Chapter 12

Long-Term Investigations in Brackish Ecosystems

Hendrik Schubert, Norbert Wasmund, and Kevin G. Sellner

Abstract Variability and complexity in brackish systems require long-term measurements in order to define base conditions, from which deviations can be ascertained. Long-term observations in three systems, lagoons, the Baltic Sea, and the Chesapeake Bay, are examined to identify system changes, unlikely detectable with sampling in single years or in temporally and spatially heterogeneous sampling. One basic condition in brackish systems is the gradient in salinity, which may be large-scale and rather stable stretching over the entire sea (marine gradient), or meso-scale and highly variable such as those in river plumes (estuarine gradient), and upwelling cells (upwelling gradient). For the first two gradients, and in some cases the third, distinct boundaries separate stenohaline taxa from more eurytopic taxa resulting in spatially explicit distributions of plankton, nutrients, and food web characteristics. The natural variability has to be ascertained through repeated long-term sampling in order to fix a baseline for shifts and trends in the ecosystem. A general trend during the last decades is cultural eutrophication, leading to increased phytoplankton biomass and sedimentation, and hypoxia in bottom water. In some areas, eutrophication was repressed in the 1990s, e.g., stabilization of chlorophyll concentrations in the Baltic Proper, recovery of macrophytes in the Darss-Zingst Bodden Chain (DZBC). In the coming years, the effects of declining nutrient loads are expected to cause a return to mesotrophic conditions in the DZBC, resulting in a return of nutrient limitation. Further monitoring will be performed to follow this unique event. It is therefore imperative that the community support long-term observations in these complex systems particularly as increasing human populations exacerbate impacts of global climate change that slowly warms waters, changes intensities and frequencies of meteorological events and responsive hydrologies, and shifts biogeographic ranges of many cosmopolitan taxa.

Keywords Abiotic limitation · Baltic Sea · Brackish Systems · Chesapeake Bay · Macrophytobenthos · Phytoplankton

12.1 Characteristics of Brackish Environments

Brackish environments are complex abiotic and biotic systems, more than just ‘something between marine and limnetic’. As ecotones, they have unique flora and fauna resulting from transitions between freshwater stenohaline cellular functions to quite adaptable euryhalinic taxa. Chemistries also shift, reflecting saline effects on particle–organic matter–ion interactions, the most obvious detected as flocculation of clay minerals into large organic-rich aggregates and the sedimentation of particle-bound phosphorus for eventual release under increasing salinity and lower dissolved oxygen concentrations.

High variability especially can be seen with respect to salinity, dependent on the precedent marine system (tidal amplitude and salinity) and the freshwater inflow regime. Daily amplitudes of >10 psu at some locations have been described. Such changes are challenges for acclimation capabilities of organisms living there, as shown by initial investigations of Remane

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(1940, 1955) who also noted that the mean salinity range influences the effects of this variability as well. A very pronounced sensitivity peak was observed around 5–8 psu, the so-called horohalinicum, where at least for animals a species minimum has been reported (Remane, 1940, 1955; Khlebovich, 1990). In general, species diversity sharply decreases down to the horohalinicum but species diversity can behave differently for individual groups of organisms: for benthic animals and phytoplankton, in general, the number of species increases again at salinities below the horohalinicum (because of increasing occurrence of freshwater species), while macrophytobenthic species numbers seem to decline further.

Salinity is only one factor that can be contrasted in freshwater or marine conditions – brackish systems exhibit large ion anomalies further restricting the range of species able to thrive and, especially in subarctic and boreal regions, brackish systems can be affected by ice scraping/ice cover phenomena, which act in two ways, mechanically as well as by diminishing light penetration.

Brackish systems (lagoons, river mouths, etc.) are mostly restricted to relatively small areas at the coast. Most of them have provided conditions favourable for human settlement and are of high economic importance (maritime industries, transport, fisheries, tourism). These human activities cause heavy deterioration of surrounding brackish ecosystems, with observed effects dependent on human impact *and* hydromorphology of the system. Examples of these cumulative impacts are obvious throughout the world, with dramatic examples in the Chesapeake and Baltic basins. For the former, the near highest water catchment area per water volume ratio of all large brackish systems insures maximum impact of land alterations on Chesapeake Bay responses while extremely high densities of human and animal activities on many Baltic and North Sea rivers guarantees excessive nutrient loads to these low salinity coastal systems. With increasing populations in catchment areas of these systems coupled with expected climatic changes in the coming 50 years, irreversible changes of the systems may occur, restricting the use of these systems for several services offered in the past.

The previously recorded deterioration of these and many other brackish systems as well as potential future stress likely from population growth and climate change support expanded observations over long time scales to assess ecological responses in these imperilled brackish systems in order to gain the knowledge needed for restoration measures and identification of long-term effectiveness of potential management actions. Long-term measurements in these nearshore systems are feasible as they are far more accessible for investigations than the open sea. Fortunately an extensive suite of investigations have been in place for some systems from all over the world over the last 30 years, resulting in several large long-term data sets.

As estuarine and other coastal waters are strongly influenced by highly variable freshwater input, upwelling events, and coastal jets, data gathered from these highly variable systems are difficult to evaluate. Quick changes and steep gradients are typical. Freshwater input from land and salt water input from the sea do create not only a horizontal but also a vertical salinity gradient in deeper waters as well. Most of the vertical gradients (light, temperature, and nutrients) are, however, not unique for brackish waters and therefore not addressed below. Of importance in the following discussion are salinity gradients, a ‘marine gradient’, an ‘estuarine gradient’, and an ‘upwelling gradient’. The horizontal salinity gradient stretching from the inner parts of a brackish sea to the outlet to the ocean, rather long in some cases, is exemplified by the Baltic Sea and the Chesapeake Bay in this chapter. The meso-scale gradients in river mouths or lagoons are referred to as ‘estuarine gradients’. The upwelling gradient refers to the intrusion of deep water of higher salinity into shallow waters, developing a meso-scale horizontal gradient.

The core of the chapter focuses on the value of long-term observations, such as those undertaken through multi-year field measurements, as critical observations to discerning patterns that would permit isolation of specific flora, fauna, and chemical signatures of these three salinity patterns. Long-term data sets for three brackish environments, i.e., lagoons, the Baltic proper, and a drowned river valley (the Chesapeake Bay), are considered for assessing unique system characteristics that otherwise would be difficult to discern with temporally brief observations.

