, the grazing of *Ciona intestinalis* in Kertinge Nor may be restricted by the stratification of the water body caused by salinity differences, as frequently seen in the Great Belt. The stratification

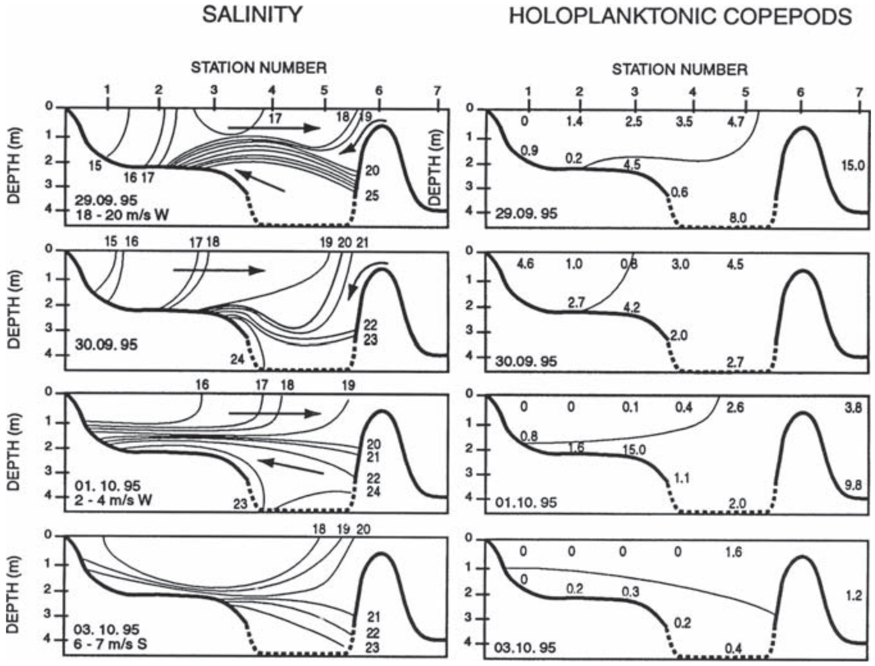

Fig. 16.8 Hydrographical situations (sketches on *left*) and the biomasses (µg C l^{-1}) of holoplanktonic copepods (*right*) on 4 days between 29 September 1995 and 3 October 1995. Wind speed and direction is indicated, and *arrows* show the direction of density-driven water circulation in the fjord. From Nielsen et al. (1997)

reduces, or even prevents, the supply of algae across the interface, decoupling the benthic filter feeders from the pelagic biomass. Thus, a key to the understanding of spatial and time dependent variations in pelagic biomasses is a knowledge of the circumstances under which coupling/decoupling of zoobenthic filter feeding take place. The hydrodynamic conditions in Kertinge Nor have been studied in detail by Riisgård et al. (1996b, 1998). The main focus of these studies was on the importance of density-driven currents in determining the grazing impact of *C. intestinalis*. Thus, it was observed that the grazing behaviour of *C. intestinalis* may at times be restricted to a boundary-layer flow created by these currents, which are in turn controlled by varying hydrographic conditions in the surrounding open sea (Fig. 16.9). It was shown that the grazing impact caused by ascidians on horizontally flowing water could be described by means of a simple numerical model. A satisfactory agreement between observations and modelled predictions emphasised the importance of filter-feeding benthos. For the idealised case, the model is expressed by the equation (Riisgård et al. 1996b):

$$Cx = C_0 e^{--(fx/Y)} \tag{3}$$

where C_x = algal concentration at a distance downstream x, C_0 = initial concentration, $f = F/v_c$; F = area specific population filtration rate of filter-feeding benthos, v_c = current velocity; and Y = depth of mixed bottom layer. The above equation illustrates how the algal concentration decreases as a function of dimensionless scales for velocity and length.

