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ORIGINAL RESEARCH ARTICLE

Ecosystem of the Polish part of the Vistula Lagoon from the perspective of alternative stable states concept, with implications for management issues

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Summary The alternative stable states concept finds broad application in reference to both terrestrial and aquatic ecosystems. For some reason, attempts to implement the concept to explain processes observed in estuaries and Baltic lagoons are very rare. Based on information included in publications issued over the last 60 years, three co-existing states were designated within the strongly elongated basin the Vistula Lagoon, namely: phytoplankton-dominated (Middle Basin), macrophyte-dominated (Elbląg Bay), and transition state balancing between the two former ones (West Basin). Regions of the lagoon representing such states are similar in terms of nutrient concentrations, but they considerably differ in terms of: exposure to wind and wave action, salinity, anthropogenic impact, and multi-level top-down regulations. The paper discusses the role of such drivers, responsible for both the maintenance of a given state, and the past transition into the present alternative state. Moreover, it presents chances for the improvement of the situation, as well as threats which can undermine them.

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1. Introduction

According to the alternative stable state theory, a given system can remain in one of multiple possible states defined by a specific composition of biocoenoses and habitat properties over ecologically-relevant timescales (Holling, 1973; Scheffer and Carpenter, 2003; Scheffer et al., 2001). During the persistence of a given state, a system of ecological feedbacks develops, counteracting the shift into another state. The transition of the ecosystem into another alternative state precedes exceeding ecosystem thresholds, and usually requires the interference of a sufficiently strong driver able to disturb the current balance, and as a consequence lead to profound transformations of the entire system. Transition states, considered unstable, can occur in between. The theory has become an important framework for understanding and managing both terrestrial ecosystems (e.g. grass-dominated vs. shrub dominated), as well as aquatic, freshwater, and marine ecosystems (e.g. clear-water vs. turbid water, kelp forests vs. urchin dominance) (review in Folke et al., 2004).

Ocean ecosystems naturally respond to environmental stress very slowly, and the rate of the occurring processes is distinguished by considerable inertia. Due to such characteristics, the majority of regime shifts in oceans unfold slowly and smooth transitions between equilibrium states are easy to overlook or ignore (Hakanson and Lindgren, 2008; Knowlton, 2004; Lyytimäki and Hildén, 2007; Petraitis and Dudgeon, 2004). The stability of open zones of oceans contrasts with the dynamics of processes occurring in coastal lagoons and estuaries. They are transitional zones where the influences of the aquatic and terrestrial, as well as freshwater and marine environment clash (Perez-Ruzafa et al., 2011). This is additionally combined with the destabilising effect of human activity, usually strongly evident in these areas. In such conditions, the risk of a shift from one state into another is particularly high (Viaroli et al., 2008). Therefore, it is important not only to define the current state of lagoons, but also to determine the rate of changes and drivers causing them, as well as the ecological thresholds exceeding of which can result in a shift to a new state (Lyytimäki and Hildén, 2007). The knowledge of such conditions can permit management of resources preventing the transition into another state, and therefore dramatic changes in the biocoenosis and the provision of ecosystem services to the coastal communities (Hughes et al., 2013; Mollmann et al., 2015). On the other hand, such knowledge can provide the basis for programmes aimed at the management or restoration of the degraded systems (Hakanson and Bryhn, 2008; Jeppesen et al., 1994; Moss, 1994).

In spite of high interest in the stable states concept among marine ecologists, attempts of its implementation aimed at the explanation of phenomena observed in the lagoons and estuaries of the Baltic Sea have been undertaken only in several cases and in a limited scope (Dahlgren and Kautsky, 2004; Munkes, 2005; Rosqvist et al., 2010). This paper is the first attempt of implementation of the theory in reference to a Baltic lagoon, taking into consideration the majority of trophic levels. It concerns the Vistula Lagoon, the second largest and one of the most thoroughly investigated lagoons in the region. The study is based on information included in publications issued over the last 60 years. The objective of the study was to organise knowledge available in the literature regarding the lagoon's ecosystem in order to provide the basis for: i. defining the (current and past) state of the lagoon in the context of the alternative state theory and regime shifts, ii. analysing drivers and buffer mechanisms maintaining a given state, with consideration of bottom-up and top-down regulations, and iii. presenting chances for the improvement of the ecological status of the lagoon, and diagnosing potential threats to the ecosystem which can undermine them. In the paper, alternative states correspond to situations in which one of the groups of primary producers is dominant, namely macrophytes (corresponding to macrophyte-dominated state) or phytoplankton (phytoplankton-dominated state) (Scheffer and Carpenter, 2003; Scheffer et al., 1993).

2. Material and methods

The Vistula Lagoon is located in the south-eastern part of the Baltic Sea. It is a strongly elongated, N—S oriented water body with a length of 91 km, width from 7 to 11 km, and surface area of 838 km^2. The eastern part of the lagoon with an area of 328 km^2 is located on the Polish side (Fig. 1), and the remaining part on the Russian side. To the north, it is separated from the open sea by the Vistula Spit — a shallow belt of sandy land with a width of 1—2 km and length of approximately 50 km. Contact with marine waters occurs through the Baltiysk Strait (the inlet length, width and depth: 2 km, 400 m and 10—12 m, respectively). The extensive surface area of the lagoon contrasts with its low depth (mean depth 2.5 m; max. depth 5.2 m).

The shoreline of the lagoon on the Polish side is weakly developed. The only bay strongly extending into the land is the Elbląg Bay, located in the south-western part of the lagoon, and fed by the Elbląg River (Fig. 1). It has an area of 7.23 km^2, and is very shallow (max. depth in the central area of the bay usually not exceeding approximately 0.8 m).

The lagoon is fed by several rivers draining an area of 23,871 km^2. In comparison to the lagoon's water surface area, the drainage area is exceptionally large (Łomniewski, 1958). More than half of the area is under agricultural use, and approximately 25% is covered by forests. The total number of residents in the lagoon's catchment slightly exceeds one million. Industry is not extensively developed.

Until the end of the 19th century, the Vistula Lagoon was nearly a freshwater basin supplied mainly by two rivers: Vistula and Pregolya. In 1895, for the purpose of protection of areas located at the mouth of the delta of the Vistula River against flood, a new mouth of the river to the Baltic Sea was dug. Moreover, a cascading system of four locks and weirs was constructed on the Nogat River (a distributary channel of the Vistula River) the main stream feeding the lagoon at the time (Łomniewski, 1958). This reduced the inflow of waters from the Vistula River to the lagoon 10 times, resulting in a gradual increase in the salinity of the lagoon waters. Nowadays, the highest salinity, reaching 6.5‰, is observed in the vicinity of the Baltiysk inlet. It gradually decreases towards the east and Western, reaching values close to zero at the mouths of the largest rivers.