12.2 System Analysis – Gradients

12.2.1 The Estuarine Gradient

The estuarine gradient not only is derived from a changing salinity but also shifts in nutrient concentration, light transmission, organic matter content, and consequently in species composition and

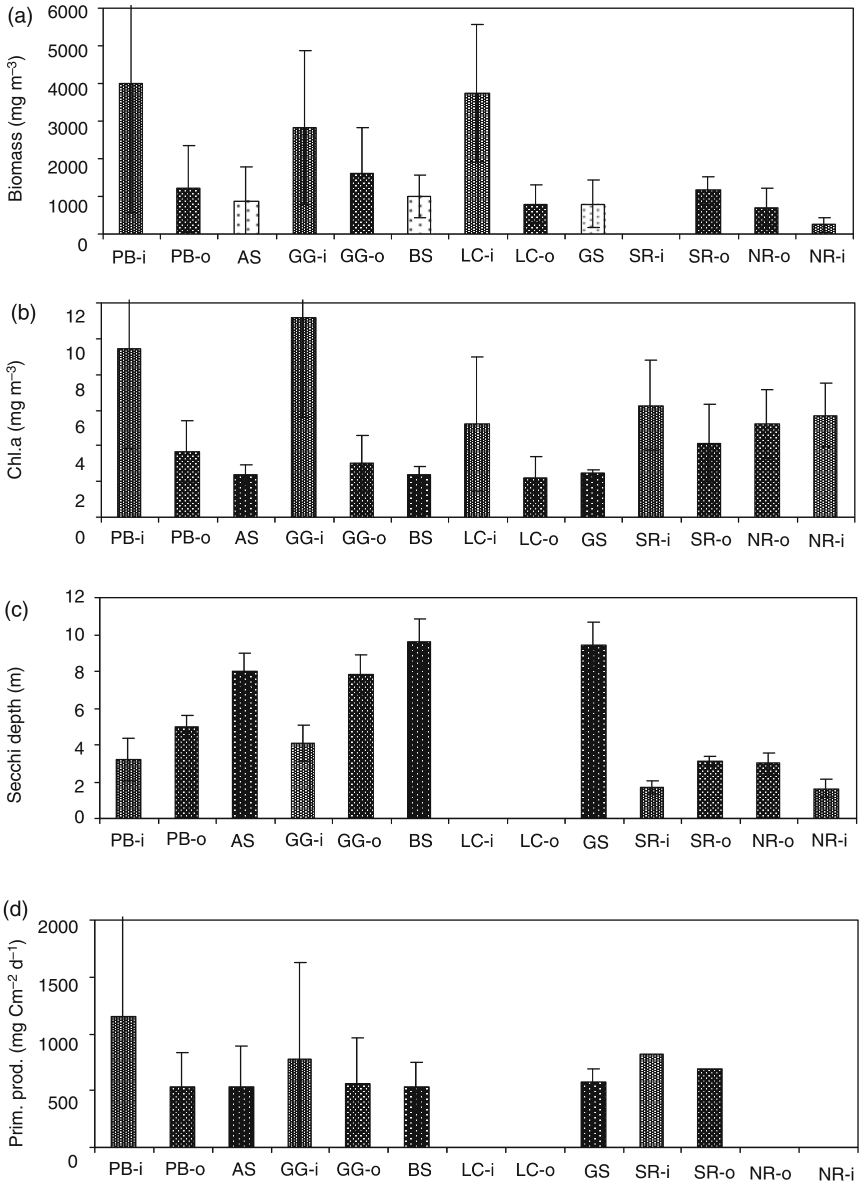

Fig. 12.1 Mean values (1993–1997) of (**a**) phytoplankton biomass, (**b**) chl *a* concentrations, (**c**) Secchi depth, and (**d**) in situ primary production in different Baltic Sea areas. The columns are represent results from short transects from the inner coastal regions (= i, columns densely stippled) to the outer coastal regions (= o) to the open sea (AS = Arkona Sea, BS = Bornholm Sea, GS = Eastern Gotland Sea, columns sparsely stippled); PB = Pomeranian Bay, GG = Gulf of Gdańsk, LC = Lithuanian coast. In the Gulf of Riga, the transect is arranged from the southern (SR) to the northern (NR) reach. The *bars* indicate confidence intervals ($p = 0.05$, $n = 5$). Primary production means from the southern Gulf of Riga calculated by pooling seasons of 1994–1997 first and estimating one combined annual average subsequently (after Wasmund et al., 2001)

trophic interactions (predators, food web structure). These different factors are interrelated and hamper causal analysis. The estuarine gradient along the Darss-Zingst Bodden Chain (DZBC) is well studied and provides an excellent opportunity to evaluate the importance of long-term measurements in system characterization. Wasmund (1990) compiled data mainly from the 1970s and found a reduction of phytoplankton biovolume from 27.9 to 3.6 mm^3 l^{-1} and phytoplankton primary production from 611 to 109 g C m^{-2}a^{-1} from the inner to the outer regions of that lagoon-like water. Further, in large river plumes (Oder, Vistula, Klaipeda Strait, Daugava), phytoplankton biomass, chlorophyll *a* concentration, and primary production were higher in comparison with offshore waters (Fig. 12.1).

In the same areas, phytoplankton composition also shifted. In a transect from the Vistula River mouth to the Gdansk Deep (Fig. 12.2), it is obvious that phytoplankton biomass declined sharply, beyond what would be expected from simple dilution. Freshwater species disappear successively, first the green algae *Coelastrum microporum*, *Dictyosphaerium pulchellum, Pediastrum* spp., and *Scenedesmus* spp., followed by *D. ehrenbergianum*. *Microcystis aeruginosa* also disappears quickly but the

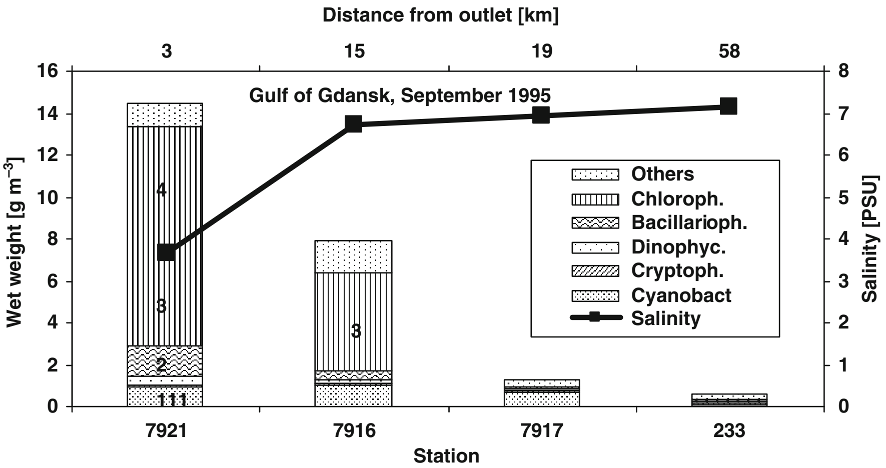

Fig. 12.2 Phytoplankton composition and salinity in surface water in a transect from the Vistula river mouth to the open Gulf of Gdansk on 14–15 September 1995. Important species: 1 = *Snowella septentrionalis*, 2 = *Aulacoseira granulata*, 3 = *Dictyosphaerium ehrenbergianum*, 4 = *Coelastrum microporum*, and *Scenedesmus* spp. (after Wasmund et al., 1999, modified)

cyanobacteria *Snowella septentrionalis, Aphanocapsa delicatissima, Pseudanabaena* sp., and *Merismopedia warmingiana* persisted until station 7917, at a salinity of 7.0 psu. Typical species of the open Baltic Proper were only found at station 233 (*Nodularia spumigena, Dinophysis norvegica, D. rotundata, Heterocapsa rotundata,* and *Chaetoceros densus*).

The Chesapeake Bay and its primary tributaries fall into this estuarine category as well. Similar changes in phytoplankton (loss of cyanobacteria, an increase in diatoms and flagellates) have been observed in the Chesapeake, exemplified in its second largest tributary, the Potomac River estuary (see below).

