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Salinity Induced Regime Shift in Shallow Brackish Lagoons

Erik Jeppesen,[1,2,*] Martin Søndergaard,[1] Asger Roer Pedersen,[1] Klaus Jürgens,[3] Agnieszka Strzelczak,[1,4] Torben L. Lauridsen,[1] and Liselotte S. Johansson[1]

[1]*Department of Freshwater Ecology, National Environmental Research Institute, University of Aarhus, Vejlsøvej 25, 8600 Silkeborg, Denmark;* [2]*Department of Plant Biology, University of Aarhus, Ole Worms Allé, Building 135, 8000 Aarhus C, Denmark;* [3]*Baltic Sea Research Institute, Warnemünde (IOW), Seestraße 15, 18119 Rostock, Germany;* [4]*Institute of Chemistry and Environmental Protection, Szczecin University of Technology, Aleja Piastow 42, 71-065 Szczecin, Poland*

Abstract

In brackish lagoons, *Daphnia* is replaced by calanoid copepods (*Eurytemora affinis, Acartia* spp.) and rotifers when a certain threshold (depending on, for instance, fish density) is reached. We hypothesize that loss of *Daphnia* induces a regime shift from clear to turbid at high nutrient concentrations. We conducted a factorial designed enclosure experiment with contrasting salinities (0–16‰), low fish predation (one three-spined stickleback, *Gasterosteus aculeatus*, m^{-2}) and three levels of nutrient loading in a shallow brackish lagoon. A change point analysis suggests a strong regime shift from a clear to a turbid state at 6–8‰ salinity at low and high loading, but not for the control. From the low to the high salt regime, chlorophyll *a* (Chla), Chla:total phosphorus (TP) and Chla:total nitrogen (TN) ratios shifted highly significantly for all nutrient treatments, and the bacterioplankton production followed the changes in Chla. These changes occurred parallel with a shift from cladoceran and cyclopoid copepod to rotifer dominance. Monitoring data from 60 Danish brackish lagoons show increasing Chla with increasing TP and TN as well as interactive effects of TN and salinity, peaking at intermediate salinity. A relatively weak effect of salinity at low nutrient concentrations and the stronger effect at intermediate high salinity are in accordance with the experimental results. However, these data suggest a lower salinity threshold than in the experiment, which may be explained by a higher fish density. Our results have implications for the management of coastal lagoons both at present and in a future (predicted) warmer climate: (1) improved water quality can be obtained by reducing the nutrient loading or enhancing the freshwater input to a level triggering a shift to *Daphnia* dominance (typically <2‰), (2) fish manipulation is probably not a useful tool for brackish lagoons, unless the salinity is below the threshold for a potential shift to a clear *Daphnia* dominated state, and (3) more abrupt changes will expectedly occur in low-saline coastal lagoons at increasing salinity during summer in a future warmer climate.

Key words: regime shift; brackish lagoon; saline; *Daphnia*.

Introduction

In recent years, regime shifts in ecosystems have become an extensively studied subject (Scheffer and others 2001; Carpenter 2003). A notable example is shallow northern freshwater lakes that

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*Corresponding author; e-mail: ej@dmu.dk

at moderately high phosphorus concentrations may have two alternative states, turbid or clear (Irvine and others 1989; Jeppesen and others 1990; Scheffer 1990; Scheffer and others 1993). The clearwater state is characterized by high abundance of submerged macrophytes, a high piscivore to prey fish ratio and often high zooplankton:phytoplankton biomass ratios, whereas in the turbid state submerged macrophytes are absent or their abundance is low, as are also the piscivore:prey fish and zooplankton:phytoplankton ratios (Jeppesen and others 2000). Piscivorous fish and submerged macrophytes are generally considered pivotal for maintaining the clear-water state, one of the reasons being that piscivorous fish indirectly contribute to a high grazing pressure on phytoplankton via predation control on planktivorous fish, whereas submerged macrophytes serve as refuge for zooplankton against fish predation.

However, eutrophic brackish lagoons behave differently and remain turbid even at high macrophyte abundance (Moss 1994; Jeppesen and others 1994). This difference has been attributed to a higher fish and invertebrate predation pressure and lack of refuge for zooplankton among plants in brackish lagoons as predators are abundant here (Jeppesen and others 1994). Generally, small three- and nine-spined sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*) are the dominant planktivores in eutrophic brackish lagoons, whereas large roach (*Rutilus rutilus*) and bream (*Abramis brama*) dominate in eutrophic freshwater lakes. Sticklebacks have several cohorts per year, whereas roach and bream reproduce only once annually. Because fish fry exert a particularly high predation pressure on the zooplankton (He and Wright 1992), the predator control of zooplankton is likely higher and lasts longer in the brackish lagoons. In addition, abundance of invertebrate predators is high in brackish lagoons. At salinities of 0.5–18‰, the shrimp *Neomysis integer* is the dominant invertebrate (Irvine and others 1990; Jeppesen and others 1994; Aaser and others 1995) and increases substantially in abundance at high nutrient levels in the brackish lagoons (Jeppesen and others 1994, 1997), which contrasts with freshwater lakes where the abundances of the invertebrate predators *Leptodora kindtii* and *Chaoborus* spp. (Hanazato 1990; Jeppesen and others 1997) decline substantially when phosphorus concentrations exceed approximately 0.25 mg TP l^{-1}. This difference has been attributed to disparity in fish predation pressure (Jeppesen and others 1994; Aaser and others 1995): *Neomysis* co-exist with small-sized sticklebacks as these mainly predate on the smallest mysids and not on the large egg-bearing females (Søndergaard and others 2000). As both *Neomysis* and sticklebacks predate on zooplankton (Worgan and Fitzgerald 1981; Delbeek and Williams 1987; Hanazato 1990), the predatory control of zooplankton is likely higher in nutrient-rich brackish lagoons than in comparable freshwater lakes, as also indicated by a lower zooplankton:phytoplankton ratio in brackish lagoons (Jeppesen and others 1994). In addition, sticklebacks and mysids occur frequently within the vegetation (Muus 1967; Jeppesen and others 1997), reducing the value for the zooplankton of using submerged macrophytes as a daytime refuge.

