Phytoplankton response to markedly changing anthropogenic pressure in the Puck Bay, Baltic Sea

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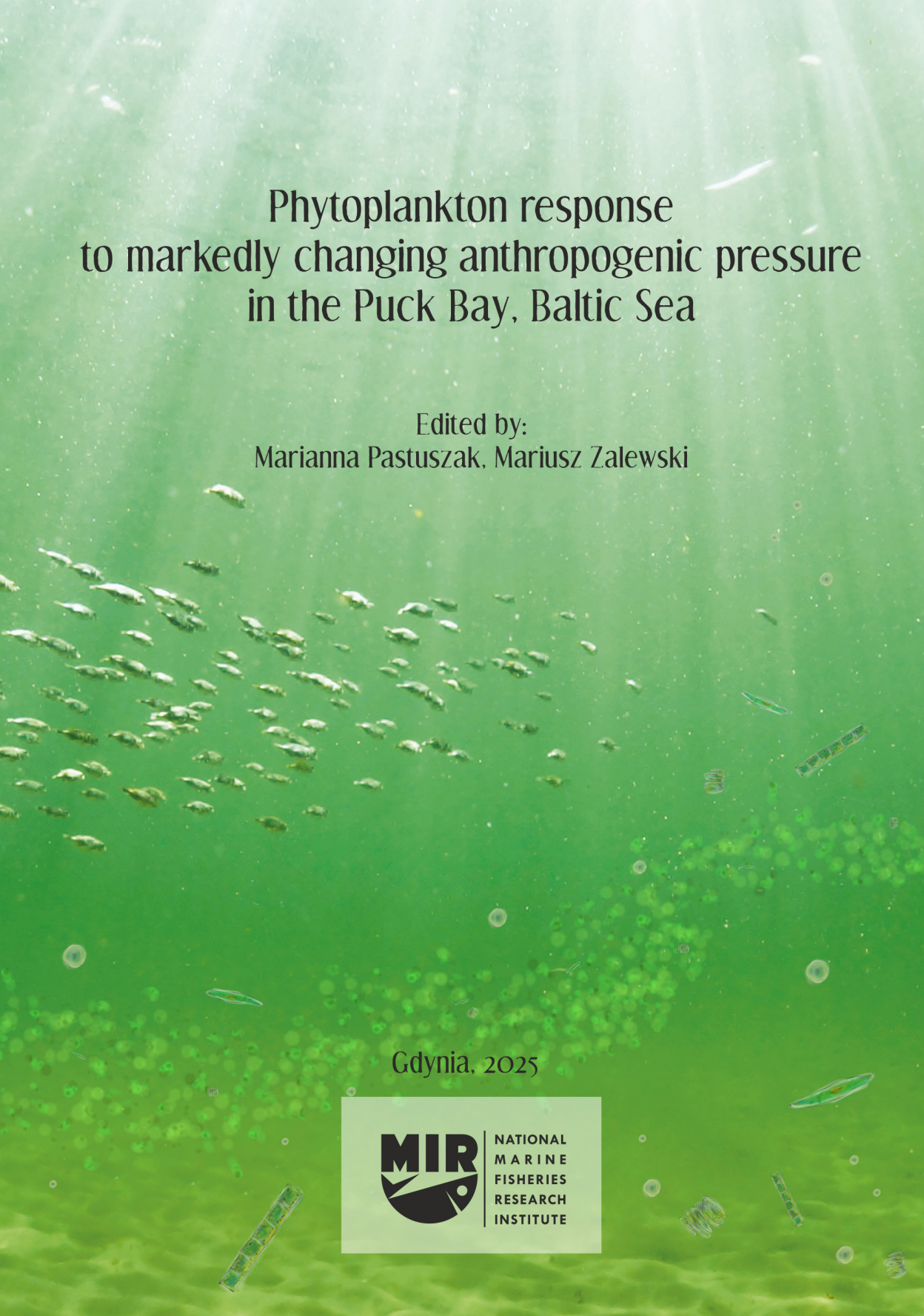

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National Marine Fisheries Research Institute, Gdynia, Poland

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INTRODUCTION

Marianna Pastuszak, Mariusz Zalewski

The Puck Bay, a semi-closed coastal part of the Gulf of Gdańsk, is a unique reservoir due to the preserved species richness of plants and animals inhabiting its bottom, the coexistence of various communities of benthic flora and fauna, and the presence of rare species of benthic plants and animals. This region, consisting of the Puck Lagoon (PL) and the Outer Puck Bay (OPB), is regarded as the most diverse and biologically valuable part of the Polish marine areas, and is a key site for a number of species that are not present along the open seacoast. It is, therefore, not surprising that this region is subject to legal protection under both national and international regulations (Chapter 1).