12.2.2 The Marine Gradient

The marine gradient originates from the inflow of oceanic water into a brackish sea. In contrast to estuarine gradients, the marine gradients are large-scale gradients occurring only in a few brackish seas, in particular the Baltic Sea. The marine gradient is less variable and mainly constitutes a salinity gradient with rather uniform light conditions, concentrations of organic matter, nutrients, etc. Therefore, it is well suited for studying the influence of salinity irrespective of the influences of other factors. Typical distribution patterns for phytoplankton are shown in Fig. 12.3, providing seasonal summaries. Some marine species like *Dactyliosolen fragilissimus, Proboscia alata*, and *Ceratium* spp. occur mainly in the western Baltic. Others, like *Peridiniella catenata, Nodularia spumigena, Aphanizomenon* sp., and *Coscinodiscus granii* are not observed in higher salinities. As expected, diversity is much higher in the western Baltic than in the central Baltic Sea, indicative of the horohalinicum discussed in the Introduction.

12.2.3 The Upwelling Gradient

Upwelling occurs in many marine waters, but the resulting gradients are rather weak. However, upwelling causes exceptionally strong horizontal gradients in stratified brackish seas and estuaries, as deep water is moved to the surface. In contrast to river water in estuarine gradients, the upwelled water has a higher salinity and lower temperature in comparison with the surrounding water. It is rather clear water containing only a few seeding cells (Gromisz & Szymelfenig, 2005) but substantial nutrients. Consequently, upwelling events lead initially to reduced biomass but may later initiate new blooms. At the upwelling frontal boundary, primary production and standing crop can be significantly enhanced (Nômmann, Sildam, Nôges, & Kahru, 1991). Kononen et al. (1996) and Vahtera, Laanemets, Pavelson, Huttunen, and Kononen (2005)

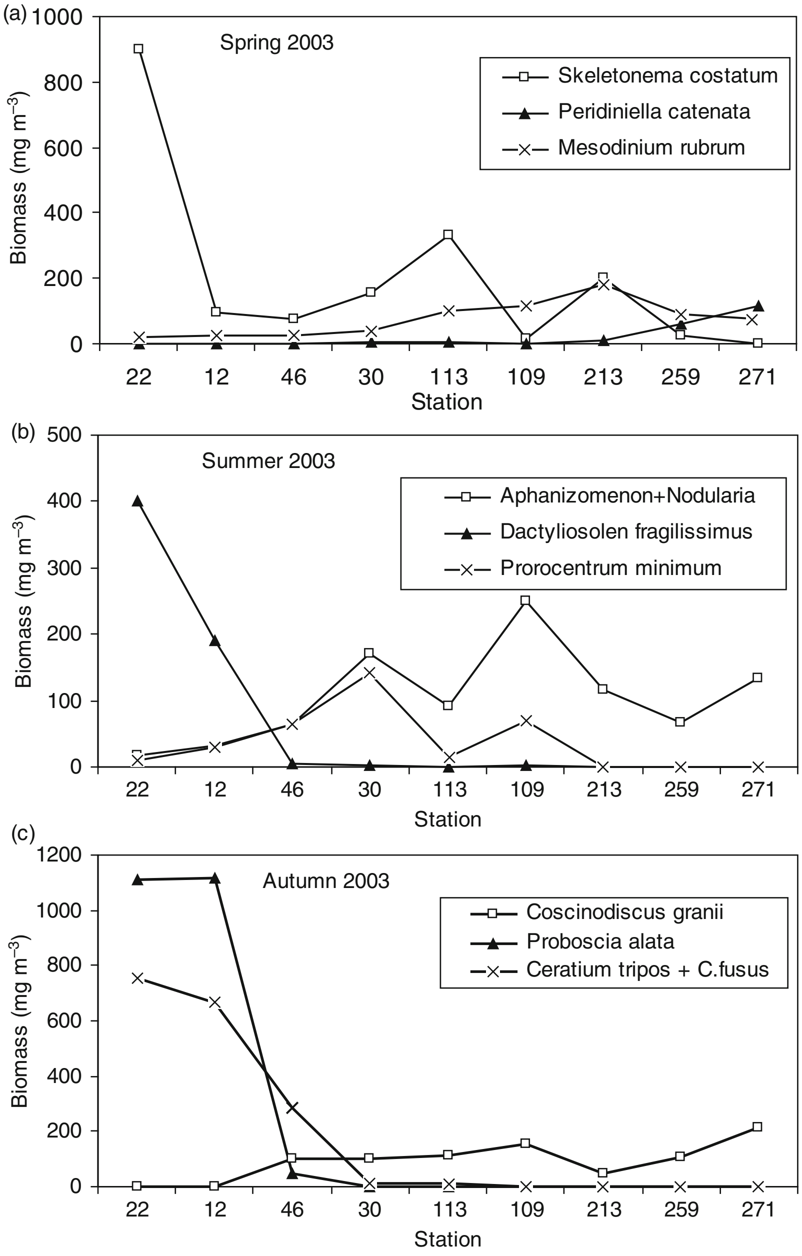

Fig. 12.3 Biomass of selected species along a transect through the Baltic Sea in (**a**) February–May, (**b**) June–September, and (**c**) October–December, 2003

described the initiation of cyanobacteria blooms in the Gulf of Finland by nutrient pulses due to vertical mixing, while several investigative teams in the Chesapeake have identified diatom and dinoflagellate (and associated chlorophyll levels) increases following summer 'tilting' of the pycnocline (see below), followed by dominance of microzooplankton grazers in response to the bloom (Sellner & Brownlee, 1990).

12.3 System Analysis – Long-Term Trends

12.3.1 Drowned River Valleys – Cheapeake Bay

The Chesapeake Bay is the brackish extension of the Susquehanna River along the mid-Atlantic coast of

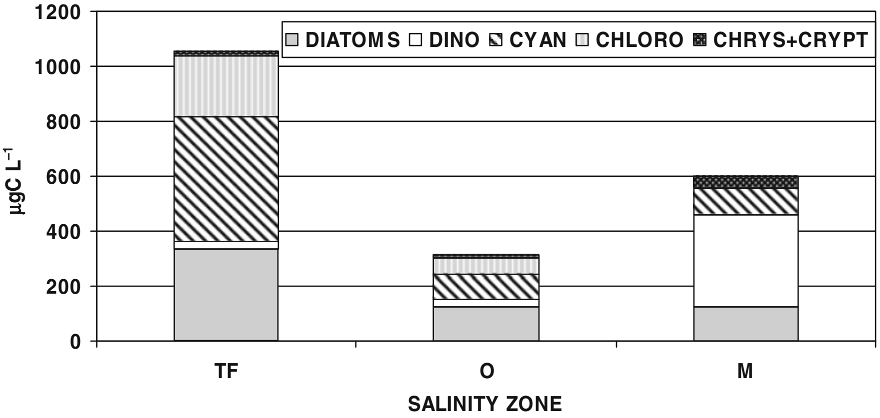

Fig. 12.4 Shift in biomass (μgC l^{-1}, averages from 1985 to 2006) of the most abundant phytoplankton groups in the Potomac River and estuary, a major tributary of the Chesapeake Bay; euglenophytes and prasinophytes not shown due to small contributions. TF = tidal fresh, 0–0.5 psu, O = oligohaline, 0.5–5 psu, and M = mesohaline, 5–18 psu

the USA. It formed after the last ice age when melting glaciers and retreating ice sheets raised sea level and flooded the lower Susquehanna River, yielding a partially stratified estuary, the current Chesapeake Bay.