The velocity of density-driven currents, as well as the importance of tidal currents and wind-mixing, for the supply of phytoplankton to the filter feeding *Ciona intestinalis* in Kertinge Nor was studied by Riisgård et al. (1998). The aim was to examine the dynamic interactions between the water column and benthic filter

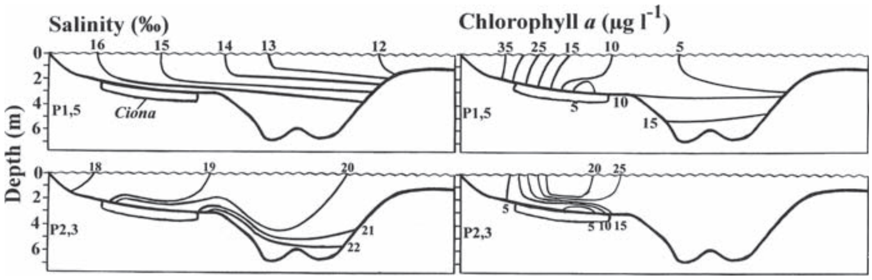

Fig. 16.9 Iso-lines for salinity and Chl *a* in Kerteminde Fjord/Kertinge Nor on two separate days (P1,5 and P2,3) in late summer 1994. The area populated with *Ciona intestinalis* in Kertinge Nor is indicated. On the first day, salinity observations (*upper left*) suggest that a 0.5 m-thick near-bottom density-driven current was flowing northwards along the bottom. The upstream Chl *a* concentration, measured to be 36 µg l^{-1}, was reduced to a downstream concentration of 5 µg l^{-1} by passing over the *C. intestinalis* bed. On the 2nd day (*lower panels*), no density-driven current was detected. The stratification, which uncoupled the benthic filter feeders, caused low Chl-*a* concentrations in the near-bottom water. However, above the halocline, a phytoplankton bloom was developing. From Riisgård et al. (1996b)

feeders in order to account for the variability of phytoplankton biomass seen in the fjord. The moderate tidal- and density-driven near-bottom currents were both estimated and directly measured by means of an underwater-video technique, and the downstream reduction in algal concentration over the ascidian bed was both measured and modelled by means of Eq. 3.

Riisgård et al. (1998) undertook a number of cruises in Kerteminde Fjord/Kertinge Nor during 1995 in order to measure salinity profiles. Over the whole investigation period, the number of clockwise and anti-clockwise circulations were almost the same, and the incidence of salinity stratifications (i.e. salinity differences > 0.2 psu between surface and bottom) in Kertinge Nor was about 50%. In September 1995, during a pronounced density-driven circulation, 'extended' cruises were performed, including collection of water samples for Chl *a* measurement. The Chl *a* concentrations in the near-bottom water above the *Ciona* bed were lower than in the upper layer, and Riisgård et al. (1998) suggested that the relatively high algal concentrations developing in the surface layers during stratification were available to the benthic grazers only if a density-driven circulation carried these algae down to the bottom. It was concluded that, although wind is a crucial force for vertical mixing and transport of phytoplankton to the bottom, the frequent salinity changes in the Great Belt give rise to density-driven currents of considerable importance for the nourishment of the filter-feeding benthos in Kertinge Nor.

Food consumption of benthic filter feeders is, in general, dependent on currents in the benthic boundary layer. In some cases, for example in calm weather or in waters characterised by very moderate tidal currents (e.g. the diurnal tide is only 0.2 m in Kertinge Nor), the near-bottom current speed may be slow: $<0.001\,\text{m s}^{-1}$. Near-bottom vertical profiles of phytoplankton caused by a dense population of filter-feeding *Nereis diversicolor* in the southernmost part of Kertinge Nor have been observed in the field by Riisgård et al. (1996c). Water samples were collected simultaneously at different heights above the bottom where *N. diversicolor* were present, and it appeared that a phytoplankton-reduced near-bottom water layer of 0.05–0.1 m in thickness developed on calm days. That such a depletion of phytoplankton in near-bottom waters plays a significant role for this worm was demonstrated in field-growth experiments performed with worms transferred to glass tubes placed at different heights above the bottom (Riisgård et al. 1996c). A reduction in growth rate of bottom dwelling *N. diversicolor* of around 10 times compared with that of worms elevated just 0.1 m above the sediment surface indicates that extremely meagre food conditions are prevalent near the seafloor.