Excessive discharges of nitrogen (N) and phosphorus (P) to the Puck Bay in the 1970s/1980s resulted in development of filamentous algae, which deposited on the bottom of the bay and limited the development of vascular plants and microalgae. As they decomposed, they caused periodic oxygen deficits in the sediments. These facts led to the collapse of the ecological balance in the bay. The most easily noticeable negative effects of these factors included a decrease in water transparency (Secchi depth), the disappearance of underwater meadows that serve as spawning grounds and growth sites for juvenile stages of many fish species, and unfavorable changes in the species structure of ichthyofauna. The Puck Bay, part of the Gulf of Gdańsk, has been subject to increasing anthropogenic pressure generated not only by direct (wastewater treatment plants - WWTPs and small rivers feeding the lagoon), but also by indirect loads of nutrients due to water/mass exchange between the bay and the open Gulf of Gdańsk fed by the Vistula River (Chapter 1). Eutrophication with its negative effects was a key problem in the Puck Bay, prior to proecological and successful undertakings aiming at nutrient loads reduction, particularly reduction of nutrient emission from local WWTPs (Bolałek and Burska, 2022b).

In 2020 and 2023, National Marine Fisheries Research Institute (NMFRI) received funding to conduct extensive interdisciplinary research in the Puck Bay. Among the many research objectives, the studies covered abiotic parameters (temperature, salinity, oxygen content, nutrients, Secchi depth) and biotic parameters (phytoplankton and chlorophyll *a*). The aim of the presented study is to evaluate to what extent the variable in time anthropogenic pressure, particularly driven by climate change, as

well as excessive in the past and declining over the last decades nutrients supply to the system, have affected the abiotic and biotic parameters in the Puck Bay, coastal ecosystem in the southern Baltic Sea. The specific objectives of our study are to: (i) use all available historical (temperature - 1972-1990; nutrients and oxygen content - 1981-1991; phytoplankton biomass and species composition - 1987-2018) and relevant our data from 2020 and 2023, to build images of changes in long-term abiotic and biotic parameters; (ii) determine the causes and the degree of long-term changes of abiotic and biotic parameters, and emphasize their interdependence; (iii) define abiotic parameters that had a significant impact on the quantitative and qualitative changes of the phytoplankton community. In our own archival resources, we had access to long-term qualitative and quantitative data on phytoplankton, and on content of chlorophyll *a*; besides, we had access to historical data published by other authors. The historical data, covering nitrate, ammonium, phosphate, temperature, salinity, oxygen content, were obtained from the monograph published by University of Gdańsk (Korzeniewski, 1993). We also used vast knowledge contained in the monograph consisting of three volumes dealing with physical, chemical and biological parameters in the Puck Bay (Bolałek and Burska, 2022a,b,c). There was no risk of compilation of the historical and our environmental data collected in 2020 and 2023, because the same sampling strategy and the same analytical methods (nutrients, oxygen) recommended by the Helsinki Commission (HELCOM, 1988; Grasshoff, 1976) were used by the parties. Moreover, the relevant laboratories from the University of Gdańsk and the NMFRI participated in both international as well as interlaboratory calibration of nutrient determination. Besides, in the 1990s, both laboratories conducted joint environmental studies in the Baltic Sea on board R/V Profesor Siedlecki, and determination of nutrients was part of the scientific program.

The considerable volume of scientific material together with graphics prompted us to prepare a monograph ***"Phytoplankton response to markedly changing anthropogenic pressure in the Puck Bay, Baltic Sea"***, providing greater opportunities for a multi-faceted discussion of our latest research results. We consider this monograph as complementary material to the historical, as well as recent research in the Puck Bay, carried out by the University of Gdańsk (Korzeniewski, 1993; Bolałek and Burska, 2022a,b,c).

