

REGIME SHIFT IN A COASTAL MARINE ECOSYSTEM

JENS KJERULF PETERSEN,^{1,5} JENS WÜRLER HANSEN,² MARTHA BROGAARD LAURSEN,² PREBEN CLAUSEN,³
JACOB CARSTENSEN,¹ AND DANIEL J. CONLEY^{1,4}

¹Department of Marine Ecology, National Environmental Research Institute, University of Aarhus, P.O. Box 358,
Frederiksborgvej 399, DK-4000 Roskilde, Denmark

²Marine Group, Environment Centre Ringkøbing, Holstebrovej 31, DK- 6950 Ringkøbing, Denmark

³Department of Wildlife Ecology and Biodiversity, National Environmental Research Institute, University of Aarhus,
Grenåvej 14, DK-8410 Rønde, Denmark

⁴Geobiosphere Science Centre, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden

Abstract. We demonstrate changes in ecosystem stable states in a coastal lagoon that are consistent with what a regime shift would hypothesize. In the nutrient-stressed Ringkøbing Fjord, Denmark, a small change in one variable (salinity) facilitated by a change in sluice management, caused a sudden regime shift from a bottom-up controlled turbid state, into a top-down controlled clear-water state. The change in dominating pathway of organic matter production from pelagic turnover to benthic-pelagic coupling was facilitated by new recruitment and growth of existing suspension-feeding clams, *Mya arenaria*. With the invasion of clams, benthic grazing became the key feature of the biological structure. Phytoplankton composition and zooplankton abundance were also affected by the change in biological structure. The small, but sudden, increase in salinity caused by the change in sluice management led to a dramatic reduction in biomass and coverage of benthic vegetation and thus affected herbivorous waterbird populations. In recent years, plant coverage has been increasing, as can be expected with increased water transparency. The regime shift has some major implications for coastal water management and revealed some conflicts between different types of nature and environmental protection legislation.

Key words: benthic vegetation; biological structure; coastal lagoon; herbivorous waterbirds; marine; regime shift; suspension feeding.

INTRODUCTION

Ecosystem change in relation to changing conditions is generally considered to be smooth with one stable state for each set of conditions. However, ecosystems may switch abruptly to alternative stable states. Ecosystem management is to a wide extent governed by the paradigm of smoothly changing ecosystems and that reductions in ecosystem pressures will lead to foreseeable improvements in ecosystem health. Thus, abrupt changes are not just a problem from an ecological point of view; they also present a management challenge.

Abrupt shifts in ecosystem stable states have been demonstrated in a number of different terrestrial, freshwater, and marine systems (Scheffer et al. 2001, Scheffer and Carpenter 2003). Such sudden changes between states may more reasonably be termed regime shifts (Hare and Mantua 2000). Regime shifts can be viewed as a consequence of reduced ability of the ecosystem to absorb perturbations. In the terminology of Holling (1973), the state of an ecosystem can be seen as a ball in a landscape, where the valleys represent

basins of attraction and their size the resilience of the system. An example of shift from one basin of attraction to another and decreased resilience is the sudden loss of water transparency and submerged vegetation in lakes and coastal marine environments subject to human-induced eutrophication (Duarte 1995). Tipping the ecosystem state over the threshold from one basin of attraction to another has often been associated with stochastic events like hurricanes or breakout of pathogens (Scheffer et al. 2001). Abrupt changes in time series of field data are not necessarily an evidence of the existence of alternative attractors, since sudden shifts may result from a stepwise change in a control parameter (Scheffer and Carpenter 2003). If the system, however, has a different trajectory when the controlling parameter decreases, compared to when it increased, there is evidence of alternative regimes. The difference between forward and backward switches is known as hysteresis (Scheffer and Carpenter 2003).

Most marine data are insufficient to conclude existence of discontinuous regime shifts, although some success has been achieved to demonstrate regime shifts caused by removing top predators (Jackson et al. 2001, Daskalov 2002) or changes in ocean circulation (Reid et al. 1998, Scheffer and Carpenter 2003, Beaugrand 2004). Other examples of marine regime shifts are the overgrowth of coral reefs (Knowlton 1992, McCook

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⁵ E-mail: jkp@dmu.dk

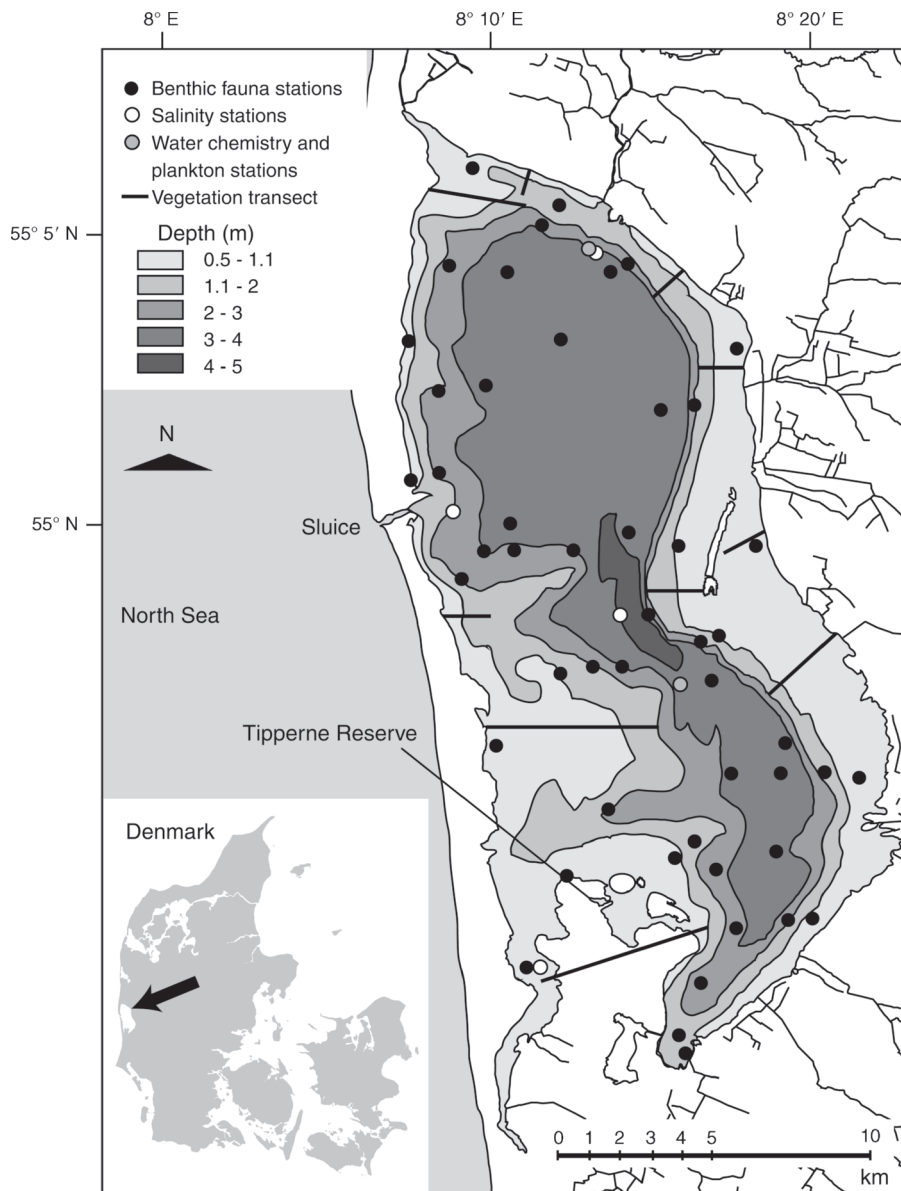


FIG. 1. Map of Ringkøbing Fjord, Denmark, including locations of sampling stations and transects.

1999, Nyström et al. 2000) and existence of multiple stable points in marine populations or communities (Lewontin 1969, Sutherland 1974). However, it has been argued that massive colonization events in, e.g., fouling communities are inappropriate examples of regime shifts unless the new state can persist through numerous generations (Scheffer and Carpenter 2003).