16.3.6 Biogeochemistry, Microphytobenthos and Macrozoobenthos

The distribution of the three nereid polychaetes *Nereis virens*, *N. diversicolor* and *N. succinea* between the shoreline and 1 m water depth in Kerteminde Fjord/Kertinge Nor was studied during the autumn of 1991 by Miron and Kristensen

(1993). The results suggested that pore water sulphide produced during sulphate reduction – the major anaerobic mineralisation process in the sediment – acts on the distribution of these species. *N. virens* was confined to low-sulfidic areas (<50 µM) and was found throughout most of the fjord system, with highest densities (>500 ind. m^{-2}) in the western part of Kertinge Nor. *N. succinea* was found in high-sulfidic sediments (from 50 to 2,000 µM) of the dense bed of mussels (*Mytilus edulis*) near the mouth of Kerteminde Fjord; *N. diversicolor* showed a broader distribution with respect to pore water sulfide and was found mainly in the southern and eastern part of Kertinge Nor.

The impact of the non-suspension-feeding *Nereis virens* and the facultative suspension-feeding *N. diversicolor* on C and N dynamics in organic-poor sediment from the innermost part of Kertinge Nor was investigated in the laboratory by Christensen et al. (2000). It was found that the oxygen consumption and DIN release were increased by a factor of 3 in sediment with *N. diversicolor*, but only by a factor of 1.5 in sediment with *N. virens*, and the deposition of particulate C and N to the sediment was up to 30 times higher in sediments inhabited by the much more actively water pumping *N. diversicolor* (see also review by Riisgård and Larsen 2005).

Rysgaard et al. (1995) studied seasonal variations in oxygen and nutrient fluxes, and denitrification in the shallow (0.5 m) southernmost part of Kertinge Nor, which has sandy sediment colonised by benthic microalgae and burrowing zoobenthos. Oxygen dynamics in the upper sediment layers were controlled by the microalgae and there was a net flux of O_2 out of the sediment during spring and autumn and a reduced efflux of NH_4^+ and PO_4^{3-} from the sediment to the water during daytime. Denitrification based on NO_3^- from the water column (D_w) occurred only in winter and spring – when NO_3^- was present in the water column – and activity was proportional to the water column NO_3^- concentration. Coupled nitrification–denitrification (D_n) in the sediment was stimulated by O_2 production during winter and spring, at which times NO_3^- and NH_4^+ were present in the water column in high concentrations. In contrast, during summer, when the concentration of NO_3^- and NH_4^+ in the water column was low, benthic microalgae inhibited D_n by competing with nitrifying bacteria for NH_4^+. D_w accounted for 80% of the total denitrification during winter, while on an annual basis, D_w and D_n each accounted for 50% of the total denitrification activity. Oxygen consumption, D_w and D_n were linearly correlated with the density of *Corophium volutator*, and all the processes studied were stimulated by the water-pumping zoobenthos. But, because the concentration of inorganic nitrogen in the overlying water and the sediment nitrification potential were both low during summer when zoobenthic density is high, Rysgaard et al. (1995) concluded that the stimulatory effect of burrowing, water-pumping zoobenthos is of minor importance to the annual denitrification budget in Kertinge Nor. Impacts of bioturbating zoobenthos (*Nereis diversicolor*, *Corophium volutator*, *Hydrobia* spp.) on sediment metabolism and nutrient fluxes in different Kertinge Nor sediments were also studied by Hansen and Kristensen (1997).

16.3.7 Fish

Around 16 species of fish have been recorded in Kerteminde Fjord/Kertinge Nor (Larsen et al. 1994). A number of fish species are found only, or mainly, in Kerteminde Fjord: *Clupea harengus* (herring), *Salmo trutta* (sea trout), *Syngnathus typhle* (pipefish), *Solea solea* (sole), *Platichtys fleses* (flounder), *Merlangius merlangus* (whiting), *Sprattus sprattus* (sprat). Other species of fish are found mainly in Kertinge Nor: *Gasterosteus aculeatus* (three-spined stickleback), *Pungitius pungitus* (nine-spined stickleback), *Myoxocephalus scorpius* (short-horn sculpin), *Perca fluviatilis* (perch), and some fish species occur in the whole fjord system, e.g. *Anguilla anguilla* (eel), *Hyperoplus lanceolatus* (sand eel), *Zoarces viviparus* (viviparous blenny), *Pomatoschistus microps* (clay goby), *Gobis niger* (black goby).

The dominating species in Kertinge Nor are three- and nine-spined stickleback. Due to their very high numbers, especially of three-spined sticklebacks, they have been suggested to play an important ecological role in Kertinge Nor, where they compete with jellyfish for zooplankton (Fig. 16.6). Only a few part-time fisherman catch fish, mainly eel (and shrimp), in the fjord system but no official fishing statistics exist.