Gravitational circulation insures mixing of fresh river water with oceanic water throughout the length of the Bay, yielding an extended estuarine gradient where large variability in chemistry and flora and fauna typify the system. Vertical and horizontal gradients in salinity lead to similar stratification in chemical processes and biotic signatures. The most marked gradient is at the freshwater–seawater interface, in the oligohaline zone of the system. In this zone, freshwater planktonic taxa experience severe osmotic stress, leading to rapid declines in abundances and dramatic shifts in taxonomic composition at salinities approximating 0.5–2 psu. For example, Sellner, Lacouture, and Parrish (1988) have documented salinity-induced aggregation and condensation of *Microcystis aeruginosa* typical of the tidal fresh Potomac River estuary, the second largest tributary to the brackish bay after the Susquehanna. The condensation leads to declining photosynthesis, loss of buoyancy control, and eventual rapid sedimentation of stressed, dense *M. aeruginosa* colonies. This loss of cyanobacteria is mimicked by similar declines in other freshwater taxa, particularly chlorophytes (Fig. 12.4).

As salinities increase to meso- and polyhaline conditions further down the estuary, a brackish flora emerges typified by cosmopolitan taxa including winter–spring diatoms *Skeletonema costatum*, *Cerataulina pelagica*, and *Rhizosolenia fragilissima* and the ubiquitous dinoflagellate *Prorocentrum minimum*. In summer, the flora shifts to euryhalinic small centric diatoms, dinoflagellates (*Karlodinium veneficum*, *Gymnodinium* spp.; see white bar in Fig. 12.4), and numerous unidentified microflagellates and cryptophytes. Interestingly, in the last decade, a filamentous cyanobacterium has also increased in the mesohaline and polyhaline bay (Hartsig, Lacouture, Sellner, & Imirie, 2007), leading to substantial cyanobacteria (picocyanobacteria and filament) contributions, 30–50%, to the summer autotrophic assemblage (hatched bar in mesohaline segment, Fig. 12.4).

These horizontal and seasonal shifts in phytoplankton vary year to year, reflecting annual variability in river discharge as well as river-delivered nutrient loads, particularly nitrogen (Malone, 1992; Harding, 1994). Long-term nitrate data collected in the upper Susquehanna River indicates a marked increase in concentration (Hagy, Boynton, Keefe, & Wood, 2004), reflecting population growth and accompanying ‘cultural eutrophication’, leading to the estuarine shifts in salinity and biomass of the phytoplankton taxa described above. Harding (1994) has described the effects of the elevated nitrate levels (Fig. 12.5) entering the upper brackish bay, largely governing the magnitude of the spring diatom bloom. This bloom thereafter governs the magnitude of summer anoxic volume via its decomposition as it settles to the bottom as largely ungrazed cells. The long-term pattern in the bay’s

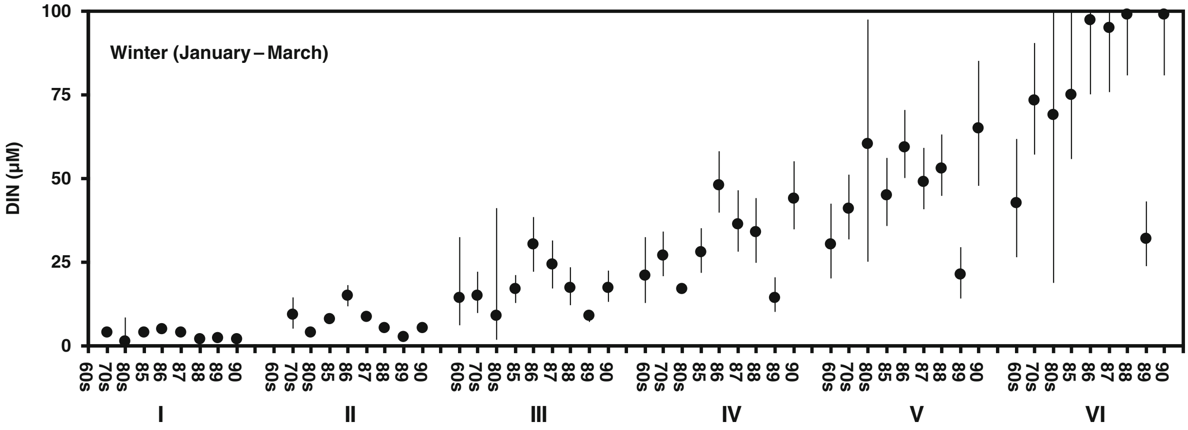

Fig. 12.5 Winter DIN concentrations (µM) by year and salinity regions of Chesapeake Bay (tidal fresh (I) to polyhaline (VI)) for 1960s, 1970s, 1980s, and individual years from 1985 to 1990. *Error bars* are 95% lower and upper confidence intervals (from Harding, 1994)

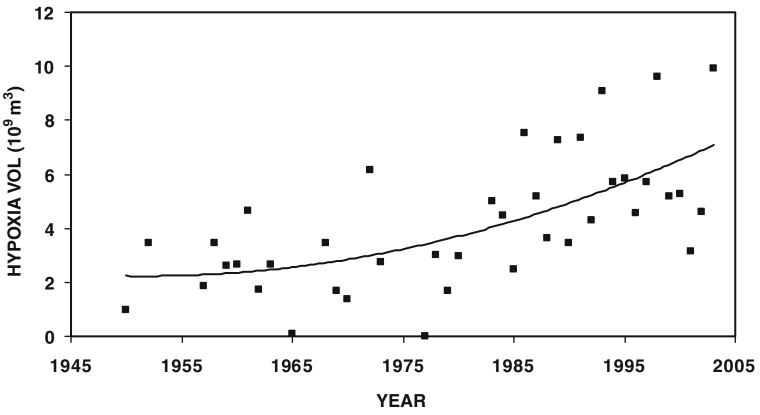

Fig. 12.6 Long-term (1950–2003) changes in bottom water hypoxia volumes in Chesapeake Bay as a function of Susquehanna River discharge (from Hagy et al., 2004)

response to increasing load and algal accumulation is now obvious through the several decade increase in hypoxic volumes in the mesohaline bay, increasing at an exponential rate (Hagy et al., 2004; Fig. 12.6). The decomposition and elevated oxygen demand, in turn, lead to high benthic flux of ammonium and phosphate, fuelling elevated summer phytoplankton biomass over the last several decades (Fig. 12.7).

These recent trends suggest that eutrophication in the brackish bay is accelerating rapidly, perhaps having passed an assimilative capacity a decade or more ago. This increasing trend in system response to nutrient load could not be identified without the multi-year observations, thereby insuring acknowledgement of a rapidly worsening system state that would not be possible with short-term discrete measurements.