On the basis of monitoring data collected by the local county and national authorities, we present an example of a change in ecosystem state in Ringkøbing Fjord, Denmark. Ringkøbing Fjord is typical for Danish estuaries, i.e., shallow, eutrophic, and highly productive (Conley et al. 2000). Water exchange with the North Sea is governed by the sluice at Hvide Sande (see Plate 1)

that has been in operation since 1931. During the 1950s to 1970s, increased use of fertilizers and drainage projects in the catchment changed the lagoon from clear water to turbid and "green." To dilute nutrient concentrations in the lagoon, it was decided to change sluice management in late summer 1995 so that the sluice was opened more often and for a longer time, leading to an increased inflow to the lagoon of saline water from the North Sea.

MATERIAL AND METHODS

Ringkøbing Fjord is a 300-km² coastal lagoon situated on the west coast of the peninsula Jutland, Denmark (Fig. 1). The lagoon is shallow with an average



PLATE 1. The sluice at Hvide Sande, Jutland, Denmark. The North Sea is in the foreground, and Ringkøbing Fjord behind the sluice. Photo credit: Hvide Sande Havn/Profil Luftfoto.

depth of 1.9 m and a maximum depth of 5.1 m. The depth interval 0–3.5 m covers 92% of the lagoon area and 38% of the area has depths of 0–1 m. Total volume is $560 \times 10^6 \text{ m}^3$. Ringkøbing Fjord has a catchment area of 3500 km^2 and freshwater run-off ranged from 1100×10^6 to $2000 \times 10^6 \text{ m}^3/\text{yr}$ in the period 1989–2004, depending on precipitation. Water residence time of the lagoon is approximately two to four months. The lagoon is situated in a flat and open landscape adjacent to the North Sea and is very wind exposed with annual average wind speeds of 7 m/s.

Most of the reported parameters were sampled in connection with regional or national monitoring programs using standard methods according to the HELCOM guidelines (*available online*).⁶ Salinity was measured at four stations weekly during the entire period. Nutrient concentrations, Secchi depth, and chlorophyll *a* were measured at one representative station in the northern part of the lagoon about 15 times per year during the period 1989–1992, about 30 times per year in 1993–1997, and about 45 times per year in 1998–2006. Additional samples were taken at a station in the central part of the lagoon in the period 1998–2006. The determination of nutrients was based on

colorimetric methods. Chlorophyll *a* was analyzed on filtered samples using spectrophotometric determination.

Phytoplankton and zooplankton were sampled at the same station as the water chemical parameters about 15 times per year in 1989–1991, about 30 times per year in 1992–1997, and 26 times per year in 1998–2006. Plankton species composition, abundance, and biomass were determined from depth-integrated samples from 1989–1997, samples from 1 m below surface from 1998–2003, and depth-integrated samples in 2004–2006. Standard factors were used for conversion of cell volume to biomass.

Benthic fauna was sampled once annually in the spring using a HAPS corer sampler (area 0.0143 m^2 [Kannevorff and Nicolaisen 1973]) taking 10 samples at 25 stations in 1989–1994, five samples at 25 stations in 1995–1997, and one sample at 50 stations in 1998–2006. Filtration capacity, defined as the total volume of water potentially filtered by the population of the soft-shell clam *Mya arenaria*, was calculated from population data sampled at 16 stations in the fall of 1998–2006 and literature values on size specific filtration rate (Riisgaard and Seerup 2003, Riisgaard et al. 2003) at a water temperature of 15°C . Clams were sampled to a sediment depth of 40–50 cm using a frame and suction pump. Abundance, size frequency distribution, and mean dry

⁶ http://www.helcom.fi/groups/monas/CombineManual/en_GB/main/

TABLE 1. Univariate analyses of 1989–2006 data regarding the shift in distribution of abiotic variables before (b: 1989–1995) and after (a: 1996–2006) changes in sluice management, and biotic variables before (b: group 1, 1989–1996; group 2, 1989–1995) and after (a: 1997–2006) the management change.

Variable analyzed	Units	Distribution	Two-sample estimates				<i>t</i> test		<i>F</i> test	
			$\hat{\mu}_b$	$\hat{\sigma}_b$	$\hat{\mu}_a$	$\hat{\sigma}_a$	$P(\mu_b = \mu_a)$	df	$P(\sigma_b = \sigma_a)$	df
Abiotic group										
Nitrogen load	10 ⁶ kg/yr	normal	6776	988	5516	1087	0.0246	16	0.8490	6, 10
Phosphorus load	10 ⁶ kg/yr	normal	158	28	132	30	0.0898	16	0.9029	6, 10
DIN	μg/L	normal	692	116	762	190	0.3934	16	0.2375	6, 10
DIP	μg/L	normal	6.2	1.3	7.5	2.2	0.1678	16	0.1951	6, 10
Summer salinity		normal	9.4	1.2	11.9	1.4	0.0010	16	0.7872	6, 10
All-year salinity		normal	7.9	1.0	9.5	1.5	0.0238	16	0.3890	6, 10
Biotic group 1										
Secchi depth	m	normal	0.69	0.18	1.87	0.31	< 0.0001	16	0.1487	7, 9
Chl <i>a</i>	μg/L	lognormal	3.87	0.35	2.25	0.28	< 0.0001	16	0.5363	7, 9
Diatoms	μg C/L	lognormal	3.93	0.88	3.47	0.81	0.2716	16	0.8059	7, 9
Cyanobacteria	μg C/L	lognormal	6.87	0.89	−1.44	1.30	< 0.0001	16	0.3321	7, 9
Chlorococcales	μg C/L	lognormal	4.94	0.39	−0.97	1.81	< 0.0001	10.1	0.0006	7, 9
Flagellates	μg C/L	lognormal	0.81	1.86	1.31	0.78	0.4910	9.0	0.0192	7, 9
Other phytoplankton	μg C/L	lognormal	3.55	0.81	2.63	0.57	0.0126	16	0.3219	7, 9
Protozooplankton	μg C/L	lognormal	2.93	0.76	2.28	0.38	0.0382	14	0.0717	5, 9
Holoplankton	μg C/L	lognormal	5.19	0.65	3.96	0.64	0.0009	16	0.9366	7, 9
Meroplankton	μg C/L	lognormal	3.37	0.54	1.84	0.85	0.0016	14	0.3362	5, 9
Vegetation depth limit	m	normal	0.76	0.03	1.35	0.14	< 0.0001	9.9	0.0003	7, 9
Polychaeta	g DM/m ²	lognormal	1.75	0.43	2.42	0.18	0.0027	8.9	0.0169	7, 9
Mollusca	g DM/m ²	lognormal	−0.92	0.76	5.00	0.59	< 0.0001	16	0.4907	7, 9
Crustacea	g DM/m ²	lognormal	−0.83	0.73	−0.51	0.75	0.3670	16	0.9594	7, 9
Other benthic fauna	g DM/m ²	lognormal	−1.73	1.02	−2.33	0.91	0.2101	16	0.7272	7, 9
Biotic group 2										
Vegetation coverage	%	normal	9.93	2.94	3.81	3.06	0.0007	16	0.9675	6, 10
Bewick's Swan	bird-days	lognormal	8.94	0.81	7.11	0.82	0.0003	16	1.0000	6, 10
Northern Pintail	bird-days	lognormal	10.7	0.55	9.01	0.86	0.0003	16	0.2838	6, 10

Notes: Salinity values reported are on the practical salinity scale. Analyses were done (1) by comparing two-sample location parameters (μ_b and μ_a ; *t* test) and scale parameters (σ_b and σ_a ; *F* test) parameters assuming independent observations in time and (2) by intervention analysis for shift in mean value, including an autoregressive parameter (ρ) on standardized observations. Parameter estimates from the intervention analysis were obtained by maximum likelihood. Parameter estimates (indicated by a hat) from the two-sample test were obtained by least squares and from the intervention analysis by maximum likelihood. Significant tests ($P < 0.05$) are in boldface type. Abbreviations are: DM, dry mass; Chl *a*, chlorophyll *a*; DIN and DIP, dissolved inorganic nitrogen and phosphorus, respectively.

mass of clams in 5-mm size intervals were determined for each station. Plant coverage and depth limit of rooted submerged vegetation were estimated once annually by divers at 25 transects in 1989–1997 and 13 transects in 1998–2006. For location of stations and transects, see Fig. 1.