Variations in salinity may, however, also affect zooplankton community structure directly. Zooplankton have different tolerance levels to salinity (Aladin 1991). Large-sized *Daphnia*, which are the main controllers of phytoplankton in freshwater lakes (Carpenter and Kitchell 1993), appear mainly at relatively low salinity (<2‰) (Jeppesen and others 1994), an exception being *D. magna*, which tolerates higher salinity (Lampert and Rothaupt 1991; Ortells and others 2005). This species, however, only seldom occurs in Danish brackish lagoons, as it is highly vulnerable to predation due to its large size (Jeppesen and others 1994). At higher salinity, grazing control is mainly exerted by small and/or selective filter feeders such as small cladocerans (*Bosmina* spp.), calanoid copepods (*Eurytemora affinis, Acartia* spp.) and rotifers (Heerkloss and others 1991; Jeppesen and others 1994). One may therefore hypothesize that a potential salinity induced shift from the clear to the turbid state will occur in a non-linear way and that the salinity threshold for such a shift depends on both predation pressure and nutrient loading. To test for non-linearity, we conducted a factorial enclosure experiment with contrasting levels of salinity (0–16‰) and nutrient loading in a shallow brackish lagoon (Lake Kogleaks, Vejlerne, North Jutland). We further used monitoring data from 60 brackish lagoons (168 lagoon years) to evaluate the generality of our results.

Materials and Methods

Enclosure Experiment

Forty-eight enclosures with a diameter of 1.2 m each were established in the shallow brackish lagoon Kogleaks (salinity 0.5‰, 50 (μg P l^{-1}, 400 μg N l^{-1}) during the first week of May 1999. The average water level in the enclosures was 0.8 m

and each enclosure had a water volume of approximately 1,000 l. The enclosures were kept open to the sediment and consisted of a clear polyethylene tube, which was attached to a plastic hoop at the top and wrapped around a metal cylinder forced into the sediment. The plastic tube was suspended approximately 30 cm above the surface between four poles by use of elastic connectors. During filling, a net (1 mm mesh size) was held underneath the bottom of each enclosure to prevent fish entrance. The net was removed again when the enclosures had reached the sediment. A net to ward off birds was suspended permanently over each enclosure. A single male three-spined stickleback was added to each enclosure to obtain a moderately low fish density (1 m^{-2}). A salt solution of NaCl, $MgSO_4$ and $NaHCO_3$ and nutrients (nitrogen as $Ca(NO_3)_2$ + phosphorus as Na_2HPO_4) were added to duplicate enclosures to give the following salinities: 0.5, 1, 2, 4, 6, 8, 12 and 16‰, and initial nutrient levels: 50 (Low), 150 (Medium) and 450 µg (High) TP l^{-1} (TN at a N:P ratio of ~10:1 by weight). The enclosures with the lowest salinity and the lowest nutrient levels received no nutrient or salt addition. To allow high salinity adapted species to develop in the more saline enclosures, all enclosures were inoculated with an identical mixture of plankton taken from three different locations: Lund Fjord (1‰), Østerild Fjord (4‰) and the Limfjord (22.4‰). The mixture consisted of phytoplankton (15 ml water from each location) and concentrated zooplankton (100 ml from originally 40 l per lake). In addition, surface 0–5 cm of the sediment (200 ml) pooled from each location was added. To maintain three different loading levels nutrients were added weekly corresponding to 0, 1.5 and 7.5 mg P m^2 day^{-1} and 0, 23 and 115 mg N m^2 day^{-1}, respectively. Due to dilution by rain the salinity typically declined over time. We therefore adjusted it fortnightly to maintain the desired levels. Typically, the reduction was less than 10% between samplings, occasionally 20–30%.

For chemical variables and chlorophyll *a* weekly samplings were conducted after 5 weeks (to allow a shift in structure to occur) from June 16 to October 1 and fortnightly for zooplankton. A tube sampler was used (length = 1.85 m, diameter = 7 cm, with a closing device at the bottom). For zooplankton, the sampling was conducted at five stations along transects distributed across each enclosure, for other variables only at a center station. For zooplankton the water was mixed in a barrel and a 5-l subsample was filtered onto a 50-µm filter and preserved in an acid Lugol's solution. Temperature and salinity were measured after stirring the enclosures gently with a paddle. To ensure comparable conditions in all enclosures throughout the experiment, macrophytes appearing in low abundances in some enclosures were removed with a hoe (*Myriophyllum spicatum* L.) or a sieve (*Lemna minor* L.) at each sampling date.