An interesting parallel in phytoplankton species selection is observed between the stratified brackish Chesapeake Bay and the open Baltic Sea. The seasonal shift from diatoms that occur in high flow, highly mixed surface waters of the winter–spring in the Chesapeake to small centrics, dinoflagellates, and cryptophytes in the summer can also be observed in the summer following wind-induced local ‘upwelling’. In the Chesapeake, a shift from westerly to northerly or southerly winds >10 m s^{-1} leads to intrusion of sub-pycnocline, nutrient-rich water (derived from the same decomposition of diatoms noted above) into shallow depths along the shore. This in turn favours rapid growth of diatoms and a quick transition to bloom-forming dinoflagellates (Fig. 12.8), not unlike the spring-to-summer transition (Malone

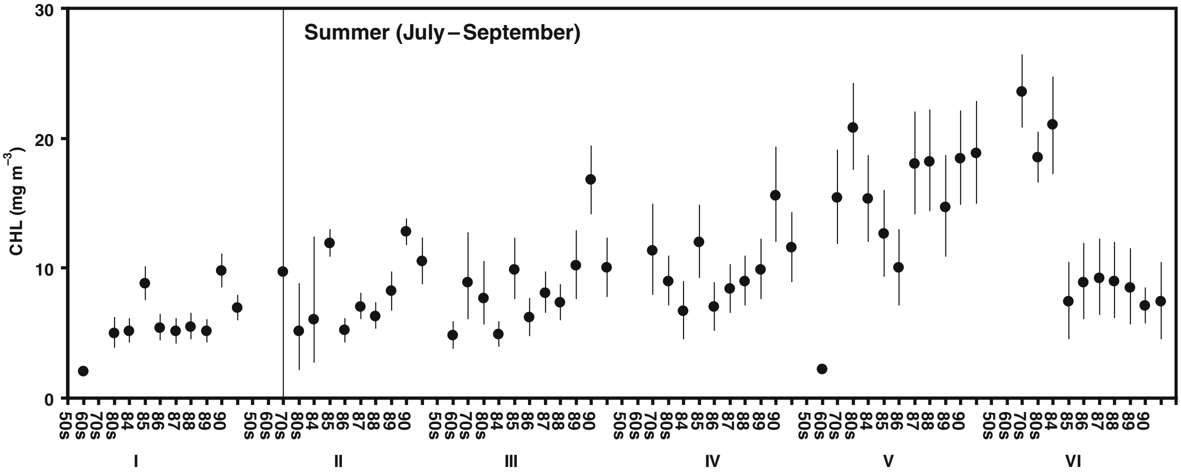

Fig. 12.7 Summer surface chlorophyll a concentrations (mg m^{-3}) in six Chesapeake Bay segments (I–VI) of increasing salinity (tidal fresh (I) to polyhaline (VI)) for the 1950s, 1960s, 1970s, 1980s, and individual years from 1984 to 1990 (*error bars* are 95% lower and upper confidence intervals) (from Harding, 1994)

et al., 1986; Sellner & Brownlee, 1990; Weiss et al., 2005).

In the open Baltic, a similar phenomenon occurs where the seasonal thermocline is displaced, enriching lighted surface waters with regenerated nitrogen (N) and phosphorus (P) with the latter giving rise to the thereafter dominant cyanobacteria *Aphanizomenon flos-aquae* or *Nodularia spumigena* (Kononen et al., 1996). In both systems, ambient flora are displaced to more opportunistic and thereafter dominant summer taxa through short-term, aperiodic wind events that alter surface mixing and nutrient availability. The importance of these event-induced shifts in phytoplankton and their subsequent dominant roles in summer production and trophic dynamics could be ascertained in the future through continuous records of nearshore trends in water temperature (satellite detection, observing systems) and subsequent species/chlorophyll responses.

This pattern for the Chesapeake likely reflects other drowned river valley system responses to increasing human population-derived land use alterations which mobilize nutrients into receiving waters and subsequent downstream advection. Once in the estuary, gravitational circulation insures substantial residence time in the brackish mixing zone, thereby favouring phytoplankton assimilation of elevated nutrient loads

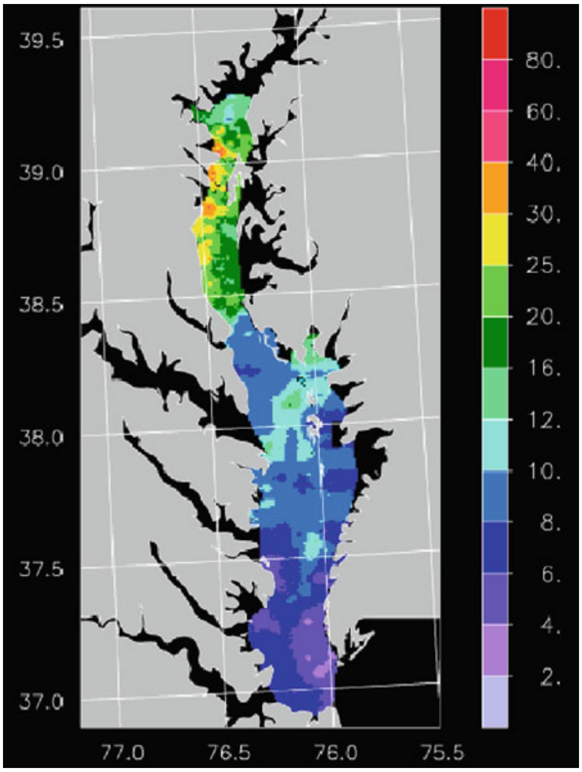

Fig. 12.8 Elevated chlorophyll a (μg l^{-1}) along Chesapeake Bay's western shore following summer pycnocline tilting, a local upwelling event (courtesy of L.W. Harding, Jr.)

and their subsequent utilization within the system prior to export to the coastal ocean.

12.3.2 Large Brackish Systems – Baltic Sea

The brackish character of the Baltic Sea (415,023 km^2, including the Kattegat; mean depth 52 m) is a function of basin geomorphology. It is connected with the North Sea only by narrow straits in the west but receives large riverine input mainly in the east. The resulting 'marine gradient' is discussed above. The sporadic inflow of North Sea water perpetuates this horizontal salinity gradient but also maintains the vertical salinity gradient because the heavier salt water flows into the deep central Baltic basins near the bottom. The resulting strong halocline is a barrier for vertical transport, leading to an oxygen deficit in deep water. Such a strong halocline is typical for deep brackish seas, e.g. also the Black Sea, and even in the Chesapeake (see above). As the halocline restricts the upward transport of nutrients, low human loads of the past centuries around the Baltic Sea likely assured that the system was largely oligotrophic. However, in the second half of the 20th century, high riverine nutrient loading from the large drainage area (1,729,000 km^2, Bergström & Carlsson, 1994) inhabited by more than 80 million people fertilized surface production and enhanced organic loading to the halocline and below, leading to the eutrophic conditions of the system now obvious in elevated summer cyanobacteria blooms.