Birds were counted at the Tipperne reserve, situated in the southern part of the lagoon (Fig. 1). The reserve includes Tipper Grund, the most important of the three shallow banks in Ringkøbing Fjord for staging waterbirds. Counts covering the entire reserve have been carried out two to six days per month since 1973 (only from March to November since 1998). Bird-days (Desholm 1998) are calculated as the mean number of birds counted per month multiplied by the number of days in the month. Only data from August through November are used, since this period is the most important time of the year for staging herbivorous waterbirds. A specific monitoring program for total plant biomass on Tipper Grund in relation to food sources for the herbivorous waterbirds was designed in

1978 (Kiørboe 1980) and has been repeated almost annually in 1984–1999 (Jensen 2000).

Statistical analysis

It was hypothesized that there could be a shift in abiotic variables from 1995 to 1996 following the changed sluice practice and that this shift may have led to a subsequent regime shift in the biological system after 1996. Time series of annual observations were investigated for changes in the distribution of six abiotic and 18 biotic variables (Table 1) by means of a two-sample *F* test for difference in variances and *t* test for difference in means with variances pooled if not significantly different. All the abiotic variables and three biotic variables (benthic vegetation coverage and bird counts of two species) were assumed to respond directly to changes in sluice management and a shift in distribution between 1995 and 1996 was investigated, whereas the shift was assumed to occur between 1996 and 1997 for all other biotic variables that responded indirectly after the colonization of soft shell clams. Benthic vegetation coverage and depth penetration were

TABLE 1. Extended.

Intervention analysis		
$\hat{\rho}$	$P(\rho = 0)$	$P(\mu_b = \mu_a)$
0.02	0.9425	0.0180
0.36	0.1413	0.0773
0.41	0.0952	0.7880
0.84	<0.0001	0.0654
0.16	0.5655	0.0007
0.30	0.2529	0.0341
0.56	0.0280	<0.0001
0.47	0.1700	<0.0001
0.72	0.0004	0.1174
−0.25	0.3213	<0.0001
−0.25	0.3208	<0.0001
0.46	0.0991	0.8905
0.09	0.7477	0.0190
0.42	0.1250	0.1694
0.08	0.7497	0.0004
0.63	0.0116	0.0956
−0.08	0.8060	<0.0001
0.03	0.9148	0.0047
0.02	0.9320	<0.0001
0.67	0.0401	0.8506
0.16	0.5470	0.2900
0.77	0.0005	0.0089
0.23	0.4194	0.0003
0.15	0.5680	<0.0001

placed in separate biotic groups because coverage responded directly to the change in salinity, whereas depth penetration was connected to Secchi depths as part of the indirect response. Herbivorous waterbirds was directly related to the availability of their food source and therefore also in the same group of biotic variables as vegetation coverage. Secchi depth was considered a biotic variable because phytoplankton was the dominating factor for water transparency. Biotic variables associated with phytoplankton, zooplankton, and benthic fauna biomass as well as the calculated bird-days typically have skewed distributions and were log-transformed prior to the analysis.

To analyze shifts in the presence of autocorrelated observations, all variables were standardized to produce normal identically distributed deviates around the overall mean of the time series. If variances were not significantly different, subtracting the overall mean and dividing by the overall standard deviation produced standardized deviates. If variances were significantly different, (1) the two regimes were standardized separately to produce standardized deviations within regimes; (2) these deviates were scaled to the common standard deviation while retaining regime-specific means; and (3) final standardized deviates were produced by subtracting the overall mean and dividing by the common standard deviation. This procedure is a modification of the ASD approach of Ebbesmeyer et al.

(1990) to ensure that deviates were approximately normal. To account for potential serial correlation the standardized deviates for all variables were analyzed using intervention analysis (Box and Jenkins 1976) with residuals being modeled as a first-order autoregressive process or AR(1).

A principal component analysis (PCA) was employed to the abiotic and the two groups of biotic variables separately to visualize a potential regime shift in several ecosystem components simultaneously. PCA reduces the dimensionality of the data to a small number of uncorrelated and possibly meaningful time series (PC scores) and loading vectors. PCA was employed to the standardized deviates using their covariance matrix. Protozooplankton and meroplankton biomasses were not measured in 1989 and 1990, and therefore excluded from the biotic PCA in order to obtain a full data matrix covering all study years. Only loadings above the expected mean if all variables contribute equally ($n^{-0.5}$, where n = number of variables) were considered. PC scores from the first principal component of two groups of biotic variables were computed to investigate potential regime shift in relation to the most important abiotic forcing variables.

RESULTS

Change in sluice management increased saltwater inflow from the North Sea from $500\text{--}700 \times 10^6 \text{ m}^3/\text{yr}$ before 1996 to $1000\text{--}1300 \times 10^6 \text{ m}^3/\text{yr}$ after 1996. This change caused a significant (Table 1) increase in mean annual salinity from 7.9 in 1989–1994 to 10.1 in 1996–2006 (Fig. 2A). The change in salinity was especially pronounced during summer (May–September), where mean salinity changed from 9.4 before to 11.9 after the change in sluice management. The changed sluice management was less efficient in the years 1998–2000, resulting in slightly lower mean annual (8.8) and summer (10.9) salinities. Salinity did not differ horizontally between the representative station in the northern part of the lagoon and a station in the central part of the lagoon (Fig. 3). Vertical differences in salinity causing stratification could only be detected in 14% of the 654 sampling days in the period 1989–2006 and most of the time, stratification periods were short, since oxygen depletion rarely occurred.

Increased salinity facilitated widespread recruitment of soft-shell clams, *Mya arenaria*, which had been present in the lagoon previously, but only in very small numbers (1–50 individuals/m² or 0.1–0.5 g dry mass/m²). The establishment of a large clam population radically changed the composition of benthic biomass (Fig. 2B). Before 1996, benthic biomass was small (4–12 g dry mass/m²) and dominated by small eutrophication tolerant polychaetes. After 1996, benthic biomass increased to 50–300 g dry mass/m² and mollusks, primarily clams, constituted more than 90% of the biomass. From the period 1989–1995 to the period after 1996, mollusks and polychaetes (from 3–10 to 9–16 g dry