In the laboratory, cladocerans and adult copepods were identified to species and rotifers to genus level in one of the two replicates from each treatment. Nauplii and copepodites were classified as cyclopoids or calanoids. If subsampling was conducted, it included at least 75 individuals of the most common species/genera (Hansen and others 1992). Zooplankton biomass was calculated using standard values of biomass for each species and life stage (copepodites and nauplii) estimated from numerous length measurements in many Danish lakes (Jensen and others 1996). Chlorophyll *a* (Chla) was calculated spectrophotometrically following extraction with ethanol (Jespersen and Christoffersen 1987). For determination of the zooplankton:phytoplankton ratio, Chla was converted to phytoplankton dry weight (DW) using a Chla:carbon(C)-ratio of 30 and a DW:C ratio of 2.2 (Jeppesen and others 1994). For soluble reactive phosphorus (SRP) we used the molybdenum blue method, for ammonia (NH_4) the phenol hypochlorite method, and for nitrate + nitrite ($NO_{2,3}$) as nitrite after cadmium reduction. Total phosphorus was determined as for SRP after persulphate digestion (Koroleff 1970) and total nitrogen as nitrite after persulphate digestion (Solórzano and Sharp 1980).

Production of heterotrophic bacterioplankton was measured on July 22 at one low and one high nutrient loading salinity gradient as ^{3}H-thymidine incorporation into cold-TCA-insoluble material (Fuhrman and Azam1982). ^{3}H-thymidine was added to water (four replicate samples) from the same bulk sample as for chemical analyses at a saturating concentration (20 nmol l^{-1} final concentration), incubated for 30 min, and stopped by addition of formalin (2% final conc). Two formalin-killed controls were used to correct for background absorption of radioactivity. For an estimation of bacterial doubling times, we used the empirical conversion factors of 2×10^{18} cells mol^{-1} thymidine (Smits and Riemann 1988).

Monitoring Data

Monitoring data from 60 lagoons (168 years, 1–4 per lagoon) distributed along the Danish coast were

used to test for generality. We used summer averages (May 1–Oct 1) from the surface water of 3–10 samples per lagoon per year. Sampling and laboratory work followed standard procedures for monitoring of Danish lakes (Jeppesen and others 2000; Kronvang and others 2005). We used all 168 datasets in the analysis without weighting them according to number of years included.

Statistical Analyses

The relationships between chemical variables (including Chla, Chla:TP and Chla:TN) and salinity were investigated by change point analyses (Seber and Wild 1989). A change point analysis estimates and tests the significance of a salinity value (change point) that splits the relationship between the response variable and salinity into two potentially different linear regression models. The change point analyses were performed on $\log_e$-transformed chemical variables to obtain homogeneity of the residual variation around the linear regression lines, and the change points were estimated by the maximum likelihood method. Significance of nutrient loading specific change points was tested by calculating a simulated exact *P*-value based on the F_{max} test statistic described in section 9.2.2 of Seber and Wild (1989). The F_{max} test statistic is the maximum over candidate change points of standard ANOVA change point specific *F* test statistics for equality of the linear regression models on each side of the change point. The null hypothesis (no change point) distribution of F_{max} is independent of all model parameters other than the change point, which makes it possible to simulate values of F_{max} under the null hypothesis and hence compute the *P*-value. We simulated 10,000 replicate values of F_{max} for each calculation of a *P*-value. Equality of change points between nutrient loading groups was tested by a standard asymptotic likelihood ratio test. An extension of the F_{max} test statistic to allow for nutrient loading specific linear regression models was derived for testing the significance of common change points for the nutrient loading groups. After determining a change point (regime shift) we tested the chemical variables for additional effects of salinity within regimes by standard analysis of covariance (ANCOVA; SAS procedure PROC MIXED, SAS Institute Inc. 2004), and for variables without significant effects of salinity within regimes, we furthermore analyzed the effect and interaction of regimes and nutrient loading. On the multi-lagoon data we conducted a multiple regression using forward selection of a series of environmental variables.

Results

Enclosure Experiment

Major changes occurred in both nutrient level and Chla along the salinity gradient, a sudden shift taking place between 6 and 8‰ (Figure 1). A change point analysis revealed that all significant nutrient loading specific change points were equal to 6‰, and they were all found in the Medium to High nutrient loading groups (Table 1). The estimated nutrient loading specific change points did not, however, differ significantly for any chemical variable. This may to some extent be due to lack of statistical power. Moreover, the same common (to all nutrient loadings) estimated change point (6 ‰) was obtained for all variables, and most of these were significant (three of the first six variables, the remaining two being computed from the first six). Thus, despite the lack of statistical power the analysis provides clear evidence of a regime shift between salinity 6 and 8‰ for all nutrient loadings and chemical variables, although a smaller difference between regimes is observed in the Low nutrient group.

$NO_{2,3}$ and NH_4 exhibited a significant effect of salinity within the groups of salinity regimes identified by the regime shift analysis ($P = 0.0125$ and 0.0312, respectively). For $NO_{2,3}$, this was due to a significant effect of salinity in the high nutrient loading group in both regimes. The estimated effect on $NO_{2,3}$ of an additional 1‰ salinity was a decrease of 16% ($CI_{95\%}$: 6–25%; $P = 0.0040$) in the low salinity regime and a 15% increase ($CI_{95\%}$: 5–27%; $P = 0.0037$) in the high salinity regime. For NH_4, the overall significance was due to an effect of salinity in the low salinity regime in the medium nutrient loading subgroup ($P = 0.0225$) and an almost significant effect in the low and high nutrient loading subgroups ($P = 0.0567$ and 0.0593, respectively). The estimated effect on NH_4 of an additional 1‰ salinity in the low salinity regime with medium nutrient loading was an increase of 19% ($CI_{95\%}$: 3–37%). For the remaining six chemical variables (Table 1), there was no significant effect of salinity within salinity regimes.