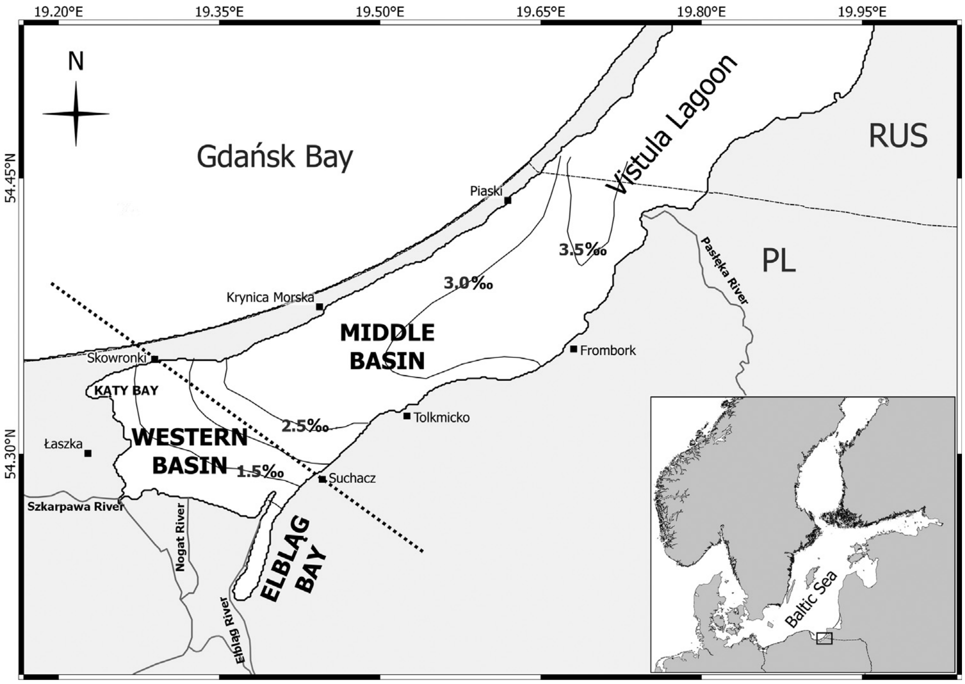

Figure 1 The Vistula Lagoon with marked oligohaline and mesohaline regions (Western and Middle basins, respectively). After Szarejko-Łukasiewicz (1959), modified.

The water level in the lagoon is subject to considerable fluctuations with an amplitude of up to 1.2 m, particularly in the period of autumn-winter storms (Chubarenko et al., 2012). They result from water exchange with the Baltic Sea and strong winds. The large surface area of the lagoon and its low depth favour continuous water mixing, and therefore intensive sediment resuspension. Sediments on the eastern and western ends of the lagoon and in its central part at a depth from approximately 2 m are muddy. Along the southern and northern shores, up to a depth of approximately 1.5—2 m, sandy fractions are dominant, locally with a small admixture of fine loamy fractions.

The lagoon is under the influence of both maritime and continental climate, with air temperature that can attain high annual amplitudes from −31°C to 36°C. The ice cover usually persists for only several days in mild winters, and from December until March in the coldest years.

Large scale research on the ecosystem of the Vistula Lagoon commenced at the beginning of the 1950s. It particularly focused on the determination of the habitat and food conditions of fish, and other issues related to fishery. In addition, monitoring research was conducted by the state environmental protection services. As a result, the lagoon became one of the most thoroughly investigated Baltic lagoons. The present paper focuses on the Polish part of the lagoon. It is based on literature, particularly published mostly after 2010, and concerning: physical—chemical properties of waters and sediments, plankton, macrophytes, macroinvertebrates, fish and birds. In the case of lack of publications from the period, older papers were used, provided that information included in them is still valid.

For the purpose of the study, the lagoon was divided into the Western and Middle basins (Fig. 1). The division was performed based on criteria such as: salinity, exposure to wind, nature of bottom sediments, and occurrence and distribution of vegetation.

3. Results

3.1. Nutrient load

Due to the large area of the catchment of the Vistula Lagoon and predominance of its agricultural use, very high amounts of nutrients are supplied to the lagoon every year. The total load from drainage basin amounts to 16 g of nitrogen and 1.2 g m^{-2} of the surface area of the water body (Witek et al., 2010). The performed balance of nutrients flow suggests that the primary source of nitrogen and phosphorus for primary producers is not the direct supply of nutrients from the catchment, but the mineralisation of organic matter, occurring in sediments and the water column, related to continuous resuspension. As a result of the mineralisation, from 15 to 20% of nitrogen, and as much as 20—40% of phosphorus contained in the sediments is released back to the water (Witek et al., 2010). The spatial distribution of nutrients in the lagoon is relatively even, with slightly increased values of N concentrations in the Middle Basin (Table 1).

According to Witek et al. (2010), the limitation of primary production with phosphorus occurs in spring, when phosphates are exhausted by phytoplankton, and nitrogen is still available. In late spring and summer, nitrogen compounds become the limiting factor, possibly favouring the development of cyanobacteria.

Table 1 Characteristics of the Western and Middle basins of the Vistula Lagoon. The physical—chemical data are the means ± SD (standard deviation) and ranges of monthly measurements at two sites located in the Western Basin and seven in the Middle Basin from May to October 2013. Data provided by the Institute of Meteorology and Water Management National Research Institute, Maritime Branch of Gdynia. SDD — Secchi disc depth.

Parameter	Western Basin	Middle Basin
Max. depth [m]	1—2	3—4
Wind exposure	From low to medium	High
Sediments	Muddy, organic	Sandy to ca. 1.5 m, deeper muddy
Salinity [‰]	1.1 ± 0.3 (0.3—1.8)	2.6 ± 0.6 (1.4—3.7)
N_{tot} [mg l^{-1}]	2.1 ± 0.8 (1.5—4.5)	2.3 ± 0.4 (1.1—3.2)
P_{tot} [mg l^{-1}]	0.11 ± 0.04 (0.06—0.18)	0.10 ± 0.04 (0.05—0.19)
SDD [m]	0.49 ± 0.20 (0.3—1.5)	0.39 ± 0.15 (0.2—0.7)
Chl.-*a* [μg l^{-1}]	48.27 ± 22.9 (13.0—93.2)	54.3 ± 23.8 (8.9—106.6)

3.2. Light availability

Water transparency measured by Secchi disc depth (SDD) is slightly higher in the Western Basin than in the Middle one, conversely as chlorophyll-*a* concentrations (Table 1). More transparent water in the Western Basin was noticed earlier by other authors (Pliński and Simm, 1978; Renk et al., 2001; Ringer, 1959). Relatively low SDD values resulted not only from the concentration of chlorophyll but also the presence of abiotic resuspended particles.