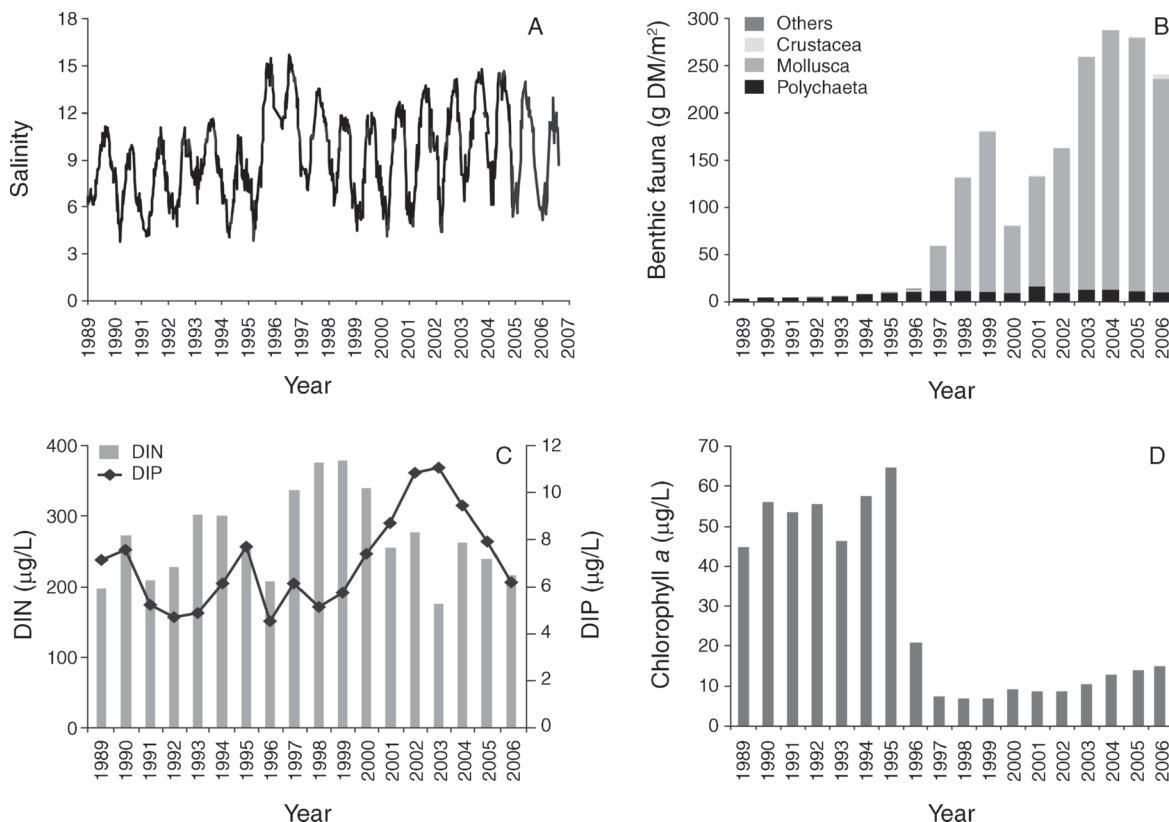


FIG. 2. Environmental parameters in the coastal lagoon Ringkøbing Fjord, Denmark, 1989–2006. (A) Volume-corrected salinity (practical salinity scale). (B) Biomass (DM = dry mass) of benthic fauna. (C) Annual mean concentrations of dissolved inorganic nitrogen (DIN, nitrite + nitrate + ammonia) and dissolved inorganic phosphate (DIP). (D) Annual mean concentration of chlorophyll *a*. (E) Annual mean phytoplankton biomass (carbon). (F) Annual mean zooplankton biomass (meroplankton not recorded in 1989–1990). (G) Summer (May–Sep) mean of Secchi depth, depth limit, and total coverage of bottom plants. (H) Occurrence of Northern Pintail (*Anas acuta*) and Bewick's Swan (*Cygnus columbianus bewickii*).

mass/m²) significantly increased their biomass whereas other fauna groups like worms or crustaceans did not experience significant changes in biomass (Table 1). The change in benthic composition was at the same time a functional shift, from a community primarily comprised of deposit feeders and scavengers to a total dominance of suspension-feeders. Benthic grazing capacity thus increased from a negligible level to one to four times the total volume of Ringkøbing Fjord daily at a water temperature of 15°C. The first major colonization of clams apparently took place in 1996, since a huge increase in abundance was observed from spring 1996 to spring 1997, just before the 1997 recruitment season (Fig. 4). This is further substantiated by the large recruitment in the second half of 1996 observed at four stations sampled with high frequency in the period 1995–1997 (Fig. 5). Abundance varied in the period after 1996 with a peak abundance of 1963 individuals/m² in May 1997 and a general decline in abundance in the period from 1998–2000, when salinity was lower (Fig. 4).

Mean annual concentration in chlorophyll *a* dropped concurrently and significantly with the increase in benthic grazing potential from 52.3 µg/L in the period

1989–1994 to 8.7 µg/L in 1997–2004 (Fig. 2D, Table 1). In the years around the change in sluice management, the change in mean annual concentration of chlorophyll *a* was especially evident with a decrease from 64.6 µg/L in 1995 to 21.0 µg/L in 1996 and 7.6 µg/L in 1997. Concentrations of chlorophyll *a* were similar in the northern and central parts of the lagoon (Fig. 3). An early spring bloom can in some years be identified, but both before and after the change in sluice management there is no recognizable seasonal pattern in chlorophyll *a* or bloom occurrence (Fig. 3). Phytoplankton composition also changed (Fig. 2E). Cyanobacteria, chlorococcales, and other phytoplankton groups experienced a significant decrease in biomass, whereas diatoms and flagellates showed no significant changes in biomass (Table 1). This implies that the relative composition changed from a phytoplankton community dominated by cyanobacteria and to a lesser extent chlorococcales, prior to the change in sluice management, to a diatom dominated community after the change (Fig. 2E). Another change was the shift within all the major taxonomic groups from dominance of large to small species. This was evident in the cyanobacteria from the

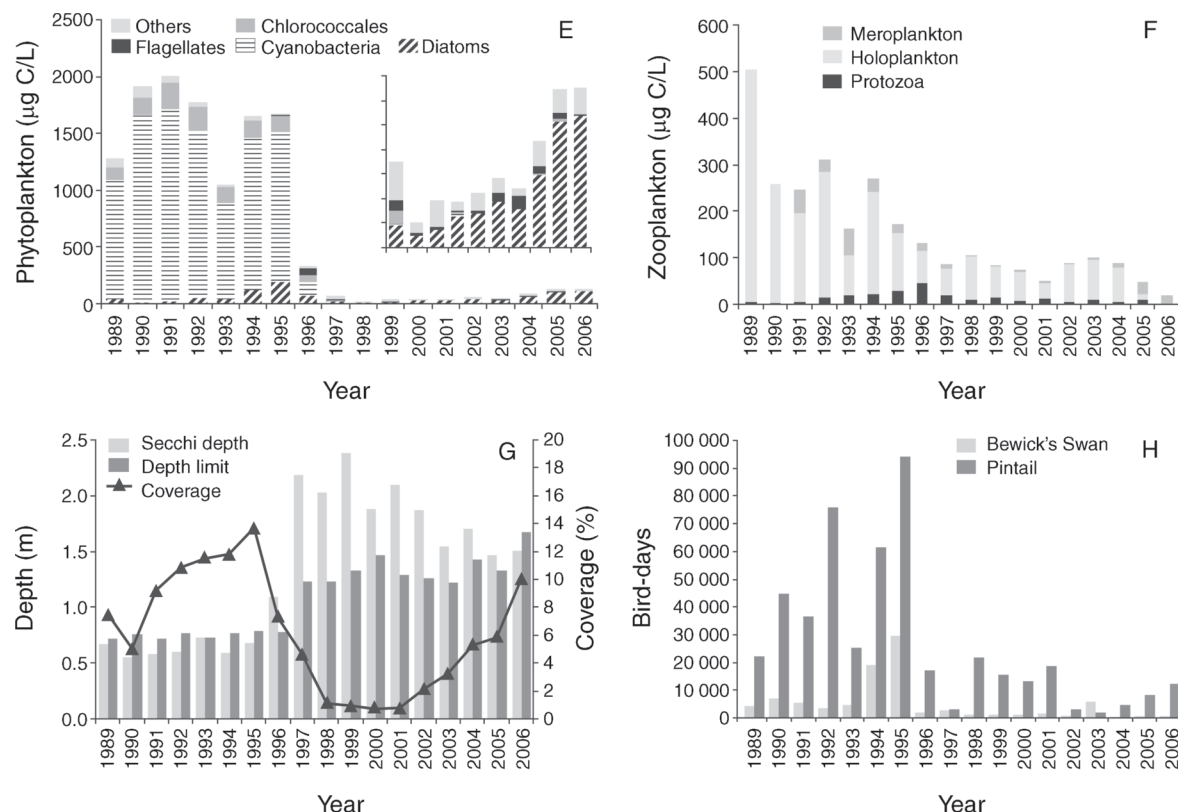


FIG. 2. Continued.

change in dominance of the colony forming species *Woronichinia cf. compacta* and *Coelomoron pusillum* to small coccoid cyanobacteria, and in diatoms from large *Thalassiosira* sp. to small (<10 µm) centric species.