For the variables TP, TN and SRP, we found no significant interaction between salinity regimes and nutrient loading ($P = 0.36$, 0.71, 0.92, respectively), but instead significant effects independent of salinity regimes and nutrient loading overall and, specifically, between high and low nutrient loading and high and medium nutrient loading, but not between medium and low nutrient loading (Table 2). Hence, for these variables the estimated differences between nutrient loading groups were

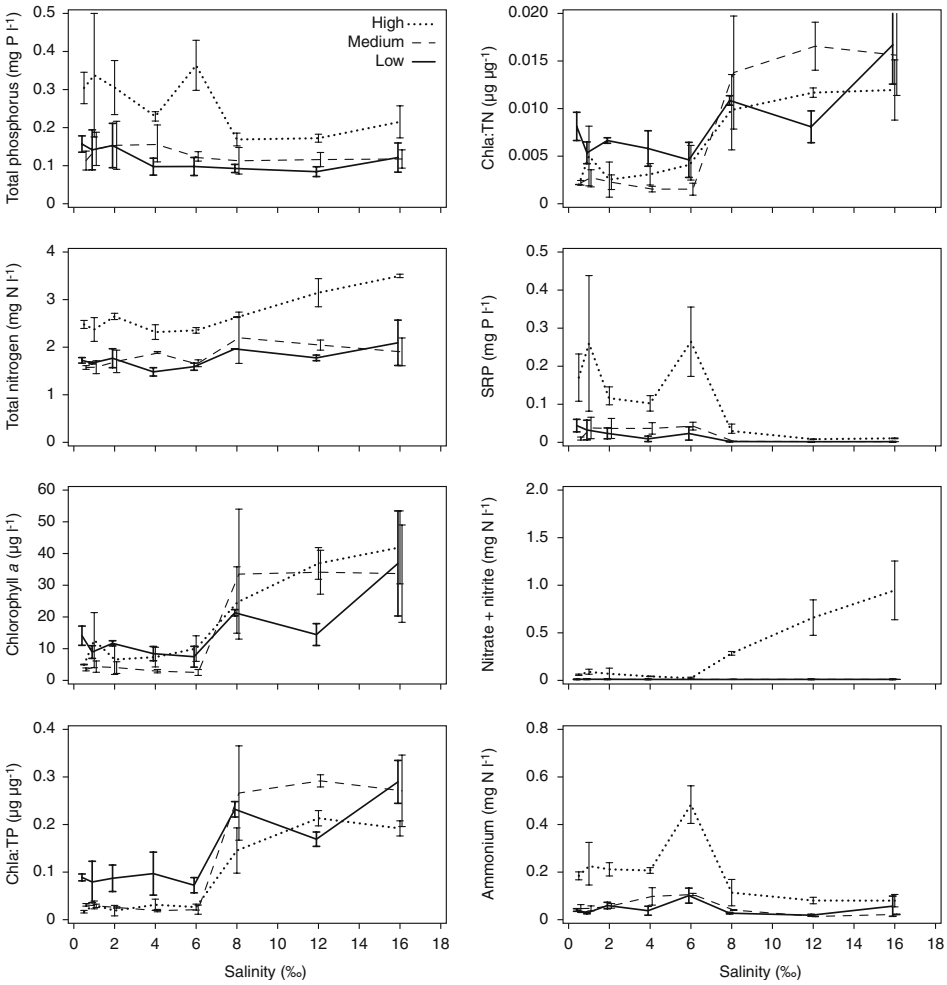

Figure 1. Mean (June 1–October 1) concentration (±SD) of various chemical variables at different salinity and nutrient loadings (low, medium, and high). Chla:TP and Chla:TN are the ratios of chlorophyll *a*:total phosphorus and total nitrogen, respectively. SRP is soluble reactive phosphorus.

Table 1. Change Point Analysis of Chemical Variables

Chemical variable	Nutrient loading specific change points			Common change point	
	Low	Medium	High	Equality of change points	Common change point
TP	8 (0.5508)	4 (0.9542)	6 (0.4548)	0.6162	6 (0.7333)
TN	6 (0.5809)	6 (0.6543)	2 (0.0541)	0.3602	6 (0.1774)
Chla	6 (0.1736)	6 (0.0055)	6 (0.8346)	1.0000	6 (0.0080)
SRP	6 (0.6751)	6 (0.0078)	6 (0.1020)	1.0000	6 (0.0051)
$NO_{2,3}$	8 (0.8118)	8 (0.4808)	6 (0.0158)	0.2078	6 (0.0918)
NH_4	6 (0.3996)	6 (0.0093)	6 (0.0155)	1.0000	6 (0.0007)
Chla/TP	6 (0.3739)	6 (0.0002)	6 (0.0649)	1.0000	6 (<0.0001)
Chla/TN	6 (0.2148)	6 (0.0008)	6 (0.8576)	1.0000	6 (0.0032)

Columns 2–4 contain change points estimated separately for each nutrient loading. Change points are represented by the highest salinity (‰) in the low salinity regime. The P-values for equality of change points between nutrient loading and the estimated common change point are given in columns 5–6. Numbers in brackets are P-values for significance of the change points.

the same in the groups of salinity regimes identified by the regime shift analysis, and the estimated differences between salinity regimes were the same in all three nutrient loading groups (Table 2).