The impacts of the increasing loads are dramatic. Elmgren (1989) described an increase in phytoplankton primary production by a factor of 1.3–1.7 from the beginning of the 20th century until the early 1980s. Kaiser, Renk, and Schulz (1981) estimated an average phytoplankton primary production of 84 g C m^{-2} yr^{-1}, which relates to 34.8×10^6 t C yr^{-1} over the entire Baltic Sea. A more recent compilation by Wasmund et al. (2001) estimated rates of 150 g C m^{-2} yr^{-1} and 62.1×10^6 t C yr^{-1}, almost a doubling within approximately two decades of the late 20th century. Similarly, chlorophyll *a* concentrations also increased in different areas of the Baltic Sea (e.g. Nakonieczny, Ochocki, & Renk, 1991; Suikkanen, Laamanen, & Huttunen, 2007). More recently, the increase seems to have levelled off in the middle of the 1990s as the former increasing trends are no longer apparent in recent time series. In the western Baltic Sea, chlorophyll *a* levels have been declining for more than 20 years (Wasmund & Uhlig, 2003).

Long-term changes were recorded not only in phytoplankton biomass and productivity but also in species composition. Wasmund, Nausch, and Matthäus (1998) described a strong decrease in the proportion of diatoms in spring blooms of the southern Baltic Proper in 1989, whereas dinoflagellates increased continuously. Despite of the high variability of the spring bloom data due to undersampling, Wasmund and Uhlig (2003) noted the same pattern for the central Baltic (Eastern Gotland Sea) using rigorous statistical analyses. The decrease in diatoms has direct implications on nutrient pools, e.g. the suddenly reduced silicate consumption in the spring bloom (see Fig. 12.9) in the southern Baltic Proper and the Gdańsk Basin (Trzosinska & Lysiak-Pastuszak, 1996) but not in Mecklenburg Bight. Despite decreasing winter silicate concentrations, diatoms are still not limited by silicate but by nitrogen, as shown by Brodherr (2006). Wasmund et al. (1998) attributed this pattern to a strong increase in winter temperatures since 1989. If the water temperature does not fall below the temperature of the highest density of the water (about 2.5°C in the brackish water of the Eastern Gotland Sea), the water column remains at least theoretically stable and therefore limited convective mixing ensues after warming in spring. Lack of mixing (stability) is disadvantageous for diatoms but beneficial for flagellates (see Harrison, Turpin, Bienfang, & Davis, 1986). The recovery of the diatoms since 2000 needs still to be investigated.

One interesting feature of the Baltic Proper is the low nitrogen: phosphorus ratio (N:P ratio), approximating eight, in the winter surface water. This deviation from the Redfield ratio (N:P = 16) is attributed to the oxycline, typical for deep brackish seas with stagnant water below the permanent halocline. In this suboxic region, denitrification and anaerobic ammonium oxidation occur, removing nitrogen from the water (Hannig et al., 2007). Moreover, phosphorus and silicate are liberated from anoxic sediments (Kuparinen & Tuominen, 2001, Conley, Humborg, Rahm, Savchuk,

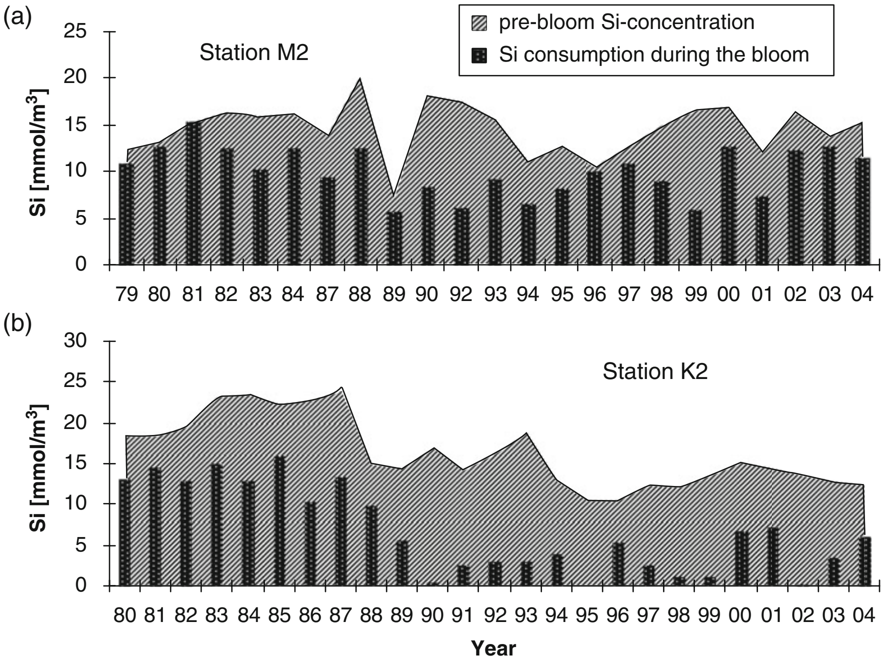

Fig. 12.9 Silicate concentration (mmol/m^3) in late winter (*line*) and difference in pre- and post-bloom silicate concentration (bars) from 1979/1980 to 2004 in (**a**) Mecklenburg Bight and (**b**) Bornholm Sea (updated from Wasmund et al., 1998)

& Wulff, 2002). The resulting decreased N:P ratios have far-reaching consequences. After the disappearance of the spring bloom, mainly by sedimentation, the inorganic nitrogen is exhausted, but a surplus of phosphorus remains in the water. Oligotrophic conditions would prevail but nitrogen-fixing cyanobacteria, mainly *Nodularia spumigena* and *Aphanizomenon* sp., grow in response to the phosphorus (see upwelling discussion above). Their growth leads to blooms, typical for the Baltic Proper in July or early August. These nuisance blooms receive high attention as they are normally toxic and restrict tourism in the bathing season. It is believed that the intensity of cyanobacteria blooms has increased, but statistical support is not yet available as data are highly variable due to high patchiness of blooms and inappropriate sampling. Satellite imagery is a useful tool especially for the monitoring of cyanobacteria blooms as they are buoyant and easily recognizable from space. From interpretations of satellite images, Kahru (1997) found large areas covered by cyanobacteria blooms in 1982–1984 and 1991–1994, which reflects an El Niño-like cycle. Trend analyses by Suikkanen et al. (2007) revealed a cyanobacteria increase in the Gulf of Finland and high singular cyanobacteria peaks in 1985, 1995, and 1996 in the Northern Baltic Proper. Mazur-Marzec, Krężel, Kobos, and Pliński (2006) stated that large-scale occurrences of *N. spumigena* were recorded for the first time in the Gulf of Gdańsk in 1994 and repeated in 2001, 2003, and 2004. Cyanobacteria blooms are not a new phenomenon in the Baltic Sea (Finni, Kononen, Olsonen, & Wallström, 2001), but they have probably intensified (Poutanen & Nikkilä, 2001).

As noted above, the importance of sub-pycnocline nutrients in Baltic summer phytoplankton and productivity is also important in summer phytoplankton production of the Chesapeake (see Fig. 12.7) with the difference, however, that the Baltic is dominated by N-fixing cyanobacteria and these are absent in the Chesapeake. As a result, the spring phytoplankton (diatom) maximum in biomass is followed by low ambient chlorophyll levels (although increasing through the last decade) but high productivity in the summer, the latter fuelled by regenerated N below the seasonal pycnocline in Chesapeake Bay and coastal areas of the Baltic. As this recycled N is introduced into surface waters through 'upwelling' (see above), short-term increases in biomass and productivity occur, visible as dinoflagellate blooms (see Fig. 12.8). It is reasonable to expect that similar disruptions of seasonal pycnoclines in the Bay's major tributaries result in temporary maxima in biomass and productivity, as sub-pycnocline N is delivered to shallow lighted depths of these systems. In the deep central Baltic areas, nitrogen fixation is the main N source for the pelagic system.