The compensation point, determined by multiplying values of SDD by the number 3 (Holmes, 1970), depending on the analysed region of the lagoon, amounted from 117 to 147 cm. The upper range corresponds to a depth at which charales were recorded in the Kąty Bay (Western Basin) in 2013 (Kornijów, 2018). Some macrophytes, however, especially of the genus *Potamogeton* in the Western Basin, grow at a depth of more than 2 m.

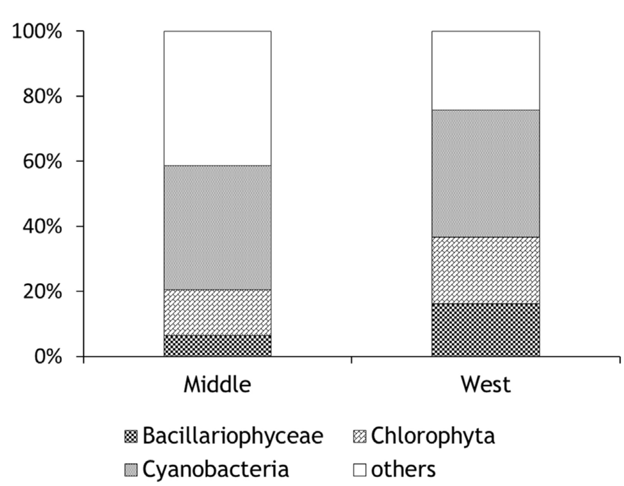

Figure 2 Relative biomass of the main phytoplankton groups in the Western and Middle basins. Mean values from the period 2010—2014, based on data collected by the Province Inspectorate of Environmental Protection in Elbląg and the National Marine Fisheries Research Institute (unpublished).

3.3. Communities

3.3.1. Phytoplankton

The phytoplankton of the lagoon is dominated by cyanobacteria, slightly more abundant in the Middle than in the Western Basin (Fig. 2). In the latter, a higher contribution is reached by diatoms and green algae. Cyanobacterial blooms occur mostly in the summer period, particularly in the Middle Basin (Dmitrieva and Semenova, 2012; Nawrocka and Kobos, 2011). They include several species which can produce cyanobacterial toxins (Rybicka, 2005).

3.3.2. Zooplankton

The structure of zooplankton abundance in both basins considerably differs (Fig. 3). Cladocera are predominant in the Western and Copepoda in the Middle Basin. Rotifera are relatively more abundant in the Western Basin. Cladocera include mostly numerous small (*Bosmina longirostris*, *Chydorus sphaericus*, *Ceriodaphnia* sp.) and large filtrators (*Diaphanosoma brachyurum* and *Daphnia* sp.), as well as predatory *Leptodora kindtii*. The most abundant Copepoda species, considered as inefficient filtrators, are *Eurytemora affinis* and *Acartia tonsa*. The highest contribution in the abundance of Rotatoria is reached by small bodied omnivorous taxa: *Keratella cochlearis*, *Keratella cochlearis tecta* and *Filinia longiseta* (Grzyb, 2012; Paturej and Gutkowska, 2015; Paturej et al., 2017).

3.3.3. Macrophytes

Emergent vegetation is well developed in both basins, forming a belt with a width from several tens to several hundred metres up to a depth of approximately 1 m (Fig. 4). Its higher qualitative variability and cover occurs in the Western Basin (Kornijów, 2018). Here, emergent vegetation occurs practically over the entire length of the shore (except for ports). In some places it is composed of two lateral belts: internal, including reed (*Phragmites australis*) and cattail (*Typha*

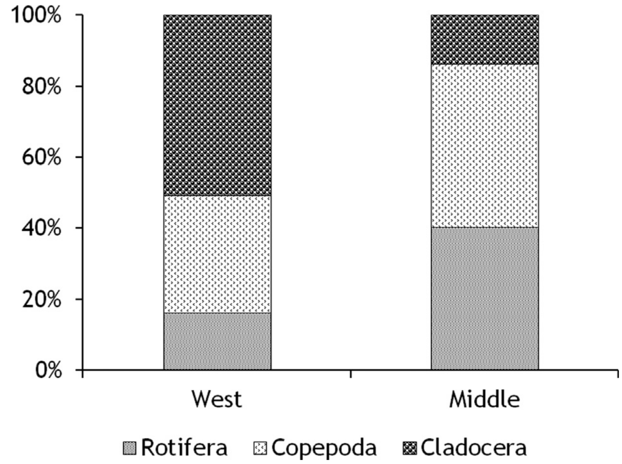

Figure 3 Relative abundance of the main zooplankton groups in the Western and Middle basins.
After Paturej and Kruk (2011), modified.

angustipholia), and external, composed of lakeshore bulrush (*Schoenoplectus lacustris*). The zone between the belts, protected from wave action, with a width from several tens to several hundred metres, includes patches of elodeids and nymphaeids. Such a vegetation pattern, developed under the influence of wave energy, is called large-lake phytolittoral.

In the Middle Basin, patches of emergent vegetation are dominated by reed. They cover approximately 80% of the shore (Pawlikowski and Kornijów, 2018). In places free from reed, sandy beaches occur, developing the psammolittoral.

Submerged and floating-leaved vegetation is well developed only in the Western Basin, and especially in the Elbląg Bay located in its southern part (Kornijów, 2018). Approximately half of the bay's water surface is covered by carpets of fringed water-lily (*Nymphoides peltata*) with an admixture of yellow water-lily (*Nuphar lutea*) (Figs. 4 and 5). Under and among them, elodeid assemblages occur, particularly composed of: Eurasian water-milfoil (*Myriophyllum spicatum*), rigit hornwort (*Ceratophyllum demersum*), Canadian pondweed (*Elodea canadensis*), horned pondweed (*Zanichella palustris*) and curled pondweed (*Potamogeton crispus*). In the remaining areas of the Western Basin, the occurrence of variable submerged and floating-leaved assemblages is limited to a relatively narrow (dozen of metres) near-shore belt (Gajewski, 2010).

In the Middle Basin, practically no nymphaeids occur, and elodeids develop resistant to water motion and drying out clusters of perfoliate pondweed (*Potamogeton perfoliatus*) with an admixture of sago pondweed (*P. pectinatus*) with a diameter from several to several hundred metres, growing up to a depth of approximately 1.2 m (Figs. 5 and 6).