For the variables Chla, Chla:TP and Chla:TN, differences between nutrient loading groups within regimes varied significantly (interaction between salinity regimes and nutrient loading; $P = 0.0026$,

Table 2. Estimated Effects (Est., %) of Salinity Regime and Nutrient Loading on Total Phosphorus (TP), Total Nitrogen (TN), and Soluble Reactive Phosphorus (SRP)

Effect	TP			TN			SRP		
	Est.	$CI_{95\%}$	*P*	Est.	$CI_{95\%}$	*P*	Est.	$CI_{95\%}$	*P*
High-sal vs. low-sal	−25	[−38; −9]	0.0039	21	[13; 31]	<0.0001	−91	[−94; −85]	<0.0001
Nutrient medium-low	12	[−11; 41]	0.3300	3	[−6; 13]	0.4942	32	[−23; 126]	0.3055
Nutrient high-low	123	[77; 180]	<0.0001	52	[39; 66]	<0.0001	780	[413; 1409]	<0.0001
Nutrient high-medium	99	[58; 150]	<0.0001	48	[35; 61]	<0.0001	567	[289; 1043]	<0.0001

Low-sal (≤ 6‰) and high-sal (>6‰). Three nutrient loadings: low, medium and high (nutrient low, medium and high, respectively).

$P < 0.0001$, and $P = 0.0011$, respectively). The estimated differences between nutrient loading groups within salinity regimes and between salinity regimes within nutrient loading groups are presented in Table 3. Interestingly, for the low salinity regime Chla:TP and Chla:TN were much lower in the enclosures subjected to medium or high nutrient loading than in the Low, whereas no differences could be discerned in the high salinity regime.

Heterotrophic bacterioplankton production (Bacpro, cells ml h^{-1}) was related to Chla (µg l^{-1}) (Figure 2). We found no significant differences between slopes among nutrient treatments ($P = 0.6444$) and when pooled together no difference occurred in the intercept either ($P = 0.2774$), the slope being, however, significant ($P = 0.0164$). The equation is:

$$\log_e(\text{Bacpro}) = 17.7 \pm 0.8(CI_{95\%}) + 0.37 \pm 0.30\ (CI_{95\%}) \log_e\ (\text{Chla})$$
$$P = 0.0204,\ R^2 = 0.33,\ n = 16 \quad (1)$$

The shift in Chla (and in heterotrophic bacterioplankton production) coincided with a major shift in the zooplankton community and in biomass. From 0.5 to 6‰, large bodied cladocerans dominated the zooplankton community, whereas rotifers dominated at 8–16‰ (Figure 3). Among daphnids, a shift occurred from dominance of several species (mainly *D. pulex*, however) at low salinities to exclusive dominance of *D. magna* at 6–8‰, among the rotifers *Notolca* dominated numerically at 8‰ and *Brachionus plicatilis* at higher salinity (Jeppesen and others 2002a). Accordingly, the total zooplankton:phytoplankton biomass ratio and the filtering zooplankton:phytoplankton biomass ratio decreased at increasing salinity (Figure 4).

Monitoring Data

The monitoring data indicate a major increase in Chla at salinities exceeding approximately 1‰ at high TP and TN, followed by a decline again at the highest salinities (Figure 5). Multiple regressions using forward selection of variables [Chla (µg l^{-1}), TN (mg N l^{-1}), TP (mg P l^{-1}), Sal (‰), log-transformed and the latter three in power 2 and 3 as well and interactions] gave the following relationship (±SD):

$$\begin{aligned}\text{Log}_e\ (\text{Chla}) = {} & 4.46 \pm 0.17 \\ & + 0.53 \pm 0.07 \log_e(\text{TP}) \\ & + 0.21 \pm 0.03(\log_e(\text{TN}) \\ & \times \log_e(\text{sal} \times 10)^2) \\ & - 0.04 \pm 0.005(\log_e(\text{TN}) \\ & \times \log_e(\text{sal} \times 10)^3),\end{aligned}$$
$$R^2 = 0.68,\ P < 0.0001,\ n = 168$$

suggesting that the salinity-nutrient interaction determining Chla is strongest for nitrogen.

Discussion

In the enclosure experiment, we found a clear regime shift from clear to turbid between 6 and 8‰ salinity at medium and high nutrient loading. The regime shift was, however, insignificant in the low nutrient loading. From the low to the high salt regime, Chla:TP and Chla:TN shifted highly significantly from very low to high levels for all nutrient treatments. The shift was accompanied by a major shift in the zooplankton community, from cladocerans and copepods to extensive rotifer dominance and a major decrease in the zooplankton:phytoplankton biomass ratio (and the filter feeding zooplankton:phytoplankton ratio) from extremely high to low levels, indicating a major

Table 3. Estimated Effects (Est., %) of Salinity Regime and Nutrient Loading on Chla, Chla:TP, and Chla:TN