It is worth emphasizing that the response of phytoplankton to the changing anthropogenic pressure over the past few decades is discussed on a local scale (the Puck Bay), but with the broad reference to disturbances occurring in the Baltic ecosystems, as well as in ecosystems beyond the Baltic Sea. In the light of current knowledge, it is undeniable that all changes occurring in aquatic and terrestrial ecosystems must

be related to global changes, i.e. climate change and the increase in air temperature and, consequently, water temperature. These issues have been widely commented on in the monograph (Chapters 1-3).

The international studies show that climate change has multiple direct and indirect potentially synergistic effects that influence the Baltic Sea species, organism communities, and ecosystem functioning through physical and biogeochemical environmental characteristics of the sea. Effects of changes in ocean temperature and chemistry may alter the physiological functioning, behavior, and demographic traits of organisms, leading to shifts in the size structure, spatial range, and seasonal abundance of population, and initiate interactions in marine food webs. The monograph shows how local and global stressors intertwine, and what effect this has on quantitative and qualitative changes in phytoplankton in the Puck Bay. These microscopic, autotrophic, planktonic organisms face a major challenge, as their exceptional sensitivity requires them to respond quickly to any environmental changes. The changing climate, contributing to rising water temperature, can affect the dynamics and timing of annual blooms. Their composition, duration, and intensity may shift, and frequent harmful algal blooms (HABs) may increasingly occur (Glibert et al., 2001). All such changes in phytoplankton development will lead to unpredictable consequences. Marine phytoplankton constitutes the base of aquatic food webs and is of global importance because it affects the abundance and diversity of marine organisms, drives marine ecosystem functioning, and sets the upper limits to fishery yields.

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1

ANTHROPOGENIC STRESSORS IN COASTAL REGIONS, THE PUCK BAY INCLUDED

Marianna Pastuszak, Tycjan Wodzinowski, Mariusz Zalewski

1. 1. ANTHROPOGENIC STRESSORS IN COASTAL REGIONS, THE PUCK BAY INCLUDED

Marianna Pastuszak, Tycjan Wodzinowski, Mariusz Zalewski

1.1. General overwiew

Coastal water bodies such as estuaries, bays or lagoons are the transitional systems located at the interface between land and sea; therefore, they are subjected to the combined modifications taking place in the atmosphere, in the oceans, and over the land surface (Streimikiene and Klevas, 2007; Sundblad and Bergström, 2014; Raimonet and Cloern, 2016; Guild et al., 2025). Studies of Möllmann et al. (2009), Möllmann and Diekmann (2012), and Reckermann et al. (2022) indicate that coastal environments, in particular heavily populated semi-enclosed marginal seas and coasts, like the Baltic Sea region, are strongly affected by human activities. Some anthropogenic stressors are naturally occurring, but they are modified by human activities i.e. climate change, hypoxia, acidification, submarine groundwater discharges, non-indigenous species, land use and cover. Some other are human-induced e.g. agriculture, aquaculture, fisheries, river regulations, offshore wind farms, shipping, chemical contamination, excessive nutrient discharges and eutrophication, dumped warfare agents, marine litter and micro plastics, tourism, and coastal management. As documented in numerous scientific papers, natural and human-induced anthropogenic stressors are interrelated to different degrees (Crossland et al., 2005; Howarth, 2008; Collie et al., 2008; HELCOM, 2009; Seitzinger et al., 2005, 2010; Robakiewicz, 2016; Friedland et al., 2019; Zaborska et al., 2019; Reckermann et al., 2022).

Estuaries and coastal areas are biogeochemical hot spots because they receive large inputs of nutrients and organic carbon from land and oceans to support high rates of metabolism and primary production (Cloern et al., 2014). Coastal areas represent a small fraction of the total oceanic area (~ 5%), but they are one of the most productive ecosystems on the Earth, and are home to diverse ecosystems that provide essential goods and services for human wellbeing (Heip et al., 1995; Costanza et al., 2007; Uitz et al., 2010; Sousa et al., 2016; Inácio et al., 2020).