12.3.3 Coastal Lagoons – Darss-Zingst Bodden Chain

The Darss-Zingst Bodden Chain (DZBC) represents a typical element of the southern Baltic coast, a shallow lagoon with substantial freshwater inflow. This results in a strong salinity gradient, superimposed with an eutrophication gradient because of the heavy nutrient load from the catchment area (for details see Schiewer, 2007). Salinity ranges between 1 psu in the innermost areas and 8–12 psu at the opening to the Baltic Sea. With a total area of 197 km^2, DZBC is a rather small system and with a catchment area/water surface ratio of 8:1, the potential natural water quality is classified as mesotrophic/eutrophic (Schiewer, 2007).

In the 1970s, intense ecological investigations were undertaken which, through time, have revealed pronounced changes in ecosystem matter flux and species dominance. The first system analysis in the mid-1970s (Schnese, 1978; see also Schiewer, 2007) revealed that the main bulk of primary production was subject to sedimentation (see also C1 – Chesapeake) and not transferred via 'classical' food web to higher trophic levels (Fig. 12.10). Since then, nutrient load has substantially increased, leading to hypertrophic conditions (Schiewer, 1998a). A decade after the initial survey, Schiewer (1990, 1998b) noted that (A) primary production had decreased, caused to a large extent by the disappearance of macrophytes, (B) the importance of the planktonic food web further declined whereas, (C) the amount of detritus was almost stable (Fig. 12.10).

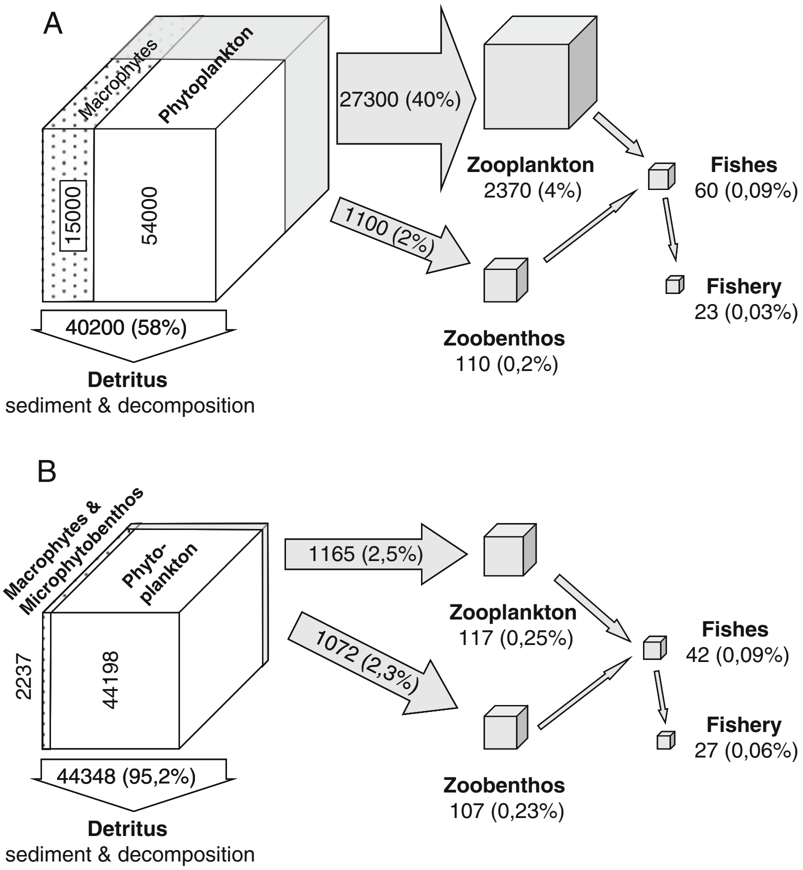

Fig. 12.10 Trophic relationships in the DZBK under (**a**) eutrophic and (**b**) hypertrophic conditions [re-drawn from Schiewer (2001); data from Schnese (1986, *upper panel*) and Schiewer (1985, *lower panel*) for the situation in the (**a**) mid-1970s and (**b**) 1981/1983]

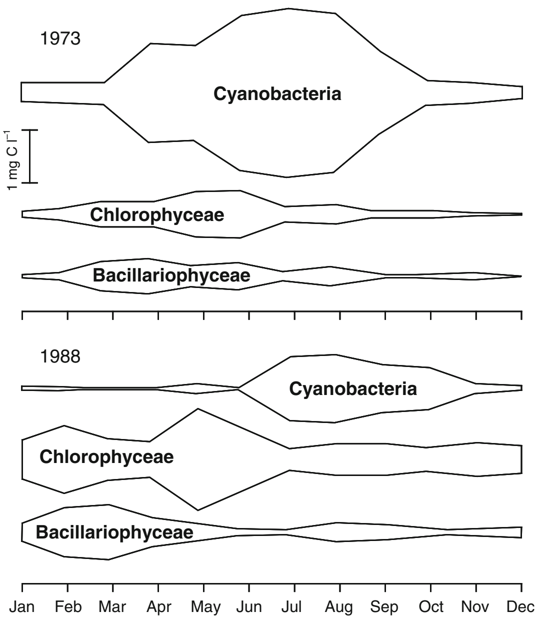

Fig. 12.11 Phytoplankton biomass (mgC l^{-1}) in the Darss-Zingst Bodden Chain under eutrophic (1973) and hypertrophic (1988) conditions (re-drawn after Wasmund & Schiewer, 1994)

Phytoplankton composition also changed. As shown in Fig. 12.11, cyanobacteria dominance retreated in the 1980s (see also Fig. 12.10), whereas chlorophytes benefited from the increased nutrient load. The declining cyanobacteria was associated with a declining pH (Wasmund & Heerkloss, 1993) and subsequent laboratory experiments with the abundant green alga *Tetrastrum* cf. *triangulare* and the cyanobacterium *Nodularia harveyana* revealed better green algae growth at low pH (7.5), while the cyanobacterium grew more rapidly at the elevated pH (9.0) (Wasmund, 1996).

The decrease of N-fixing species, however, can be interpreted as a sign of N-delimitation due to increased nutrient loads, i.e. with abundant N, there is no competitive advantage for diazotrophic cyanobacteria. The larger proportion of cyanobacteria as picocyanoplanktonic species seemed to be responsible for the marked decrease in trophic connectivity, shown already in Fig. 12.10. A regime shift in the same period has also been observed for the open sea (Wasmund et al., 1998, see also C2).

At the end of the 1980s, the common view, therefore, was that the DZBC system suffered strong light limitation as a result of elevated phytoplankton biomass and shading which in turn diminished macrophyte growth and led to a detritus-oriented food web. Reduced macrophytes further reduced productivity of the system, leading to sediment instability even further reducing irradiance availability for the macrophytes as well as phytoplankton.