Salt regime	Nutrient loading	Chla			Chla:TP			Chla:TN		
		Est.	$CI_{95\%}$	*P*	Est.	$CI_{95\%}$	*P*	Est.	$CI_{95\%}$	*P*
Low-sal	Medium-low	−66	[−79; −46]	<0.0001	−69	[−78; −56]	<0.0001	−67	[−79; −50]	<0.0001
Low-sal	High-low	−30	[−56; 13]	0.1408	−71	[−80; −59]	<0.0001	−53	[−69; −27]	0.0011
Low-sal	High-medium	109	[30; 237]	0.0031	−7	[−34; 33]	0.6908	44	[−6; 122]	0.0908
High-sal	Medium-low	39	[−25; 157]	0.2834	19	[−25; 87]	0.4465	33	[−24; 131]	0.3072
High-sal	High-low	51	[−18; 179]	0.1814	−21	[−50; 25]	0.3108	−5	[−46; 65]	0.8443
High-sal	High-medium	9	[−41; 101]	0.7867	−33	[−58; 5]	0.0800	−29	[−59; 24]	0.2251
High-sal vs. low-sal	Low	126	[31; 292]	0.0045	186	[90; 329]	<0.0001	93	[18; 217]	0.0104
High-sal vs. low-sal	Medium	839	[442; 1525]	<0.0001	1002	[634; 1554]	<0.0001	680	[376; 1179]	<0.0001
High-sal vs. low-sal	High	387	[181; 743]	<0.0001	689	[426; 1084]	<0.0001	285	[135; 532]	<0.0001

Low-sal (≤ 6‰) and high-sal (>6‰). See also legend to Table 2.

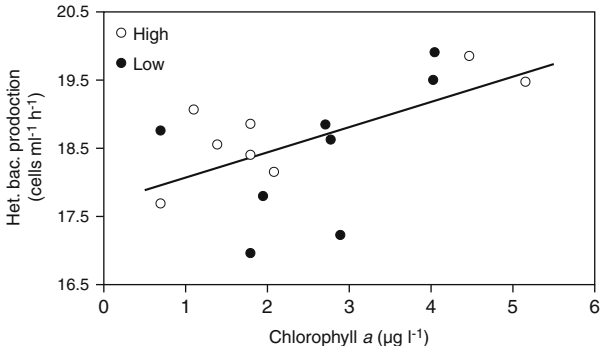

Figure 2. Relationship between heterotrophic bacterioplankton production and chlorophyll *a* (log_e transformed) on July 22 in control and high nutrient loading enclosures. One sample (four replicates) from each of the eight salinity groups.

reduction in zooplankton grazing pressure on phytoplankton. We selected a relatively low fish predation (1 fish m^2), which allowed the salinity tolerant *D. magna* (Lampert and Rothaupt 1991; Ortells and others 2005) to dominate at intermediate high salinity (4–6‰). By contrast, summer monitoring data from 36 brackish lagoons in Denmark show that loss of *Daphnia* typically occurs at 2‰, above which level brackish calanoids, such as *Eurytemora affinis*, *Acartia* spp. and rotifers, become dominant (Jeppesen and others 1994), suggesting a lower salinity threshold for loss of daphnids than in the low-fish enclosures presented here. This difference may be attributed to the higher fish densities usually found in brackish lagoons (Pont and others 1991; Jeppesen and others 1994). At higher fish predation, a lower threshold for a shift to non-cladoceran dominance will likely exist, as *D. magna* is highly susceptible to predation due to its large size (Brooks and Dodson 1965). Support for this hypothesis comes from a parallel enclosure experiment conducted in the same lagoon, run at 2‰ and high nutrient level, but with contrasting densities (0–16 m^{-2}) of male three-spined stickleback (Jakobsen and others 2003, 2004). Jakobsen and co-workers found a shift from clear at less than 2–3 fish m^{-2} to turbid state at more than 6.5 fish m^{-2}. However, whether the shift in their study occurred gradually or abruptly could not be determined, because fish densities in the mid-range, which turned out to be the critical ones, were low due to fish kill. In contrast to the results of the survey study, we only found few brackish water calanoids at high salinity; *E. affinis* was present but never abundant, and *Neomysis integer* densities were low. Instead the density of salt tolerant rotifer species was high. We have no explanation of this poor development of *Eurytemora* and *Neomysis* in our enclosures at high salinity.

We found that Chla:TP and Chla:TN were overall 53–71% lower at medium and high nutrient loading (Chla 30–60% lower) than at low nutrient loading in the low salinity regime, whereas no difference was found for the high salinity regime. The pattern seen at low salinity has also appeared in other experiments conducted in freshwater lakes with high grazer abundance, and this might reflect that grazers when facilitated by benthic food (sediment or enclosure walls) may maintain high abundance and consequently a continuously high grazing pressure on the phytoplankton. In clear-water shallow lagoons benthic and periphytic (if plants are abundant) production may be high and such facilitation therefore potentially important (Vander Zanden and others 2002, 2005; Vadeboncoeur and others 2002, 2003; Jeppesen and others 2002b). Support for benthic/periphytic facilitation of zooplankton comes from stable iso-