Human activity, changing society, and climatic changes mutually influence each other and have a huge impact on anthropogenic pressure on the natural

environment on the globe. These changes affect functioning of terrestrial and aquatic ecosystems on the Earth (Bennett et al., 2001; Bongaarts, 2009; Zalasiewicz et al., 2010; Bowes et al., 2016; Povilaitis et al., 2018; Bartosova et al., 2019; Pihlainen et al., 2020; Wenng et al., 2020). Humans have become a very important force in the Earth system, demonstrating that emissions (gaseous, liquid, and solid) are the cause of numerous environmental issues, including major global reorganizations of the biogeochemical cycles (Mackenzie et al., 2002; Viitasalo and Bonsdorff, 2022; Guild et al., 2025).

The twentieth century is characterized by the global dynamic growth of human population (Bongaarts, 2009) associated with growing production of wastewaters, increasing demand for food, therefore intensification of agricultural production in terms of livestock population requiring more fodder, thus higher crop yields achieved by increasing application of fertilizers. In 2019, nitrogen fertilizers accounted for more than 56 percent of the total global consumption, whereas phosphate and potash fertilizers held shares of 24 and 19 percent, respectively (Ritchie et al., 2022). Lu and Tian (2017) state that since 1961 the global rates of N and P fertilizer use per unit cropland area have increased by approximately 8 times and 3 times, respectively. Nausch et al. (1999) report 17-fold and 8-fold increases in the consumption of mineral nitrogen and phosphorus fertilizers in the Baltic Sea drainage basin in 1950-1988, with some decreasing tendency in the years that followed. On both, a global and local scale, the increase in nitrogen (N) and phosphorus (P) loads in various water reservoirs is associated with an increase in the use of mineral fertilizers and the intensity of animal production (Ruttenberg, 2003; Erisman et al., 2013; Sharpley et al., 2013). The gains in food production came at a cost, leaving a significant environmental footprint on the ecosystem; increased nitrogen and phosphorus emissions resulted in adverse effects in inland waters and coastal marine regions (Nixon et al., 1996; Howarth et al., 1996; Håkanson and Bryhn, 2008; Howarth, 2008; Seitzinger et al., 2005, 2010; Friedland et al., 2019; Reckermann et al., 2022).

The broadly understood growing anthropogenic pressure since the Industrial Revolution has become a contributor to global climate change (Ritchie et al., 2020, 2023a,b, 2024; IPCC, 2021; Pastuszak et al., 2021). Scheffers et al. (2016) present numerous examples of case studies of observed global climate change impacts on terrestrial and aquatic biomes and found evidence that the climate change is now affecting most biological and ecological processes on Earth. These processes encompass genetics, organisms physiology and life history, population distributions and dynamics, community structure, and ecosystem functioning. Scheffers et al. (2016) also document that in total, 82% of 94% ecological processes show evidence of being affected

by climate change, whereas the percentage of processes within levels of organization varies from 60% for genetics to 100% for species distribution.

Anthropogenic climate change, fueled by rising greenhouse gas emissions (GHG) and extensive land-use changes, is driving profound shifts in Earth's ecosystems, putting their vital services and biodiversity at risk (Guild et al., 2025). Climate change, manifesting by e.g. increasing air and water temperature, extreme events such as floods, droughts, wild fires, storms, and heat waves, sea-level rise, altered crop growth, and disrupted water systems, has a range of ecological, physical, and health impacts (Trenberth, 2011; Stillman, 2019; Heshmati, 2020; Guild et al., 2025). Climate change affects the hydrological cycle and possibilities for agricultural production thereby influence transport, transformations of nutrients and their losses to the environment (Bouraoui et al., 2002; Øygarden et al., 2014; Ockenden et al., 2016). In marine environment, climate change is responsible for shifts in temperature, water circulation and its stratification, deoxygenation, which is bound to occur in a warming and more stratified ocean, and ocean acidification (Polovina et al., 2008; Gruber, 2011; Oschlies, 2019; Li et al., 2020; Garcia-Soto et al., 2021). All these changes contribute to qualitative and quantitative marine ecosystem changes, already observed in various parts of the globe. Some of them are abrupt and are known as regime shifts (Bennett et al., 2001; Möllmann et al., 2009; Hoegh-Guldberg and Bruno, 2010; Doney et al., 2012; Möllmann and Diekmann, 2012; Salinger, 2013; Viitasalo et al., 2015; Von Storch et al., 2015; Reid et al., 2016; Meier et al., 2022).