This view was supported by the results of repeated macrophytobenthos inventories, irregularly investigated since 1895; the first thorough mapping was done in the early 1970s (for an overview see Blümel et al., 2002). In the late 1980s, macrophyte cover was reduced already by >70% (Lindner, 1978) and in the early 1990s, Schiewer (2001) reported that there were only a few remnants left of the former rich macrophytes. However, this statement, made on the basis of a 1993 mapping campaign, had to be revised in 1995, where a massive spread, particularly charophytes, were observed all over the DZBK (Yousef, 2000). Since then, macrophyte cover has increased to levels almost comparable to coverage noted in 1970s (Schubert et al., 2004). Interestingly, with respect to phytoplankton as well as dissolved nutrient concentrations, the situation has not changed much since 1990. Sediment phosphate pools still nourish massive phytoplankton development irrespective of the reduced nutrient loads from the catchment area (Schlungbaum, Baudler, & Krech, 2001).

Schumann (1993) analysed nutrient limitation of the DZBC by means of microcosm studies. Figure 12.12 shows the annual cycle of limitation events which can be described as follows:

After physical limitation by temperature/ice cover/light, rapid phytoplankton growth diminished both P and N, resulting initially in combined limitation by both macronutrients. However, the nutrient pool was sufficiently large to prevent effective zooplankton top-down control. After exceeding a N:P of 15, phosphate release from the sediment increased P-concentrations through onset of N-limitation of the still abiotic controlled (physical factors and nutrient – N) phytoplankton community, causing also a switch to diazotrophic cyanobacteria.

As can be seen from these kinetics, there is no general limitation scheme for these systems, but a complex succession of different limitation stages. These findings fit well with the 'PEG-model' derived from limnetic systems, which also describes a succession of multiple limitation stages occurring over the year in the planktonic system (Sommer, Gliwicz, Lampert,

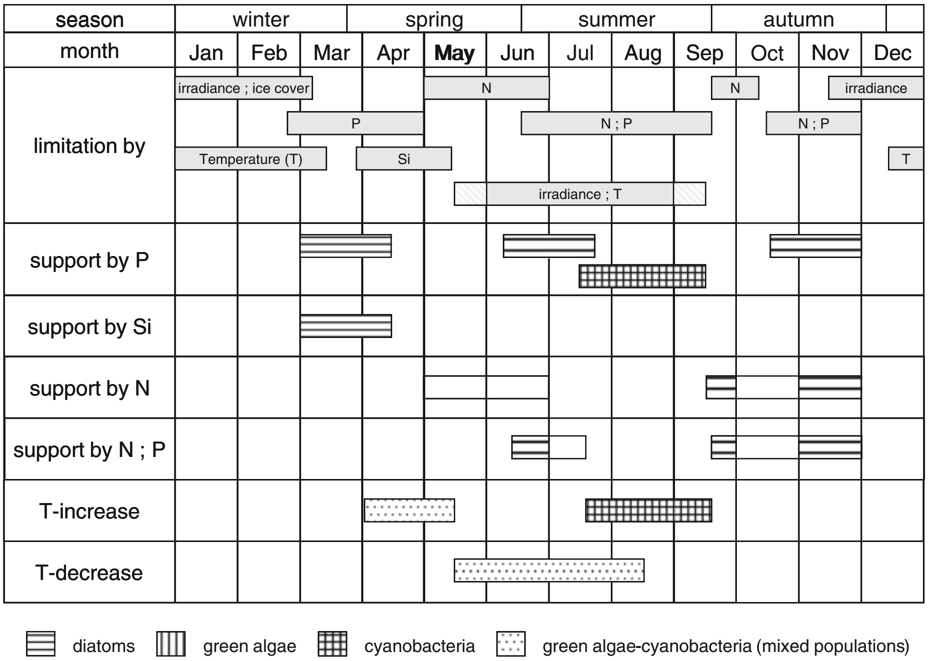

Fig. 12.12 Phytoplankton limitation pattern in the Darss-Zingst Bodden Chain. The limitation pattern was investigated by microcosm experiments with plankton samples from the Darss-Zingst Bodden Chain, in which the respective factors were increased/added for a 6-day period (for details see Schiewer, 1988)

& Duncan, 1986). However, the PEG model does not cover the hypertrophic conditions of the DZBC. Field investigations carried out in the mid-1990s showed that not only light limitation was responsible for the low trophic connectivity. In addition, an increased importance of the microbial loop caused a high turnover of nutrients and organic matter in the pelagic system. As a consequence, productivity of the system is no longer nutrient controlled; nutrient availability only controls species composition. It has been shown by several authors that under hypertrophic conditions irradiance availability and/or temperature follow nutrient availability as the controlling factor in such brackish systems (Schiewer, 2001; Schubert, 1996; Schubert & Wasmund, 2005). However, the mechanisms underlying (particularly) temperature dependency of planktonic biomass development are not yet understood and require further investigation (Schubert & Wasmund, 2005).

In the coming years, the effects of declining nutrient loads are expected to cause a return to mesotrophic conditions in the Darss-Zingst Bodden Chain, resulting in a re-onset of nutrient limitation. Further monitoring will be performed to follow this unique event.

12.4 Conclusions

Irrespective of hydromorphology-based differences and the large variability of almost all parameters typical of brackish waters, long-term studies of the three systems revealed some common features. First, the main driver for changes observed was anthropogenic in origin; irrespective of year-to-year or even decadal changes in weather conditions, eutrophication alone explains a large portion of the changes observed in ecosystem functioning of the systems. With respect to the specific eutrophication effects, decoupling of trophic interactions, leading to increased sedimentation and deposition, seems to be a general system response to increased nutrient availability. The specific changes in phytoplankton composition are more complex. At present, the switch from P- to N-limitation in the Baltic, indicated by an increase of diazotrophic cyanobacteria, can be interpreted as the first sign of hypertrophication. A further increase in nutrient loads may, as shown in C3, lead to light limitation even in shallow systems, conditions where diazotrophic Cyanobacteria are no longer favoured. However, there are several questions still to be answered: the effects of silica depletion in the Baltic Sea as well as the phenomenon of accelerated eutrophication in Chesapeake Bay are of general interest, but also specific details as the kinetics and the time lag in re-mesotrophication of the German coastal lagoon are ecological questions requiring long-term investigations.

Summarizing it can be stated that, beside the general vantage of long-term ecological studies to provide a robust backbone from whose output-specific investigations enable deeper understanding of system behaviour, such studies in brackish systems are requirements without alternatives. As shown in all three examples, the variability in brackish systems does not allow reliable detection of system shifts by point-to-point comparisons. Irregular mixing events can provoke development of dinoflagellates in Chesapeake Bay, and patchiness of cyanobacteria blooms in the Baltic in summer months, while year-to-year variation in weather conditions modulate the effects of nutrient limitation, etc. The latter effect probably will be of greater importance in future as global climate change gradually selects for new species and accelerates kinetics for most biogeochemical processes. Detection of the effects of global climate changes in highly variable systems requires not only profound knowledge about responses to 'non-climate drivers' but also robust data that bound system responses for 'pristine' weather-induced variability over several decades. Only long-term data can provide this analytical potential for detecting change.

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