16.4 Odense Fjord and Kerteminde Fjord/Kertinge Nor: Protection Measures and Environmental Objectives

16.4.1 International Protection Measures

The European Union (EU) Water Framework Directive encompasses all surface waters, stipulating that all water bodies will have to fulfill “good ecological status” by 2015, meaning that only slight deviations from undisturbed conditions will be acceptable. The whole of the inner Odense Fjord and the western part of the outer fjord has been designated as an international nature protection area – Natura 2000 site – according to the EU “Habitats” and the “Birds” directives. In these areas, “good preservational status” must be achieved for the species and habitat types selected following the directives. In Denmark, the whole country has been designated as nutrient-sensitive area due to the “Nitrates” and “Urban Waste Water” directives, meaning that outlets from point sources and diffuse sources to all surface waters are basically regulated by national measures pursuant to these directives, i.e the Aquatic Action Plans I, II and III. No areas of the fjord are highlighted for protection following the “Bathing Water” or “Shellfish” directives. The international Helsinki Convention encompasses the Baltic Sea and adjacent fjord areas, and thus includes Odense Fjord and Kerteminde Fjord/Kertinge Nor. The ministerial declaration of the Convention aims at a 50% reduction in nutrient outlets and a ‘generation target’ of reducing outlets of hazardous substances to near zero.

16.4.2 National Protection Measures

In Denmark, the water quality of coastal waters is administered at the regional political and administrative level, i.e. the counties, through a Regional Plan that is revised every 4 years. In this plan, the objectives of water quality, and measures to protect and enhance water quality, are decided politically. Due to the natural qualities of Odense Fjord and Kertinge Nor, the northwestern part of Odense Fjord and Kertinge Nor have been designated as “reference areas for scientific studies” (stringent quality objective) in Fyn County’s Regional Plan for 2001–2013. The quality objective for the remainder of the fjord is “fish waters for angling and/or fishery” and, where natural conditions permit, “spawning and/or nursery grounds for fish” (general/basic quality objective). The fjord is also encompassed by a number of other national and regional protection regulations, focusing especially on the impact of public access, hunting and fishing.

Denmark as a nation has been progressive with respect to the introduction of legislation designed to reduce eutrophication. In 1987, measures were adopted to reduce nitrogen and phosphorus input to the sea by 50 and 80%, respectively, within the following 5 years (Richardson 1996). The goals with respect to phosphorus reduction and nitrogen reduction from wastewater treatment were indeed met on time (see Fig. 16.2). But the desired reduction in runoff of nitrogen from agricultural land and the ecological quality objectives defined for the coastal waters have not yet been fulfilled (Rask et al. 1999; Iversen et al. 1998; Conley et al. 2000; Ærtebjerg et al. 2003). New measures are thus being considered for the purpose of further reducing, primarily, the run off from diffuse sources (agriculture and scattered dwellings), in order to also fulfill international requirements pursuant to e.g. the Water Framework directive, and the Birds and Habitat directives. This reduction demand on nitrogen is considered to be important for the marine environment because nitrogen is the primary limiting nutrient in Danish coastal waters, as is most pronounced in open areas (Ærtebjerg et al. 2003). A close connection between nitrogen concentration and phytoplankton biomass may therefore be expected. The median phytoplankton biomass in Danish fjords and coastal waters is about 5 μg Chl *a* l^{-1} and the biomass is coupled to the total nitrogen concentration (Sand-Jensen et al. 1994). During the summer period, total nitrogen concentrations can account for about 60% of the variability in Chl *a* concentrations (Sand-Jensen et al. 1994). The remaining 40% variation, however, is likely to be due to the complicated interplay between hydrography and filter-feeding zoobenthos, and nutrient competition with ephemeral macroalgae, etc. as demonstrated for Odense Fjord and Kertinge Nor in the present case study. Knowledge about the interactions between currents, wind- and biomixing, density-driven circulation, macrophytes and filter-feeding animals, may explain the otherwise unaccountable large variations in phytoplankton biomass. Such insight is of great importance for marine monitoring programmes using Chl *a* as a parameter in the assessment of environmental conditions.

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