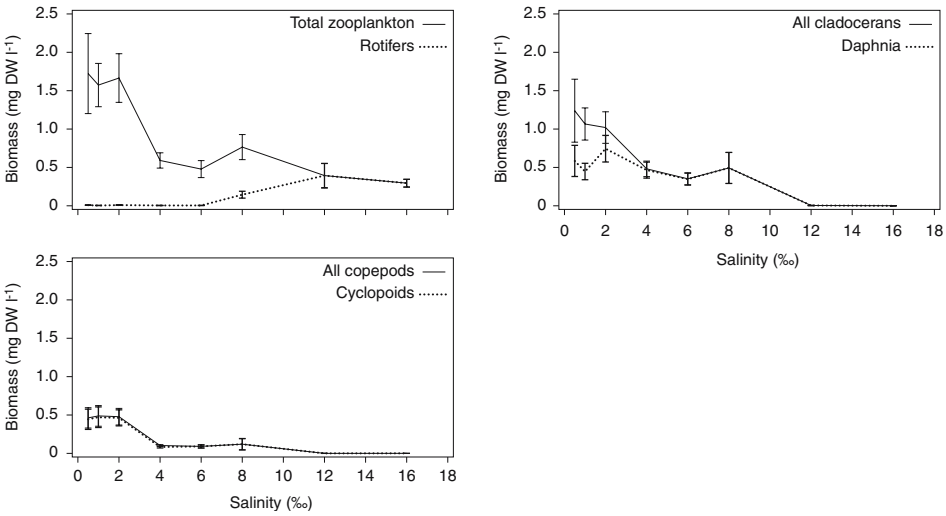

Figure 3. Mean (June 1–October 1) zooplankton biomass and groups of zooplankton at different salinity treatments. Mean values (±SD) data from the three treatments are also shown.

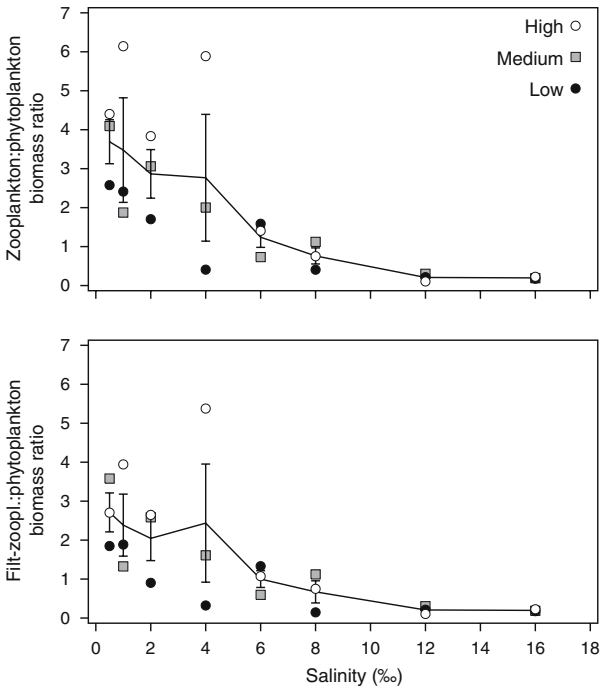

Figure 4. Mean (June 1–October 1) total zooplankton:phytoplankton biomass ratio and biomass of filter-feeding zooplankton:phytoplankton biomass (±SD) at different salinity treatments. We used phytoplankton biomass from the enclosures with zooplankton data only. Also shown are the values for the different nutrient treatments (low, medium, and high).

tope analyses (Jones and Waldron 2003) and grazing experiments (Jeppesen and others 2002b). Our results support the idea that the cascading effects of reduced predation on zooplankton are strongest in eutrophic lakes (Pace and others 1999; Jeppesen and others 2003), but emphasize that this seems not to be the case in high salinity regimes dominated by rotifers.

Besides being affected by nutrient loading as expected we also found that TP, TN and SRP differed between the salinity regimes, TP and SRP being higher and TN lower in the high salinity regime. NH_4 tended to be higher in the low salt regime and nitrate to increase at high nutrient loading in the high salinity regime. Higher NH_4 and SRP (and thus TP) in the low salinity regime probably reflect lower uptake in algae, and for NH_4 likely also the high grazing pressure by zooplankton, as important differences in oxygen between enclosures were not observed (data not shown).

The heterotrophic bacterioplankton production was significantly related to Chla as seen in many other studies (Cole and others 1988) and was independent of nutrient loading (low versus high loading). It was also visible in increasing bacterial abundance at higher salinities (K. Jürgens, unpubl. data). Although only based on a limited set of data it is reasonable to assume that the heterotrophic bacterioplankton production shows a salinity regime shift, as is the case for Chla. This may reflect both the lower Chla in the low salt regime, but likely and more importantly also the high cladoceran grazing pressure (high zooplankton:phytoplankton ratio). Cladocerans exert a strong top-down control on bacterioplankton as seen in studies from shallow Danish freshwater lakes with similarly high zooplankton:phytoplankton ratios (Jürgens and Jeppesen 1997; Jeppesen and others 2002b). A shift occurred also in bacterial community composition, as seen from analysis by fluorescent in situ hybridization (FISH): beta-proteobacteria dominated at salinities up to 6‰, whereas alpha-proteobacteria were the major