Regime shifts are commonly defined as large, abrupt, persistent changes in the structure and function of an ecosystem (Möllmann et al., 2009; Casini, 2011; Möllmann, 2011). The synchrony and time of occurrence of regime shifts in the Northern Hemisphere (the North Sea, the Baltic Sea, the Mediterranean Sea, the Black Sea, the Biscay Bay, the western part of the Atlantic Ocean, the northern Pacific) at the turn of the 1980s and 1990s suggest one common driving force, i.e. climate change (Hare and Mantua, 2000; Scheffer et al., 2001; Daskalov, 2002; Alheit et al., 2005; Casini et al., 2008; Möllmann et al., 2009). Möllmann et al. (2009) and Diekmann and Möllmann (2010) performed a multivariate analysis in the following subregions of the Baltic Sea: Gulf of Riga, the Gulf of Finland, the Bothnian Bay, the Bothnian Sea, and coastal regions. Despite large differences in environmental parameters among those regions, a change of regime was detected in all of them between 1987 and 1989. Based on studies in the Black Sea, Daskalov (2011) concluded that the regime shift is the result of external driving forces (climate change, invasion of non-indigenous species, overfishing, eutrophication), as well as due to internal perturbations in the structure and functions of the ecosystem (replacement by other species, top-down

and bottom-up trophic cascades, changes in distribution). Multiplied driving forces cause that one force (e.g. uncontrolled fishing) weakens the internal balancing forces (resilience), while the other one (e.g. sudden climate change) gives the final impulse to rearrange the ecosystem (Möllmann, 2011). Very extensive studies carried out by Reid et al. (2016) confirm that the 1980s regime shifts, represented a major change in the Earth's biophysical systems, from the upper atmosphere to the depths of the ocean, and from the Arctic to the Antarctic, and occurred at slightly different times around the world (great majority in the late 1980s). Reid et al. (2016) also conclude that this event was triggered by rapid global warming and by anthropogenic, plus natural forcing, the latter associated with the recovery from the El Chichón volcanic eruption. Reid et al. (2016) are of the opinion that the shift in temperature is considered the main forcing for a cascade of abrupt environmental changes. Temperature, as pointed out, is fundamental for most chemical, physical and biological processes; in a biological context, temperature modulates all processes, including the physiology, reproduction, development, occurrence, behavior, disease and phenology of organisms, at cellular to ecosystem scales.

Tomczak et al. (2015) performed integrated trend assessment studies in the Gulf of Gdańsk, including the Puck Bay, for the years 1994-2010, which obviously did not cover the 1980s, the latter found as a turning point in some large subregions in the Baltic Sea and beyond (Möllmann et al., 2009; Diekmann and Möllmann, 2010; Reid et al., 2016). Tomczak et al. (2015) did not report a regime shift in the Gulf of Gdańsk, but emphasized important changes in drivers and biological components of the ecosystem, and the changes occurred between the late 1990s and the early 2000s. The reported changes were driven by a combination of anthropogenic pressures (e.g. nutrient loadings and fisheries) and possible interactions with climatic disturbance.

1.2. Puck Bay - its natural value, threats, and legal protection

The Puck Bay, a semi-closed coastal part of the Gulf of Gdańsk (Fig. 1.1), is a unique reservoir due to the preserved species richness of plants and animals inhabiting its bottom, the coexistence of various communities of benthic flora and fauna, and the presence of rare species of benthic plants and animals. This region is regarded as the most diverse and biologically valuable part of the Polish marine areas, and is a key site for a number of species that are not present along the open seacoast (Węsławski et al., 2009).