3.3.4. Macroinvertebrates

In both basins, in terms of density, benthos is dominated by detritivorous Tubificinae and larvae of Chironomidae (Kornijów and Pawlikowski, 2015; Rychter and Jabłońska-Barna, 2018). Bivalve *Dreissena polymorpha* is locally encountered on hard bottom. Invasive crabs *Rhithropanopeus harrisii* prefer more saline Middle Basin and *Eriocheir sinensis* overgrown areas, and mouths of rivers (Jabłońska-Barna et al., 2013; Wójcik-Fudalewska and Normant-Saremba, 2016). The biomass structure is dominated by two alien species: bivalve clam *Rangia cuneata* and polychaete *Mareznelleria* sp. (Ezhova et al., 2005; Rychter and Jabłońska-Barna, 2018; Warzocha et al., 2016). The nectobenthos of near-shore

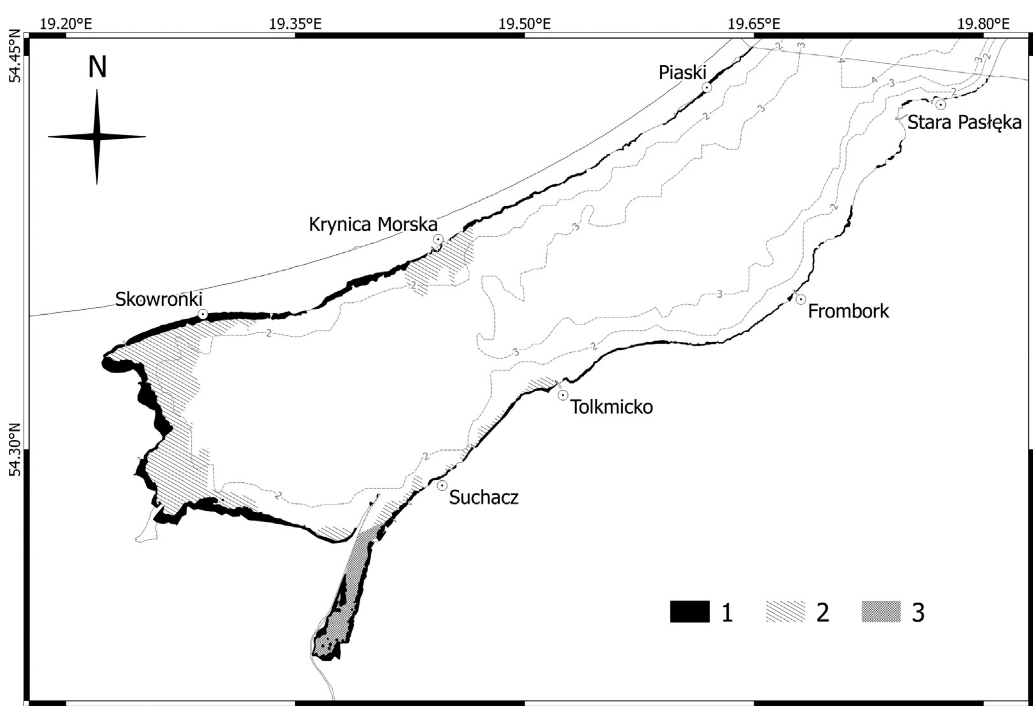

Figure 4 Distribution of emergent vegetation (1), and vegetation with dominance of submerged (2) and floating leaved (3) macrophytes in the Vistula Lagoon.
According to Gajewski (2010).

Figure 5 Poor vegetation in the southern part of the Middle Basin shore; monotonous belt of *Phragmites australis* and scattered patches of *Potamogeton perfoliatus*, 2013.08.02 (to the left), and diverse and luxuriantly developed vegetation in the Elbląg Bay (Western Basin); extensive patches of *Nymphoides peltata* and *Myriophyllum spicatum,* 2012.07.27 (to the right).

shallow areas covered with vegetation, except for the least saline parts of the Western Basin, includes abundant predatory shrimp *Palaemon elegans* and filter feeder mysid *Neomysis integer.*

3.3.5. Fish

The ichthyofauna of the lagoon is composed mostly of freshwater species (Nermer et al., 2011; Psuty and Wilkońska, 2009). Marine fish such as flounder (*Platichthys flesus*), turbot (*Scophthalmus maximus*), and Atlantic herring (*Clupea harengus*) occur in the lagoon periodically and mostly in the Middle Basin. The former two practice irregular food migrations. Herring arrives in spring (March—May) and autumn (September—October) for spawning. In those periods, the fish may constitute approximately 80% of harvested fish biomass.

Non-piscivores (except for herring) in the lagoon are dominated by ruffe (*Gymnocephalus cernua*) and roach (*Rutilus rutilus*) (Fig. 7). In the Western Basin, bleak (*Alburnus alburnus*), European smelt (*Osmerus operlanus*) and silver bream, and in the Middle Basin three-spined stickleback (*Gasterosteus aculeatus*) are also abundant. Greater differences between the two parts of the lagoon occur in the dominance structure of piscivorous fish. An evident division of influence is observed — pikeperch dominates in the Middle, and perch in the Western Basin (Fig. 7).

The percentage of piscivores in the total biomass of planktivorous and predatory fish in the Western Basin amounts to 31% throughout the year (Nermer et al., 2011). In the Middle Basin, their percentage is similar (32%) with the exception of spring and autumn when herring arrives for spawning. Then the value is very low (2%).

3.3.6. Birds

The lagoon together with the adjacent wetlands overgrown by reed beds and riparian forests, and river mouths constitute a well-known refuge of water and wetland birds. The most abundant herbivores include ducks (among others: *Netta rufina*, *Anas clypeata*, *Anas platyrhynchos*, *Anas querquedula*,

Figure 6 Strong winds in the Middle Basin lead to extremely low or high water levels persisting from several hours to several days. Their destructive force limits the possibilities of colonisation by macrophytes, 2013.07.10.

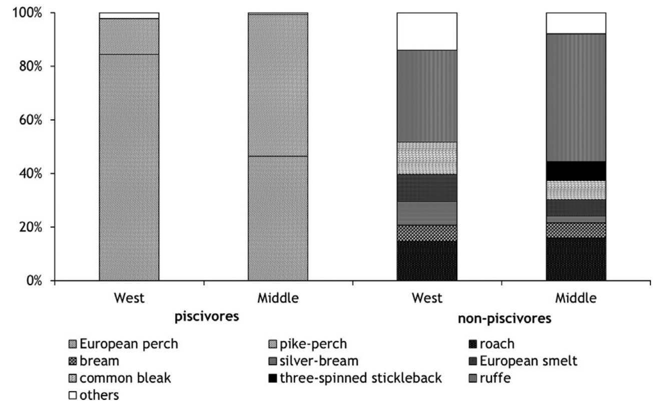

Figure 7 Relative abundance of piscivores (to the left) and non-piscivores without herring (to the right) in the Western and Middle basins.
Based on the data in Nermer et al. (2011).

and *Aythya ferina*), Canada goose (*Branta canadensis*), coot (*Fulica atra*), and mute swan (*Cygnus olor*) (Goc and Mokwa, 2012). The highest numbers of birds, estimated for a total from several to several tens thousand individuals, occur in the Western Basin, particularly in the Elbląg Bay and at the mouth of the rivers. Predatory birds feeding on fish particularly include white-tailed eagle *Haliaeetus albicilla* the abundance of which including juvenile individuals is estimated for 40—50 individuals, seagulls (*Hydrocoloeus minutus*), terns (*Chlidonias niger, C. hybridus*), herons (*Ardea cinerea, Egretta alba*, *Botaurus stellaris*, *Ixobrychus minutus*), grebes (*Podiceps cristatus*) and cormorants (*Phalacrocorax carbo*). The cormorant colony, one of the largest in Europe, is estimated for approximately 11,000 couples (Goc and Mokwa, 2012).