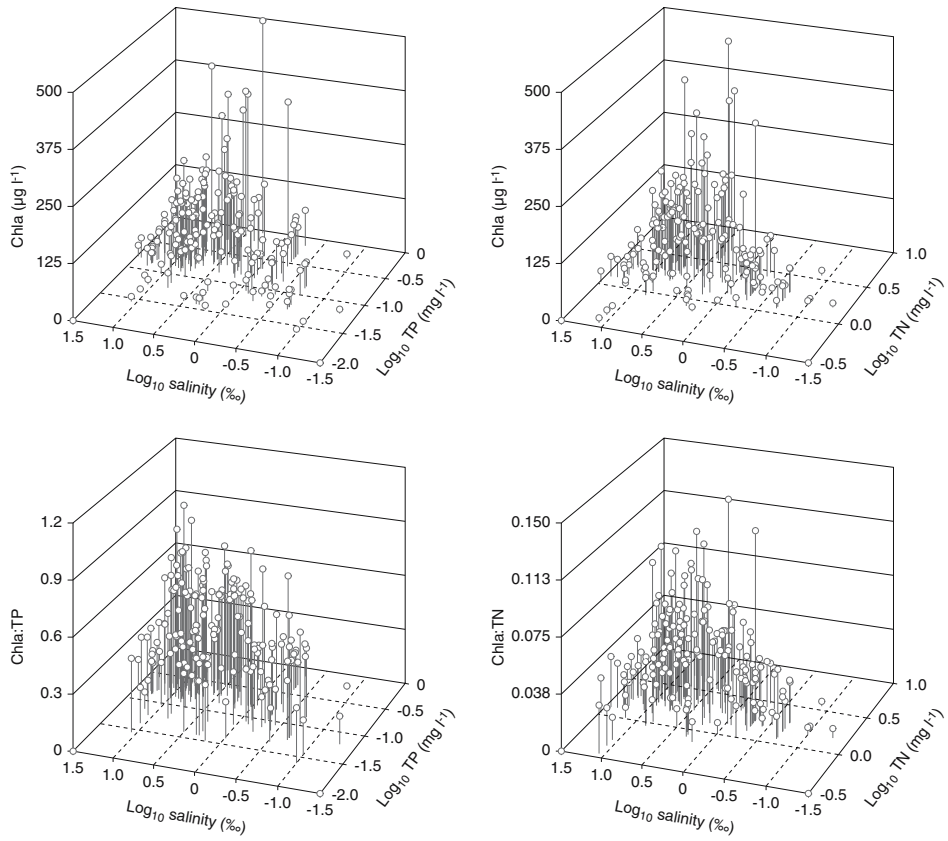

Figure 5. Mean (May 1–October 1) *Upper*: chlorophyll *a* concentrations versus $\log_{10}$ of salinity and total phosphorus and nitrogen, respectively. *Lower*: The same for the ratio of chlorophyll *a*:total phosphorus and nitrogen, respectively, in 60 Danish brackish lagoons (168 lagoon years).

group at higher salinities (K. Jürgens, unpubl. data).

Regime shifts are easier to provoke in enclosure experiments than in natural systems as interactions will be stronger in a limited space and without the natural spatial heterogeneity (Schindler 1998). The monitoring data presented here (Figure 5) apparently suggest a smoother pattern in nature, although there is a tendency for a non-linear response in Chla:TN to increasing TN at salinities above 1‰. Compiled monitoring data from many lagoons may, however, give the wrong impression of the response type, as variations in, for instance, morphometry and retention time may lead to an apparent smoother pattern in multi-lagoon comparisons than in studies of single locations subjected to year-to-year changes in salinity. That abrupt changes actually occur in the field is supported by a study in shallow brackish Lake Ørslevkloster, Denmark (Jeppesen and others 1997). Here, a major shift from turbid to clear water occurred when summer mean salinity decreased from 1.5–3 to 0.5–1‰. The shift was accompanied by an abrupt shift from a calanoid-rotifer community to a *Daphnia* dominated state, a major decrease in Chla and the Chla:TP ratio and a major increase in the zooplankton:phytoplankton ratio and Secchi depth, all of which are indicative of enhanced grazing by zooplankton (Jeppesen and others 1997). Another example is Lake Lemvig, Denmark, that showed a complete shift in the zooplankton community, from freshwater to brackish species dominance from one year to the next and back again in connection with a slight shift in salinity from 1 to 3‰ and then back to 1–2‰ in the following year (Jeppesen and others 1994). The monitoring data show increasing Chla with increasing TN and TP and interactive effects of nitrogen and salinity, peaking at intermediate salinity. The relatively weak effect of salinity at low nutrient concentrations and stronger effect at intermediate high salinity are in accordance with our experimental results. However, the salinity effect sets in at lower salinity than in our experiment, which may be explained by the low fish predation in the experiment. In contrast to the experimental results, the regression indicates declining effects at the highest salinity. A likely explanation is that the monitored lagoons with higher salinity are more open and tidal influenced systems with higher exchange rates and also a different fauna (e.g., occurrence of marine mussels)

than the more closed brackish lagoon systems at intermediate salinity, which may lead to lower Chla (Møhlenberg 1995) than expected from the experiment. Our experimental results can therefore not be transferred to open tidal systems that might be strongly influenced by filtration from mussels.

Our results have implications for the management of coastal lagoons now and in a future potentially warmer climate induced by global warming. As we found a turbid state at even a low fish density in the high salinity enclosures, restoration of turbid saline brackish systems can most likely only be achieved by reducing the nutrient loading or by enhancing the freshwater input to a level triggering a shift to *Daphnia* dominance. Reducing the salinity to below 2‰ to improve water quality has, based on our results, been recommended for and now successfully applied in an artificial brackish lagoon located in the nature reserve The Eastern Vejler: *Daphnia* spp. appeared in the targeted Lake Selbjerg and the water cleared up (Jeppesen and others 2002a). Our findings also indicate that fish manipulation, a well-known restoration measure in freshwater lakes, will not be a useful tool for brackish lagoons, unless the salinity is below the threshold for a potential shift to a clear-water state. Managers may also expect major changes to occur in coastal lagoons if they become more saline during summer in a future warmer climate, a factor to be considered when setting the target for ecological quality. Small changes in salinity may create major changes in trophic state.

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