Concentrations of dissolved nutrients did not change significantly with the change in sluice management (Fig. 2C, Table 1). Annual mean concentration of dissolved inorganic nitrogen (DIN) increased from 569 µg/L in 1996 to 921 µg/L in 1997 and peaked in 1999 with 1037 µg/L, but concentrations of DIN have since then generally been declining and have approached the pre-1996 levels. There has been a distinct seasonal pattern in DIN concentration with low and potentially limiting concentrations during summer, but there was no difference in concentrations between stations (Fig. 3). The number of days with potential N limitation (<28 µg DIN/L (Fisher et al. 1992) was in the range of 100–150 d/yr both from 1989–1994 and from 1996–2006. Concentrations of dissolved inorganic phosphorus (DIP) developed in a pattern similar to DIN, with an increase in concentrations after the change in sluice management, but with recent levels approaching concentrations in the early 1990s. DIP concentrations varied seasonally with low and potentially limiting concentrations during spring and summer, but with no difference in concentration between stations (Fig. 3). Number of days with potential P limitation (<6.2 µg

DIP/L [Fisher et al. 1992]) was in the range 200–300 d/yr in 1989–1994 and in the range 100–250 d/yr in 1996–2006.

Changes in nutrient load from the watershed did not follow a trend similar to the nutrient concentrations (Fig. 6). Loads of both phosphorus and nitrogen were low in 1996, 1997, and 2003, primarily due to low levels of precipitation. Nitrogen load to Ringkøbing Fjord was significantly higher in the period 1989–1995 with an average load of 6776×10^6 kg/yr compared to 5516×10^6 kg/yr after 1996, but no significant change in P load could be found (Table 1).

Zooplankton biomass was reduced from >160 µg C/L before 1996 to 50–106 µg C/L after 1996 and all zooplankton groups had significantly reduced biomass after 1996 (Table 1; note, however, that protozoa- and meroplankton was not significant when corrected for autocorrelation), but no visible change in species composition was observed (Fig. 2F). Since 1992, low biomass in winter and early spring, peak biomass of microzooplankton around April–May, and peak biomass of mesozooplankton around June–July and again in autumn have characterized the seasonal pattern in zooplankton development. Filtration capacity of zooplankton rarely exceeded primary production except occasionally in spring and early summer.

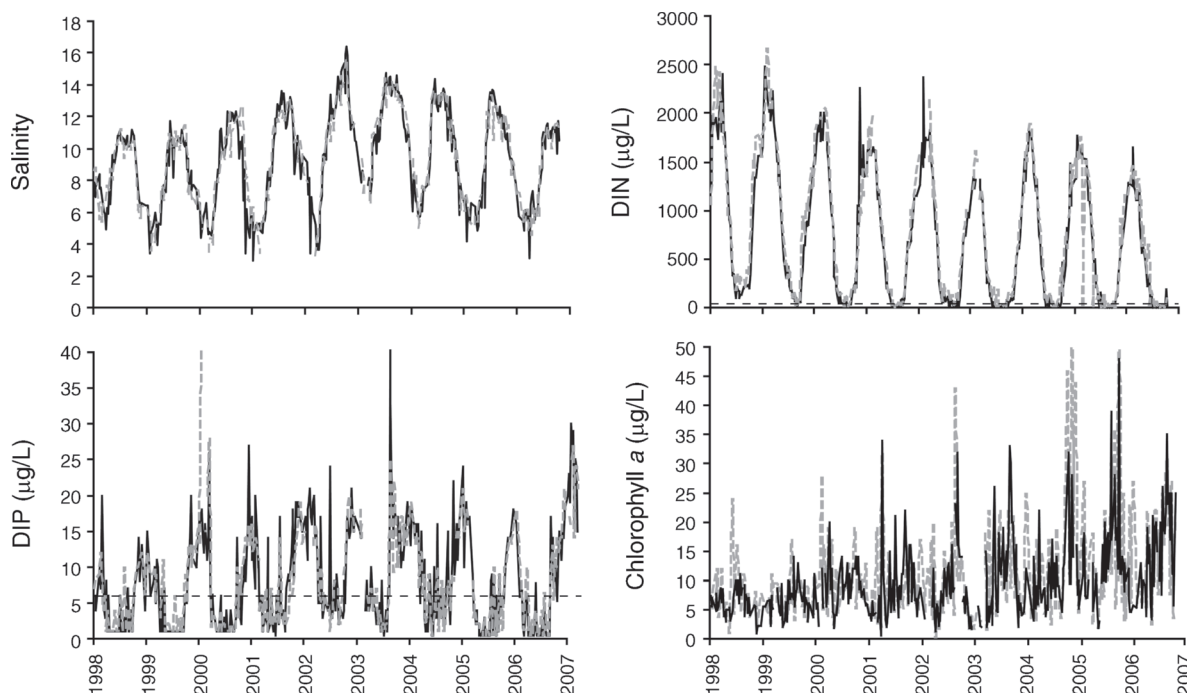


FIG. 3. Salinity (practical salinity scale), DIP, DIN, and chlorophyll *a* at 1 m depth measured at two stations, northern (solid black line) and central (dashed gray line), in Ringkøbing Fjord in the period 1998–2006. Horizontal dashed lines indicate potential nutrient limitation.

The reduced phytoplankton biomass led to an increase in light penetration and thereby increased the depth limit of submerged, rooted, benthic vegetation penetration significantly from 0.6–0.8 m in the period before 1996 to 1.2–1.7 m in the period 1997–2006 (Fig. 2G, Table 1). Coverage of benthic vegetation, however, decreased drastically from a mean total coverage of 9.9% for the entire lagoon before 1996 to 0.9% coverage in 1998–2001 when coverage was lowest. Plant coverage has increased since then and was 9.9% in 2006, but mean coverage was still significantly lower in the period 1996–2006 compared to the period 1989–1995 (Table 1). Sago pondweed *Potamogeton pectinatus* and to a lesser extent spiral ditchgrass *Ruppia cirrhosa* dominated the benthic

vegetation before 1996. After 1996, spiral ditchgrass and eelgrass (*Zostera marina*) have increased their relative proportion of the benthic vegetation, but eelgrass still constitutes only a minor part of the benthic vegetation. After 1996, there has been a reported increase in occurrence and abundance of macroalgae, especially sea lettuce (*Ulva lactuca*), but biomass and coverage have not been determined consistently.

Abundance of Northern Pintail (*Anas acuta*) and Bewick's Swan (*Cygnus columbianus bewickii*), which are specialist feeders on sago pondweed seed and below-ground tubers, respectively (Nolet and Drent 1998, Clausen et al. 2002), decreased drastically from 1995 to 1997 and was significantly lower in the period after the change in sluice management compared to before the change (Fig. 2H, Table 1). The data for vegetation

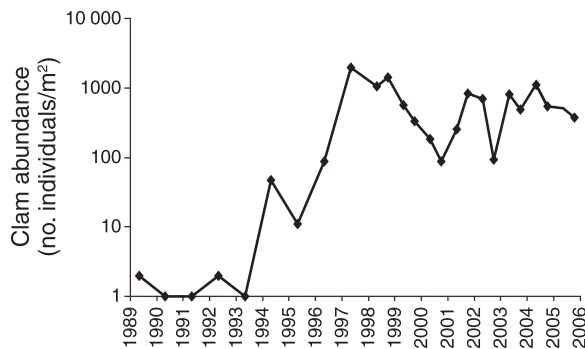


FIG. 4. Mean abundance of the clam *Mya arenaria* in Ringkøbing Fjord in 1989–2006. Data are from stations used for benthic fauna sampling; note the log scale.

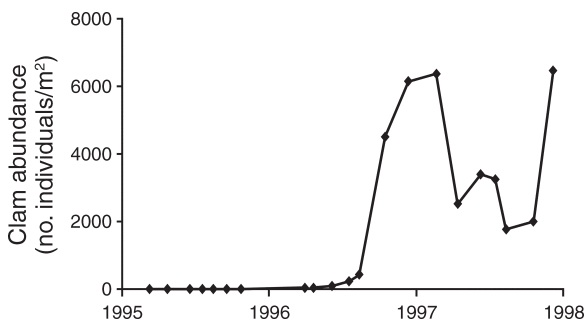


FIG. 5. Mean abundance of *Mya arenaria* at four stations in Ringkøbing Fjord sampled with high frequency in 1995–1997.