4. Discussion

4.1. Alternative states and driving forces

The recorded differences in primary producers, and especially in the development of macrophyte communities between designated parts of the lagoon allow for ascribing a different alternative state to each of them (Table 2). The Western Basin currently shows the features of the transition state, the Elbląg Bay located in its south part — the macrophyte-dominated state, and the Middle Basin — the phytoplankton-dominated state.

Only the Elbląg Bay has retained its macrophyte-dominated state until now. It is the most freshwater region,

Table 2 Characteristic features determining the alternative status of distinguished basins. EMV — emergent vegetation, SUV — submerged vegetation, FLV — floating-leaved vegetation.

Parameter Status	Western Basin (Elbląg Bay) Macrophyte-dominated	Western Basin (other area) Transition state	Middle Basin Phytoplankton-dominated
EMV	A continuous belt, with domination of: *Phragmites communis*, *Schoenoplectus lacustris* and *Typha angustifolia*	A continuous or two parallel belts composed mostly *P. communis* and *S. lacustris*	Intermittent monospecific belt of *P. communis*
SUV	Vast patches rich in species, with domination of *Ceratophyllum demersum* and *Myriophyllum spicatum*, covering over 40% of bottom surface	From large patches (*Nitellopsis obtusa*) (Bay Kąty) to several dozen metres belts of outside emergent macrophytes (mostly *Potamogeton perfoliatus* and *C. demersum*	Small or medium-sized scattered patches of *P. Perfoliatus* and *Stuckenia pectinata*
FLV	Extensive beds, mostly of *Nymphoides peltata* with admixture of *Nuphar lutea*, covering about 80% of water surface	From extensive (Bay Kąty) to small stands, mostly *N. lutea*	Hardly present (*N. lutea*)
Phytoplankton	Elevated percentage of diatoms, cyanobacterial blooms occasional	Elevated percentage of diatoms and chlorophytes, cyanobacterial blooms frequent in summer	High percentage of cyanobacteria, cyanobacterial blooms frequent in summer
Transparency	From high to medium	From medium to low	Low

largely isolated from the influence of the main basin of the lagoon. At least since the 1950s emergent vegetation has surrounded the bay with a wide and almost continuous ring, and nymphaeids and elodeids have covered more than half of the bottom area (Pliński, 1995; Pliński et al., 1978, and own observations). The macrophyte-dominated state in the bay is maintained in spite of many years (1970—1990) of strong nutrient supply by the Elbląg River (Cieśliński, 2002), as well as supply of faeces of thousands of individuals of waterfowl (Goc and Mokwa, 2012). The vegetation is evidently not impoverished as a result of herbivory by birds, frequently considered as the cause of failure of restoration measures (Phillips et al., 2016).

The literature data suggest that the present transition state of the remaining area of the Western Basin has been lasting since the early 1980s. Before, the area showed many features of macrophyte-dominated state, similarly as the Elbląg Bay. A very wide belt of emergent vegetation of several hundred metres over km-long sections was divided by an open water zone developing large-lake littoral. It was inhabited by luxuriantly developed floating-leaved and submerged vegetation, including extensive meadows of various species of charales (Pliński et al., 1978; Szarejko, 1955). The external belt of helophytes is currently residual, and submerged vegetation severely impoverished qualitatively has been limited to an intermittent belt of approximately a dozen metres wide on the external side of the emergent vegetation.

The shift of the prevailing area of the Western Basin from the macrophyte-dominated to transition state probably occurred as a consequence of interference from many human interactions. For several decades the waters had been supplied with domestic and industrial sewage. The 1970s was also a period of intensified application of mineral fertilisers. As a consequence, the concentration of nutrients in water gradually increased (Margoński and Horbowa, 2003; Różańska and Wiktor, 1978). This, however, did not lead to more prosperous development of phytoplankton (Latała, 1978; Pliński and Simm, 1978; Renk et al., 2001; Witek et al., 2010), probably due to bad light conditions caused by resuspension and substantial dynamics of salinity and water level fluctuations. Notice that the shift from the macrophyte-dominated to phytoplankton-dominated state did not occur in the Elbląg Bay in spite of an approximate, or even higher load of nutrients (Cieśliński, 2002). Therefore, the shrinkage of macrophytes with gradually increasing nutrient load, the mechanism suggested by some authors (Dahlgren and Kautsky, 2004; Krause-Jensen et al., 2008; Munkes, 2005), probably was not determined by excessive development of algae.

Another concept assumes that the shift from one state to another occurs as a result of the disturbance of the environment's resilience (defined as the magnitude of perturbation that a system can absorb) caused by a strong external driver (Holling, 1973). Based on such an assumption, the nutrients are not the driver themselves, but they influence the threshold for the actual drivers causing the switch (Folke et al., 2004; Moss, 2007; Phillips et al., 2016). In the analysed case, there must have been at least several such drivers with combined and synergistic effects. The most important one seems to be the effect of hydro-engineering dredging works, conducted for several years in the first half of the 1980s along the western shore of the lagoon. Their side effect is always strong water turbidity, as well as release of nutrients and pollutants from sediments over a considerably larger area than that directly affected by such works. After conducting the works, part of the phytolittoral with elodeid and nymphaeid assemblages disappeared (Chmara, 2012; Goc and Mokwa, 2012). The negative effect of dredging works on the vegetation is confirmed by the disappearance of the extensive meadows of *Nitellopsis obtuse* in 2014 in the Kąty Bay. The works had been conducted one year before at the mouth of the Elbląg River and at the inlet to the Kąty Bay. The dredging must have affected not only plants, but also other organisms. For example, its long-term negative effect on the spawning grounds of pikeperch, and a strong decrease in its abundance in the Vistula Lagoon was documented by Borowski and Dąbrowski (1998). This might have resulted in the weakening of the cascade effect. Already before, in the 1950s and 1960s, the positive effect of predatory fish on the environment had been strongly limited due to the collapse of the population of pike (Psuty-Lipska and Borowski, 2003).