The 1970s and 1980s were characterized by the lack of proecological activities in agricultural sector, as well as the lack of proper water and sewage management in Poland (Pastuszak et al. 2012a,b, 2014, 2016, 2018a,b), the Puck Bay catchment included (Kruk-Dowgiałło and Szaniawska, 2008). Excessive discharges of nitrogen and phosphorus and consequently high concentrations of nutrients in the Puck Bay (Bolałek et al., 1993) resulted in development of filamentous algae, which deposited on the bottom of the bay and limited the development of vascular plants and microalgae. As they decomposed, they caused periodic oxygen deficits in the sediments. These facts led to the collapse of the ecological balance in the bay (Kruk-Dowgiałło and Opioła, 2009). The most easily noticeable negative effects of these factors include a decrease in water transparency, the disappearance of underwater meadows that serve as spawning grounds and growth sites for juvenile stages of many fish species, and unfavorable changes in the species structure of ichthyofauna (Morawski, 1982; Pliński, 1990; Kruk-Dowgiałło, 1991).

The main forms of legal nature protection in the Puck Bay catchment area are landscape parks: Nadmorski Park Krajobrazowy and Trójmiejski Park Krajobrazowy. Apart from the above-mentioned parks, there are other forms of nature protection, both surface (nature reserves, ecological sites, protected landscape areas) and individual (natural monuments) (Cieśliński et al., 2022a,b). In addition, a large part of the Puck Bay is protected under the Natura 2000 network. The entire Puck Lagoon (PL), the adjacent part of the Outer Puck Bay (OPB), and the strip of coastal waters along the southern shore of the Hel Peninsula, ("PLH 220032 Puck Bay and Hel Peninsula"), are protected under the Habitats Directive (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora). One of the main objects of protection in this area is the habitat "1160 Large and shallow bays" covering the entire Puck Lagoon and part of the Outer Puck Bay. The entire area of PL and OPB is also part of the area "PLB 220005 Puck Bay", which is protected under the Birds Directive (Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds). The latter Directive assures protection of a number of breeding and migratory birds species (Piwowarczyk and Wróbel, 2016; Cieśliński et al., 2022a,b).

The Puck Bay, similarly to other coastal water bodies (e.g. Streimikiene and Klevas, 2007; Sundblad and Bergström, 2014; Raimonet and Cloern, 2016), is the transitional system located at the interface between land and sea, which remains under local, but also global anthropogenic pressure, as proven in the text hereafter.