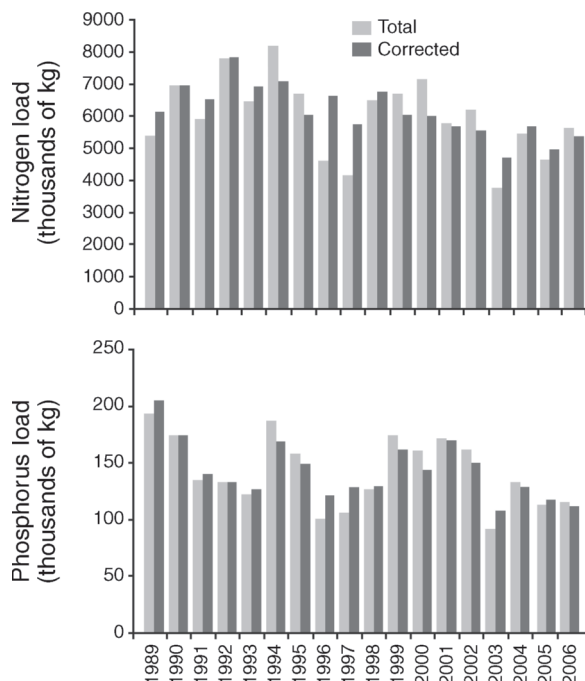


FIG. 6. Load of nitrogen and phosphorus to Ringkøbing Fjord in the period 1989–2006, shown as total load and load corrected for precipitation. Atmospheric deposition is included in loads.

coverage data in Fig. 2 is based on sampling throughout the lagoon, while bird numbers are only from Tipperne, the most important waterbird area in the southern part of the lagoon. Analysis of a more comprehensive data set on vegetation biomass and bird numbers from Tipperne compiled in the period 1978–1999 shows close correlations between biomass of benthic vegetation and occurrence of Northern Pintails and Bewick's Swans (Fig. 7). Several generalist feeders on benthic vegetation such as Mute Swan (*Cygnus olor*), Eurasian Wigeon (*Anas penelope*), and Eurasian Coot (*Fulica atra*), all experienced a decline in occurrence concomitant to the decline in vegetation coverage, and displays similar correlations between bird-numbers and vegetation biomass at Tipperne (data not shown). The data in Fig. 7 only include the first three years after the change in sluice management, but nevertheless support that lower numbers of Northern Pintail, Bewick's Swan, and the other herbivorous waterbirds after 1996 most likely can be explained by the lower bottom coverage of food plants in recent years (Fig. 2G, H).

In the multivariate ecosystem analysis, the first principal component (PC1) for the abiotic variables explained 55% of the total variation with nitrogen load ($r = -0.48$), salinity in summer ($r = 0.50$) and mean annual salinity ($r = 0.50$) as the most important loadings. PC2 for the abiotic variables accounted for 19% of the total variation and described mainly variations in phosphorus load and concentration, whereas DIN was

main contributor to PC3 (15%). More than 80% of the total variation could be explained by the first three principal components of the first group of biotic variables (Table 1). Secchi depth ($r = -0.31$), chlorophyll ($r = 0.32$), cyanobacteria ($r = 0.33$), chlorococcales ($r = 0.39$), vegetation depth limit ($r = -0.37$), polychaetes ($r = -0.33$), and mollusks ($r = -0.33$) were the most important loadings to PC1 (54% of variation). Diatoms ($r = 0.57$), crustaceans ($r = 0.42$), and other benthic fauna ($r = 0.33$) were the most important loadings to PC2 (15% of variation), whereas PC3 (12%) mainly accounted for changes in flagellates ($r = -0.49$), vegetation depth limit ($r = 0.47$), polychaetes ($r = -0.35$), crustaceans ($r = 0.35$), and other benthic fauna ($r = -0.41$). For the second group of biotic variables, PC1 was an average of the benthic vegetation coverage ($r = 0.57$), Swans ($r = 0.57$) and Pintails ($r = 0.58$) accounting for 71% of the total variation, whereas PC2 (15%) described the difference between vegetation coverage ($r = -0.67$) and Swans ($r = 0.74$).

Only the PC1s for the two groups of biotic variables reflected systematic variation in relation to the abiotic variables (Fig. 8), whereas higher-order principal components were not related to abiotic forcing (data not shown). Both groups of biotic variables demonstrated a shift in PC1 around 1996 that was not linearly related to the abiotic forcing. The two separate clusters in PC1 for the biotic variables indicate a shift between 1995 and 1997 with 1996 as an intermediate year. This shift was mainly manifested through increasing Secchi depth, vegetation depth penetration, polychaetes, mollusks, and decreasing chlorophyll including cyanobacteria and chlorococcales as the most important loadings of PC1 for the first group of biotic variables. Decreases in benthic vegetation coverage and herbivorous waterbirds characterized the shift in the second group of biotic variables. Distances between the two clusters remained

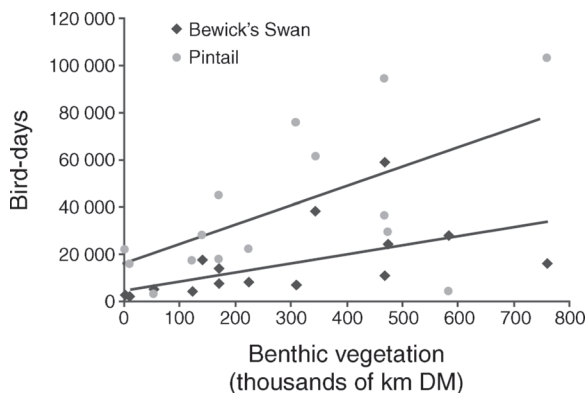


FIG. 7. Correlations between occurrence of Northern Pintail (*Anas acuta*) and Bewick's Swan (*Cygnus columbianus bewickii*) and biomass (dry mass) of benthic vegetation in the period 1978–1999. Bird-days express the total use of a site, in this case the sum of average counts per month multiplied by the number of days in each month, for August–November. Correlations are significant ($P < 0.01$).

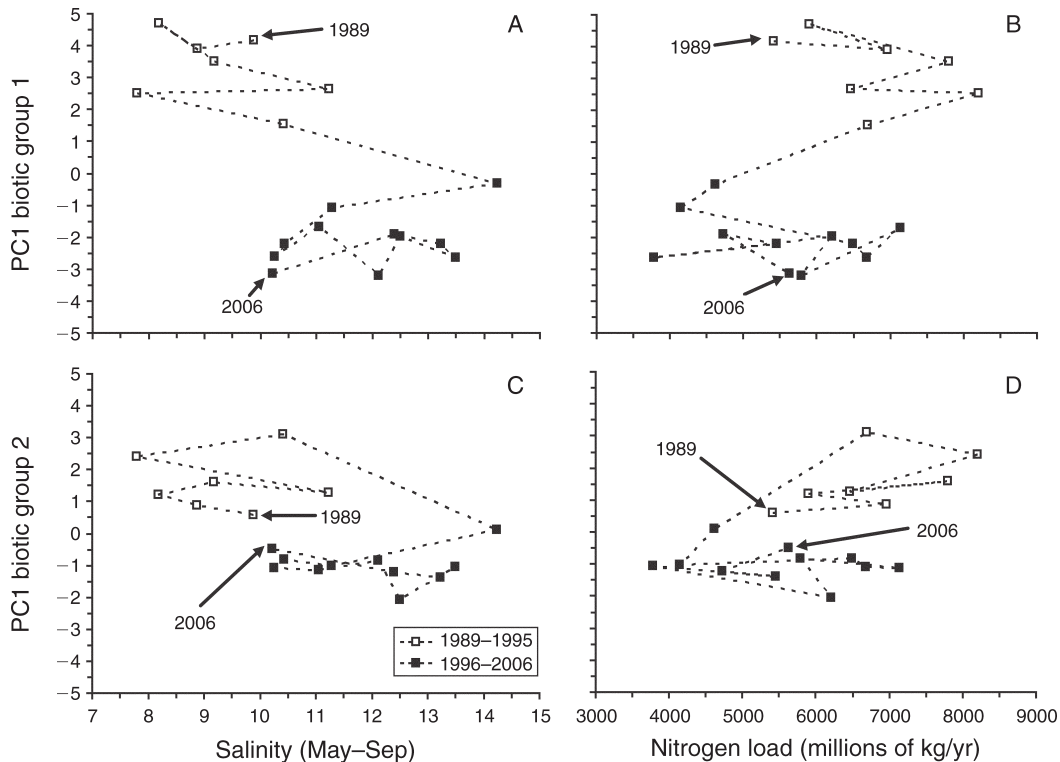


FIG. 8. First principal component scores for the two groups of biotic variables related to the most important loadings of PC1 for the abiotic variables (yearly salinity is not shown, but it responded similarly to summer salinity; Table 1). Scores are connected to show the trajectories in time. The key to symbols in panel (C) pertains to the entire figure. Salinity is measured on the practical salinity scale.