Chemical compound tributyltin could have also contributed to the degradation of the vegetation. In the 1970s and 1980s it was commonly applied for the protection of nets against invasive hydroid *Cordylophora caspia* almost throughout the lagoon. Tributyltin proved to be harmful not only for invertebrates and fish, but also for plants (Brooke et al., 1986). Sayer et al. (2006) suggest that this compound may promote the replacement of macrophytes by phytoplankton through reducing populations of grazing organisms in water bodies already affected by eutrophication.

Whereas shading by periphyton does not seem to be a driver completely eliminating macrophytes, it undoubtedly contributed to the worsening of the plants' condition. Weakened plants could more easily yield to the pressure of omnivorous/herbivorous invertebrates (Bakker et al., 2016; Hidding et al., 2016). Next to crustaceans (Chinese mitten crab *E. sinensis*, dwarf crab *R. harrisii*, and spinycheek crayfish *Orconectes limosus*), they also include several species of Amphipoda. The latter reach considerably smaller sizes, but they inhabit plants in enormous numbers, so their cumulative effect can be substantial (Kornijów, 1996).

The Western Basin currently remains in a transition state balancing between the phyto- and macrophyte-dominated state. Periodically, underwater meadows of elodeids and charales develop over extensive areas, particularly in the Kąty Bay protected from wind. Further dredging works, however, lead to their repeated destruction. Each time, this entails the loss of a chance, or at least long-term delay, of gradual, progressing eastwards, improvement of water quality. The plants, and particularly charales, play an important role in the restoration of degraded water bodies, influencing sedimentation and nutrients concentration (Blindow et al., 2014; Van den Berg and Coops, 1999). In addition macrophytes stabilise and oxygenate sediments, and therefore limit internal supply of phosphorus compounds. Moreover, they compete with phytoplankton for nutrients, have an allelopathic effect on algae, and provide habitat structure limiting the strength of the top-down effect of fish on zooplankton, controlling the development of phytoplankton (e.g., Blindow et al., 2014; Moss et al., 1996; Phillips et al., 2016).

The Middle Basin is phytoplankton-dominated, and has remained as such for at least 60 years. Currently, similarly as in the 1950s (Ringer, 1959), its bottom is overgrown by locally large-sized (several hundred metres in diameter), although together not exceeding 5% of the littoral area, patches of *P. perfoliatus*, particularly along the southern shore. Beginning from July, the surface of plants is covered by a thick layer of periphyton. Its abundance can be explained by complete lack of snails (unpublished), considered as the most efficient grazers (Underwood, 1991). The time of the existence of shaded elodeids and nymphaeids in the central part of the lagoon was reduced, and currently lasts for approximately three months (Pawlikowski and Kornijów, 2018). This is a typical manifestation of excessive fertility of the water body, called the "sandwich effect" (Sayer et al., 2010) due to the fact that the period before the appearance of plants and after their disappearance is characterised by strong development of phytoplankton.

The tendency for higher than average concentrations of phytoplankton in more saline Middle Basin can be related to different dominance structure of filtering zooplankton, higher predation pressure on zooplankton, and in consequence lower grazing capacity than in the less saline western part of the lagoon (Jeppesen et al., 1994; Moss, 1994). In contrast to the Western Basin, in the Middle one, crustation zooplankton does not include efficient filter-feeding cladocerans such as: *Daphnia* sp., *Bosmina* sp., and *Ceriodaphnia quadrangula*. Instead, it is dominated by omnivorous *E. affinis* and *A. tonsa*, prosperous in estuaries with highly suspended particulate matter dominated by non-living particles (Richman et al., 1977; Tackx et al., 2003). In the absence of Cladocera, efficient filtrators Rotatoria predominate, freed from food competition. Due to lack of elodeids, water turbidity remains the only refuge for zooplankton against fish predation (Horppila and Liljendahl-Nurminen, 2005). In addition to freshwater fish, stickleback *G. aculeatus* and ziege *Pelecus cultratus* constitute permanent components of the planktivorous ichthyofauna. In spring, zooplankton is additionally strongly affected by Baltic herring *C. harengus* (Dmitrieva and Semenova, 2012; Grzyb, 2012) spawning in more saline regions of the lagoon (Nermer et al., 2011). First, zooplankton is eaten by shoals of adult fish, and then for at least approximately three months also by their larvae and fry until they leave the lagoon. The larvae reach very high densities, even up to more than one hundred individuals per m^3 (Grzyb, 2012), and are able to remove approximately 50% of zooplankton standing stock (Naumenko, 2009). This is probably the cause of the strong decrease in the abundance of zooplankton observed in June (Grzyb, 2012). In addition to planktivorous fish, in the more saline Middle Basin in the open water zone, predatory cladocerans *Cercopagis pengoi* are occasionally abundant, and in the littoral phytophilous crustaceans *N. integer* and *P. elegans*. They may exert an additional top-down impact on zooplankton (Jeppesen et al., 1994; Lehtiniemi and Gorokhova, 2008; Lesutiene et al., 2014; Moss, 1994). In consequence, higher cumulative predation by invertebrates and fish may lead to low zooplankton/phytoplankton ratio, and accelerate eutrophication processes.

The above discussion concerns the role of different drivers in the transition from one state to another, or in the maintenance of the already existing one in the designated parts of the Vistula Lagoon. It is also worth mentioning the top-down causal factor common for the entire lagoon area, particularly strong from the mid 1980s. That includes piscivorous birds, including large white-tailed eagle and many smaller such as: herons, seagulls, grebes, and in particular cormorants — highly efficient predators, even in turbid waters (Gremillet et al., 2012). They control the abundance of mainly small fish such as: ruffe, roach, round goby, or stickleback (Stempniewicz et al., 2003). It is estimated that only the cormorants themselves eat from 1.2 to 2.1 tonnes of fish annually, a biomass comparable to that harvested by fishermen (Kornijów, 2018). Whereas fishermen catch large and economically valuable fish, cormorants mainly prey on small planktivorous species. This may result in the cascading effect leading to reduced pressure of small fish on zooplankton and an increase in zooplankton grazing on phytoplankton. Remains of undigested fish are not returned to water in the form of faeces. They are deposited on land. Therefore, cormorants also contribute to continuous export of nutrients from the aquatic environment. There is at least one example of water quality remarkably improved by the activity of cormorants (Leah et al., 1980).

4.2. Implications for the theory

According to the alternative stable states theory, an ecosystem can remain in one of the states in a broad range of nutrient concentrations (Scheffer et al., 1993). The Vistula Lagoon constitutes an interesting case in which at very approximate nutrient concentrations, but under different hydromorphological, hydrological, and anthropopressure conditions, three different, alternative states developed and co-existed in a single water body. Such a theoretical possibility was earlier considered by Knowlton (2004). Drivers considered to determine the distinguished alternative states are listed in an arbitrarily accepted order (from the most to the least important) in Table 3.