large for the first group of biotic variables despite that ranges of variation in the forcing variables were overlapping. However, distances between the two clusters for the second group of biotic variables were smaller with a tendency for the most recent year to approach the level at the beginning of the time series.

DISCUSSION

From 1995 to 1997, a dramatic change in biological structure of Ringkøbing Fjord took place. The ecosystem of the lagoon changed from a nutrient-driven, turbid, green-water state to a grazing-controlled, clear-water state. The post-1996 stable state was the result of two parallel and only slightly related chains of events. Invasion of clams led to a different biological structure affecting both benthic fauna and plankton biomass and composition. As shown in the PCA, the distance between clusters of these biotic variables in the period before and after the change in sluice management remains so large that there are strong indications of different stable states. In contrast, the development in benthic vegetation and associated herbivorous waterbirds appears to be reflecting a strong perturbation of a single basin of attraction and benthic vegetation coverage may not yet have reached its new stable equilibrium.

The change in ecosystem state from a strongly bottom-up controlled green state to a clear-water grazer-controlled state was triggered by the change in salinity, but high nutrient loading in decades, and not salinity per se, was responsible for the pre-1996 state. It may thus represent an unstable equilibrium rather than an alternative attractor, despite the relatively long period with the same biological structure. Alternatively, this state can be characterized by having low resilience (Scheffer et al. 2001, Scheffer and Carpenter 2003). Similarly, the top-down controlled clear-water state after 1996 represents an unstable equilibrium as long as the high nutrient load persists. With a high nutrient load, stochastic events such as severe oxygen depletion or outbreak of a disease could kill the clams, resulting in disappearance of the top-down control and hence a return, however temporary it may be, to the green and turbid regime. Resilience of the new state can be promoted by reduction in nutrient load and by an increased coverage of vegetation, thereby channeling a larger part of the nutrients into benthic primary production.

If pre-1996 sluice management were re-established, an immediate dramatic reduction in clam population density and extension might not be the outcome. Adult clams can tolerate salinities down to 4–5 (Matthiessen

1960, Strasser 1999), whereas survival of larvae and juveniles is very limited below salinities of 9–10 (Matthiessen 1960, Stickney 1964). A return to pre-1996 summer salinities will thus affect recruitment but with a high grazing potential from the remaining clam population, the clear-water state can persist for several (three to eight) years until the population dies off.

For benthic vegetation, the rapid decline in coverage was likely a result of the small but sudden step in a controlling parameter (salinity) for a highly local population that had not encountered summer salinities >12 for decades. The species sago pondweed can tolerate higher salinities and theoretically should not be inhibited by the present salinity conditions (Katrud 1990, Adams et al. 1992), but the sudden although relatively small increase in salinity apparently did not provide suitable conditions for a distinct local population. Alternatively, an undiscovered disease may have affected the pondweed population in the same period. Sago pondweed coverage has increased in the years 2000–2006 where relatively stable summer salinity regimes prevailed. In addition, other more salinity tolerant species have increased their coverage, as would be anticipated (Healy 1997), and coverage of total benthic vegetation has almost reached pre-1996 levels. In fact, the potential for vegetation coverage has increased due to improved transparency (Duarte 1995). If sluice practice is changed back to pre-1996 conditions, it can not be predicted how benthic vegetation will develop, since the present populations of benthic vegetation are adapted to the new salinity regime and responses to changes in salinity seem difficult to predict for Ringkøbing Fjord vegetation.

Bird occurrence has not responded proportional to the post-2000 increase in plant coverage. This apparent discrepancy can be explained by a mismatch between geographical coverage of vegetation surveys and bird counts of Pintails and Swans in the lagoon. Vegetation has been mapped throughout the lagoon, while bird numbers were only counted at Tipperne in the southern part of the lagoon. The overall vegetation recovery is actually composed of a better recovery in the northern and eastern parts of the lagoon, and poorer recovery in the southern and western parts of the lagoon. Hence bird numbers are still low in Tipperne where vegetation recovery has been slower. Concurrent with the development in vegetation coverage and bird numbers is a change in nutrient flow and recycling in the lagoon. Kiørboe (1980) estimated an annual production of 968 Mg ash-free dry mass of submerged aquatic vegetation (SAV) at Tipper Grund in 1978 and estimated that herbivorous waterbirds consumed 30% (range 15–60%) of this. Due to the observed linearity between bird numbers and SAV biomass one might assume that waterbirds still consume the same percentage of SAV produced, but with lower biomass of SAV, the importance of the SAV–waterbird interaction for

nutrient recycling in the lagoon has been lower after 1996.

Phytoplankton species composition was radically changed in 1996. Before 1996, it was a community characterized by large forms and mainly colonial cyanobacteria and after 1996, it was a community common to Danish estuaries (Conley et al. 2000) with a more diverse assemblage of groups but mainly small forms. The change in size composition from large to small forms can be explained by the huge benthic grazing, which will remove particles up to the millimeter scale and will favor small, fast-growing species (Petersen 2004). The explanation for the change in species composition is less obvious since the slight change in salinity is probably not enough to create unfavorable conditions for the cyanobacteria species. It is possible that pre-1996 conditions with high phytoplankton biomass have resulted in nutrient limitation, favoring nitrogen-fixing cyanobacteria, as the mean summer DIN:DIP ratio changed from below before 1995 to above the Redfield ratio after 1996 (data not shown). It is also possible that the pre-1995 conditions with a combination of high biomass/primary production and low salinity can have created high pH values, which would favor cyanobacteria (Shapiro 1990). There are, however, no systematic measurements of pH to verify this hypothesis. How a change in sluice management back to pre-1996 conditions would affect phytoplankton community structure cannot be predicted from the present data, since several factors may have been involved in the structuring of the community.

We have stated that the change in biological structure of the system can be explained primarily by the invasion of filtering clams. A prerequisite for the clams playing a major role is that they have access to the phytoplankton. Since the lagoon is shallow and exposed it can be assumed that the water column is often mixed. Stratification was rarely encountered and oxygen depletion (defined as $<4 \text{ mg O}_2/\text{L}$) could only be detected in 2% of the sampling days (data not shown), indicating that stratification usually is a short-term phenomenon. Further similarity between stations regarding concentrations of chlorophyll and nutrients indicates that the lagoon is very homogenous in terms of water column parameters and that the northern monitoring station is representative for the lagoon.

There may be other causes for the reduction in phytoplankton biomass than benthic filtration. Due to low precipitation nutrient run-off was low concomitant with the regime shift in 1996–1997 and there was a significant lower nitrogen load in the period before, compared to after the change in sluice management. For a number of reasons it is, however, not likely that the reduced load is responsible for triggering a shift from green turbid to relatively clear water. Area loads to the lagoon area in 1996–1997 of around $15000 \text{ kg N}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ and $400 \text{ kg P}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$ (corresponding to 70% of the preceding years) are still high loads, even

TABLE 2. Mean concentrations of dissolved (DIP) and total (TP) phosphorus, dissolved (DIN) and total (TN) nitrogen, chlorophyll *a* (Chl *a*), and phytoplankton biomass (Phyt) sampled at the northern representative station.

Date	TP ($\mu\text{g/L}$)	DIP ($\mu\text{g/L}$)	TN ($\mu\text{g/L}$)	DIN ($\mu\text{g/L}$)	Chl <i>a</i> ($\mu\text{g/L}$)	Phyt ($\mu\text{g C/L}$)	<i>Mya arenaria</i>	
							Abundance (no. clams/ m^2)	Biomass (g DM/ m^2)
1994	117	6	1843	823	59	1653	51	0.3
1997	54	6	1488	921	8	69	1982	46
Ratio†	-2	1	1	1	-7	-24	39	154
1 Jun–15 Aug 1996	75	4	843	66	29	673	245	5
15 Oct–31 Dec 1996	60	11	1735	1370	8	36	5297	67
Ratio†	1	3	2	21	-4	-19	22	15

Notes: Data on abundance and biomass (DM, dry mass) of clams *M. arenaria* are from 25 stations in 1994 and 1997 and four intensively sampled stations in 1996. In 1996, summer and winter values are compared. The numbers of times that parameters increased or decreased are shown as positive and negative ratios, respectively.

† The ratio of the earlier value to the later value in each pair.

compared to eutrophic Danish estuaries (Conley et al. 2000), and loads to Ringkøbing Fjord reached pre-1996 levels in 1998–2002 without an increase in phytoplankton levels. Further, a low run-off in 2003 did not result in a decrease in biomass of phytoplankton. Examining the concentrations of dissolved nutrients similarly show no decreasing trend in the years around the change in ecosystem state. Nitrogen limitation occurred more frequently before than after 1996 and there is no long-term trend or difference in concentrations of phosphorus or occurrence of P limitation that can account for the huge reduction in standing biomass of phytoplankton. It is thus most likely that the low runoff in 1996–1997 is coincidental with rather than the cause for the regime shift.

To further investigate the potential role of nutrients for the change in ecosystem state, a comparison of key parameters in the period before and after the change is shown in Table 2. Comparing 1994 with 1997 shows that phytoplankton biomass decreased, whereas concentrations of inorganic nutrients remained constant. Concentrations of DIN and DIP were not reduced from summer to autumn/winter in 1996, but increased like in most other years, while phytoplankton biomass decreased dramatically. Chlorophyll *a* has in most years, both before and after 1995, not decreased in a similar way during winter. The data do not support nutrient limitation to be the cause for the sudden change in ecosystem state.

Before 1995, zooplankton could in theory control phytoplankton during periods of the year. However, zooplankton did not effectively have access to all of the phytoplankton in the years before 1995, because a large fraction of phytoplankton biomass was represented by large colonial cyanobacteria that are not accessible for zooplankton (Hansen et al. 1997). Further, taking into account that zooplankton filtration was high and potentially controlling a limited part of the year, whereas chlorophyll *a* was constantly high through all seasons both before and after 1995, it is unlikely that zooplankton has triggered the change in ecosystem state. Zooplankton may, however, have been important

during the transition and especially in 1996 in reducing levels of phytoplankton.

Ringkøbing Fjord has previously experienced large changes in salinity due to variation in water exchange with the North Sea (Spärck 1936). In 1910, a channel was dug at Hvide Sande causing an increase in salinity to 15–30 in the lagoon and the channel was closed again in 1915 reducing salinity to 7–11. On both occasions, a major change in fauna composition was observed, primarily manifested by colonization of mussels and clams and their subsequent decline in abundance after closure of the channel (Spärck 1936). Though data are scarce on phytoplankton and mainly qualitative rather than quantitative, there is no indication that these historical changes in salinity were associated with major changes in phytoplankton biomass.

A return to pre-1995 sluice management has not been allowed politically so, strictly speaking, there is no proof that a regime shift took place in Ringkøbing Fjord since hysteresis (Scheffer et al. 2001, Scheffer and Carpenter 2003) has not been shown. As argued above, a return to pre-1996 sluice management may not be expected to lead to an immediate collapse of the clam population. Recruitment of clams can be seen as an on-off mechanism in connection with changing sluice management, whereas the adult population can tolerate pre-1996 salinity conditions and will thus persist in the lagoon for a period. Such a time delayed response can be considered a different return trajectory compared to the shift in 1996 eventually leading to elimination of top-down control, but not necessarily as a nonlinear shift from one basin of attraction to another, which is a requirement for hysteresis (Scheffer et al. 2001). The pre-1996 conditions are however, the result of a (supposedly) gradual deterioration of the original clear water state of the lagoon (Spärck 1936) due to an increased load of nutrients and the post-1996 conditions can in some respects be considered a return to this state albeit through a different trajectory. We have demonstrated existence of different stable states for the same forcing variable (eutrophication) through an abrupt transition (Beauregard 2004) caused by invasion of clams and are

thus in line with many reported examples of marine regime shifts (e.g., Hare and Mantua 2000, Jackson et al. 2001, Collie et al. 2004). But we have not demonstrated regime shifts in the rigid definition (Scheffer et al. 2001) including demonstration of hysteresis in relation to the introduction of clams. The question is if hysteresis at all can be demonstrated in open natural (marine) systems, when this example in a relatively confined and partly controlled lagoon using an extensive (though limited in time) data set does not comply with the rigid definitions.

The change in ecosystem state in Ringkøbing Fjord has some of the same characteristics as the changes in biological structure occurring in North American lakes after invasion of zebra mussels (e.g., Strayer et al. 1999) or the invasion of clams in San Francisco Bay (Cloern 1982, Alpine and Cloern 1992). In contrast to both lakes and San Francisco Bay, clams are not alien to Ringkøbing Fjord and were already present in the lagoon before 1996. In addition, the invasion of clams was not at the expense of other benthic fauna groups that maintained or even increased their biomass. Like invasive clams and zebra mussels, the population of *M. arenaria* has been able to accomplish further recruitment after the initial increase in abundance and now several cohorts are present. The population can be characterized as rejuvenating, which is another requirement for a genuine regime shift (Scheffer and Carpenter 2003). In fact, the population of clams in the lagoon has experienced several successful recruitments since 1996 (data not shown) and differs from the cyclic pattern normally observed for *M. arenaria* in the Wadden Sea area (Beukema et al. 2001).

The reported change in ecosystem state has major implications for ecosystem management. The post-1996 regime in Ringkøbing Fjord is in many ways closer to favored objectives of environmental protection than before the change in sluice practice. This applies to indicators like water transparency and vegetation depth limit. The apparent improvements were, however, not a result of a reduction in anthropogenic pressure and the reduced resilience of the system due to nutrient loading has not been solved. In addition, the reduction in herbivorous waterbirds in the years following the change in sluice management represents a nature conservation problem because the southern part of Ringkøbing Fjord is designated as a Ramsar site under the Convention on Wetlands and as a Special Protection Area for Birds under the European Union Birds Directive (79/409/EEC) and several of the species specifically listed in the designations forage on benthic vegetation. From a bird protection point of view, the pre-1996 sluice management was preferable to the years just after the change in sluice management, when a drastic decline in sago pondweed coverage resulted in declined bird populations. From a water body management point of view, e.g., according to the European Union Water Framework Directive (200/60/EC), a return to the turbid green state would, however, not be admissible.

This apparent contradiction between nature conservation and environmental protection may be solved by the current gradual increase in plant coverage and show that patience may be required of managers and politicians. Similar conflicts between different management perspectives may very well be the result of regime shifts in other coastal areas.

Well-described sudden shifts in ecosystem states, as in Ringkøbing Fjord, are important in several aspects: (1) they can be used to enhance our understanding of ecosystem states and regime shifts that hitherto have been few reported for the marine environment (Collie et al. 2004); (2) they are important reminders of the lack of predictability of coastal ecosystems and should serve as warnings for simplified water body management (Folke et al. 2004, Groffman et al. 2006); and (3) they can be used to establish models of ecosystem thresholds in order to improve the predictive capacity of ecosystem behavior, thereby providing additional knowledge to support policy makers and the decision-making process (Muradian 2001).

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