The dominant driver regulating the structure and processes occurring in the lagoon seems to be wave exposure. Only inconsiderable wave action, such as that in the sheltered Elbląg Bay, permits the existence of the macrophyte-dominated state (Figs. 4 and 5). In the exposed central part of the basin, where waves periodically reach a height of up to 1.5 m (Chubarenko et al., 2012), such a state is very unlikely, irrespective of the level of nutrient concentrations (Coops et al., 1991). The destructive effect of wave action on macrophytes and other organisms is magnified by substantial water level fluctuations reaching up to 1.2 m, which periodically permit eroding of deeper located parts of the bottom (Fig. 6). Moreover, wave energy causes resuspension which on the one hand worsens the light conditions and constrains the re-establishment of macrophytes (Green and Coco, 2014; Lawson et al., 2007), and on the other hand magnifies the internal supply of nutrients (Sondergaard et al., 1992), stimulating the development of phytoplankton and periphyton. The Vistula Lagoon can be therefore included to typical coastal water bodies, maintained first of all by physical constraint (Perez-Ruzafa et al., 2011). Water salinity is the second in terms of strength of effect. It determines the structure of biocoenoses, including the contribution of filtrators and predators, and indirectly affects the strength of top-down regulation (Jeppesen et al., 1994; Moss, 1994). The next driver, third in terms of "importance" are bottom-up regulations. They influence the development of vegetation and associated biota

Table 3 The major drivers at four-scale magnitude (low, medium, significant, high) of the distinguished states in particular areas of the Vistula Lagoon.

Area Status	Western Basin (including Elbląg Bay) Macrophyte-dominated/transition state	Middle Basin Phytoplankton-dominated
Wind and wave exposure	From low to medium — shores protected to the west	High — unprotected shores, periodically strong winds from the Baltic Sea, storms
Salinity	From low to medium — salinity < 2 PSU, periodical inflow of more saline waters from the east	High — salinity > 2—5 PSU
Bottom-up forces	From high (nutrient supply by bird faeces in Elbląg Bay) to medium — inflow of nutrients from rivers, periodical resuspension and internal supply of phosphorus	High — permanent resuspension and internal supply of phosphorus compounds
Anthropogenic impact (fishery, toxins, boating, pollution, hydro-engineering works	From low (Elbląg Bay as a reserve) to high until the first half of the 2000s, currently moderate	High until the first half of the 2000s, currently moderate
Multi-level top-down regulations	Significant — very abundant: piscivorous birds, strong pikeperch and perch population, effective grazers (Cladocera)	Medium — very abundant: piscivorous birds, strong pikeperch and perch population, numerous but ineffective phytoplankton grazers (Copepoda, Rotatoria)
Pressure of predators on zooplankton	From low (refuge effect by vegetation structure in Elbląg Bay) to medium — mainly freshwater fish	High — freshwater and marine fish, predatory crustaceans
Herbivory on elodeids/nymphaeids	High — abundant: waterfowl, crayfish, insect larvae, amphipods	Low — low density of waterfowl, abundant: crayfish, insect larvae, amphipods. No snails

particularly in regions of the lagoon protected from wind. A similar conclusion was presented by Viaroli et al. (2008) investigating the role of different drivers determining the state of eutrophic Mediterranean coastal lagoons.

The importance of the drivers concerning trophic interactions, summed up in Table 3 was discussed in Section 4.1.

4.3. Implications for management

The aforementioned drivers with proposed hierarchical order of importance (Table 2) constitute a mutually supplementing system determining the current state of particular regions of the lagoon (Table 2). Their knowledge can be helpful in the development of programmes concerning: restoration measures, environmental impact assessments, or sustainable management of the lagoon's resources. The specification of guidelines for the improvement of the ecological state for particular areas of the Vistula Lagoon should consider not only the presence of the aforementioned drivers, but also conditions such as: the vast surface area of the lagoon, shallowness of its basin and the related susceptibility to resuspension, and already strengthened feedback mechanisms (among others: dominance of phytoplankton, high percentage of cyanobacteria, fine-grained stirred-up sediments difficult to colonise by macrophytes, presence of hydrogen sulphide in sediments as the effect of excessive concentration of organic matter, and high top-down pressure on zooplankton). They can slow down the improvement processes or even make them impossible. The above suggests the obvious conclusion that the possibilities of improvement of ecological conditions in the lagoon, including causing the shift from the phytoplankton-dominated to macrophyte-dominated state, are very limited. It is practically impossible to reduce the strength of the first driver in the hierarchy, namely wave exposure. The application of solutions aimed at limiting the destructive effect of waves, proposed for lakes, e.g. deepening, wind reducing barriers, sand capping of the sediment, changes in the water level, and alterations to the shoreline profile (Penning et al., 2013) is hardly possible in the case of the Vistula Lagoon due to its size. Therefore, it is worth emphasising the role the reed rush in the lagoon plays in wave attenuation and development of habitat conditions. The wide belts of reed occurring on many sections of the Vistula Lagoon, with a mean density of 70 stems $m^{-2} \pm 18$ SD, can substantially modify water insolation, temperature, and oxygenation, as well as the grain size and chemical composition of sediments (Pawlikowski and Kornijów, 2018). Nearshore reed beds, similarly as submerged vegetation, are also important for the protection of shores against erosion, and as a filter for nutrients and organic material flushed from the catchment (Berthold et al., 2018; Christianen et al., 2013; Moller et al., 2011; Rupprecht et al., 2017). Due to this, all human activities should be conducted in a way minimising the impact on both aquatic and riparian vegetation.

According to English and Danish researchers (Jeppesen et al., 1994; Moss, 1994), water quality can be considerably improved by a reduction of salinity to a level below 2‰. It can even lead to a switch from the phytoplankton to macrophyte-dominated state. It may seem that the postulate of a decrease in water salinity in the Vistula Lagoon is not feasible considering the scale of the undertaking. Examples of practical application of such a solution in coastal lagoons are known, however. In the Ringkøbing Fjord on the western coast of Denmark, water salinity is driven by sluice management. Due to a small change in water salinity over a period of two years, the ecosystem changed from a nutrient-driven turbid green water to a grazing-controlled clear water (Hakanson and Bryhn, 2008). Notice also that in the past, human activity has already led to a substantial change in the salinity of the Vistula Lagoon, unfortunately involving its increase. This occurred over the last hundred years, after the construction of locks and weirs in the early 20th century, blocking the inflow of the Vistula River to the lagoon, and redirecting the main river water masses directly to the Baltic Sea. It is justified to claim that the reduction of the inflow of waters from the Vistula River to the lagoon in the 20th century saved the ecosystem from total degradation in the period 1970s—1990s when the inflowing rivers were extremely polluted and resembled sewers (Glasby and Szefer, 1998). The currently existing hydro-technical infrastructure would probably permit a controlled increase in the supply of freshwater to the lagoon and a decrease in salinity. The analysis of the justification of such a solution, similarly as the resulting far-reaching consequences, exceeds the thematic scope of this paper.

According to Jeppesen et al. (2007), measures other than a decrease in salinity, including those leading to a change in the dominance structure of fish and strengthening of the cascade effect, are inefficient in the case of salinity exceeding 2‰, and do not result in the improvement of water quality. Consider, however, that sustaining the current pressure of zooplankton on phytoplankton requires keeping the abundance of planktivorous/omnivorous fish on a relatively low level, possibly through the maintenance of numerous stock of predatory fish with relevant age structure (Eriksson et al., 2009; Sieben et al., 2011). In the case of the Vistula Lagoon, this particularly concerns pikeperch and perch. Their contribution in the total biomass of planktivorous and predatory fish in the lagoon for most of the year amounts to approximately 30%. It is assumed that effective top-down pressure, which can translate into efficient phytoplankton control by zooplankton through the cascade effect, requires at least 50% share of predators in the fish biomass (Moss et al., 1996). In the analysed case, also very strong pressure of piscivorous birds needs to be taken into account, including cormorants having a synergic effect on fish populations, together with predatory fish.

Pikeperch, unlike pike, is a species well adapted to turbid waters due to the specific eye structure and well developed sense of smell (Sandstrom and Karas, 2002). Although perch is a typically visual predator, well adapted to macrophyte dominated habitats (Kornijów et al., 2016), it also thrives in the lagoon, perhaps due to the fact that strongly increased water turbidity only occurs periodically as a result of resuspension. Both of the species control the abundance of not only small planktivorous fish, but also zooplanktivorous crustaceans *N. integer* and *Palaemon elegance* (unpublished). Unfortunately, in spite of more than a threefold reduction of the number of fishing vessels in the 2000s, and implementation of a number of restrictions concerning fishing gears and catch limits, the population of both of the species has been showing symptoms of overfishing over the recent years. This is suggested by a relatively high contribution of individuals only from two or three age classes (age groups 3—5), and low contribution of those with large sizes (Psuty and Wilkońska, 2009). The situation is so serious it may lead to the collapse of the populations of those species of key importance for the functioning of the lagoon. On the other hand, as a result of lack of interest of fishermen (and shortage of large pikeperch), the populations of cyprinid fish: roach and bream, include numerous older individuals. At this stage of life, they are benthivorous, and can intensify bioresuspension (Tatrai et al., 1997). Moreover, they contribute to the spawning success of the population, and their planktivorous juvenile stages increase the feeding pressure on zooplankton. It is therefore needed to limit and control the abundance of large cyprinid fish which remain outside the feeding spectrum of the currently dominating age groups of perch and pikeperch. A solution could be a decrease in the fishing pressure on pikeperch, and an increase in the size-limit. An increase in the abundance of European catfish, present in the lagoon, through fish stocking could be considered, too. The fish, however, grows slowly and over a long period of time. In the conditions of substantial fishing pressure, this largely limits the chance of reaching sufficient sizes by a high number of individuals to efficiently control the population of large cyprinids. Meanwhile, next to fishermen, also white-tailed eagles, numerous in the area, may play a substantial role in controlling the abundance of large cyprinids (Ekblad et al., 2016).

Considerable improvement of water quality and transformation of biocoenosis might occur independently from human measures as a result of the bio-engineering activity of the alien bivalve *R. cuneata*. This thermophilous clam originating from the Gulf of Mexico has been present in the Vistula Lagoon for approximately 8 years. It reaches a length of 4—5 cm and shows fast rate of growth of even 20—25 mm in the first year of life. As a non-selective filtrator, it feeds both on phytoplankton and abioseston. Harsh winters lead to high mortality of the clam population. However, it rapidly regenerates in the following years (Kornijów et al., 2018; Warzocha et al., 2016), reaching abundances of up to 1000 ind. m^{-2} The literature provides examples of positive effect of *R. cuneata* on sediment stabilisation, limiting the development of phytoplankton, and as a consequence improvement of water transparency and reconstruction of elodeid assemblages (Cerco and Noel, 2010; Shaffer et al., 2009). Considering the relatively long time of water retention and small depth of the Vistula Lagoon, the occurrence of a similar effect can be presumed. This is suggested by the observation in 2017 of the co-occurrence of very high density of *Rangia* in the central part of the lagoon (mean: 1147 $\pm$ 353 SD) and exceptionally high Secchi disc depth values in August and September (180 and 140 cm, respectively; own unpublished data) as compared to the multiannual mean value amounting to only approximately 40 cm.

Taking into consideration local hydromorphological and hydrological factors, as well as the composition of biocoenoses, the Western Basin, most freshwater part of the Vistula Lagoon seems to have the greatest chance for restoring the macrophyte-dominated state. The process would probably be already advanced if not for the dredging works conducted every several years. Further hydro-technical works planned for the period 2018—2022 can have a similar effect on the environment, but at a considerably greater scale of the entire lagoon. They involve digging the canal through the Vistula Spit, and construction of a waterway with a depth of 5 m, width from 60 to 100 m, and length, depending on the finally arranged location, from 9 to 26 km in the western part of the lagoon. The execution of the waterway itself, and its further necessary periodical deepening (due to the shallow character of the water body and susceptibility to resuspension) may lead to serious cascade of changes in the environment and food chain, resulting in complete degradation of the ecosystem (Kornijów, 2018).

The phytoplankton-dominated state present in the major area of the Vistula Lagoon does not mean that the situation cannot become even worse. In the conditions of both the macrophyte-dominated and phytoplankton-dominated states, a broad spectrum of habitat conditions can occur, depending on among others the dominance structure of primary producers (Moss et al., 1996). Consequences of the phytoplankton-dominated state of extremely degraded hypertrophic water bodies are various, and always troublesome. Chlorophyll-*a* concentrations can be even several times higher than in the Vistula Lagoon. High concentrations of cyanobacterial toxins are maintained throughout the year, constituting a threat to the wildlife and people. The species diversity of biocoenoses is strongly reduced. The fish stock is limited to several economically useless species, and the smell of decomposing algae extends many kilometres around the water body. Such situations are encountered in hypertrophic lakes and lagoons (Pawlik-Skowronska et al., 2008; Witek et al., 2010). In spite of remaining in the phytoplankton-dominated state over the majority of its area, the Vistula Lagoon still shows features of a eutrophic and not hypertrophic water body (Margoński and Horbowa, 2003; Nawrocka and Kobos, 2011; Witek et al., 2010), and it can remain this way under the condition of sustainable use of its resources and conducting pro-ecological investment policy, if not considering the possibilities of improvement of the state of the lagoon, at least aiming at not increasing the current environmental threats.

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