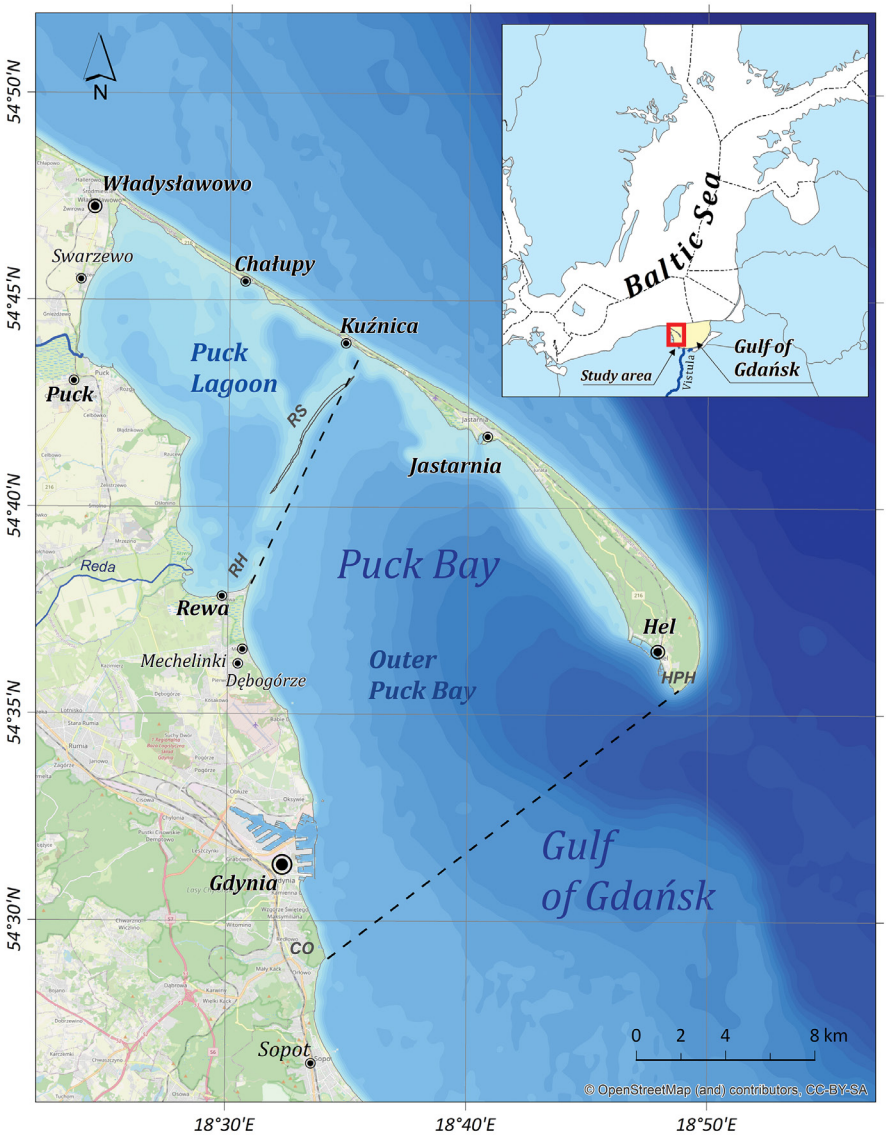

Fig. 1.1 The Puck Bay - region of studies conducted by NMFRI throughout 2020 and in June-November 2023; CO - Cape Orłowski, HPH - Hel Peninsula Headland, RS - Rybitwia Shoal, RH - Rewa Headland (source: map drawn by Lena Szymanek, NMFRI)

1.3. Puck Bay - local anthropogenic pressure generated by nutrient discharges

The Puck Bay (Fig. 1.1) remains under strong impact of the open part of the Gulf of Gdańsk, both in terms of water and nutrient exchange (Bolałek et al., 1993; Cyberski and Szefler, 1993). The Vistula River, one of the seven largest rivers feeding the Baltic Sea, shapes the hydrological conditions of the Gulf of Gdańsk and introduces large loads of pollutants (Kruk-Dowgiałło and Szaniawska, 2008; Zaborska et al., 2019), and substantial loads of nitrogen and phosphorus (Pastuszak et al., 2012a,b, 2016, 2018a,b). Significant nutrient discharges from wastewater treatment plants (WWTPs), serving not only permanent residents in the bay catchment, but also huge numbers of tourists in the summer, are also of great importance. Nutrient emission from the diffuse sources i.e. agricultural sector in the Puck Bay catchment, to a lesser extent, but also contributes to overall nutrient loads introduced to the bay (Cyberski et al., 1993; Kruk-Dowgiałło and Opioła, 2009; Dzierzbicka-Głowacka et al., 2019; Wojciechowska et al., 2019; Kalinowska et al., 2020; Burska et al., 2022). Dybowski and Dzierzbicka-Głowacka (2023) carried out modeling studies focused on impact of nitrate and phosphate discharged from land to the Puck Lagoon (Fig.1.1). The conclusion of these authors is that loads of $N\text{-}NO_3$ and $P\text{-}PO_4$ discharged from the land is not negligible but insignificant as compared with indirect impact of nutrient discharges by the Vistula River.

OPB remains under direct impact of inflowing water from the open Gulf of Gdańsk, both in the surface and bottom layer, as well as under impact of the Vistula water inflowing mainly in the surface layer (Nowacki, 1993a,b; Nowacki et al., 2009; Matciak et al., 2011). As further proven by the authors, an important role in the water and mass exchange between the Gulf of Gdańsk and OPB, and between OPB and PL is played by the upwelling phenomenon which can be identified by different characteristics e.g. salinity, nutrient concentrations, oxygen content (see Chapter 2), or water transparency (Matciak et al., 2011).

1.3.1. Declining anthropogenic pressure (nutrients) from WWTPs

Quality of WWTPs effluents plays an important role in supplying the Puck Bay with anthropogenic nutrients, as proven by Cyberski et al. (1993). These authors compiled a balance sheet for the period 1988-1990 and showed that the key source of N and P discharges to the bay were from inefficient WWTPs, and in particular the

largest former sewage collector in Mechelinki (Fig. 1.1). In 1988-1990, overall loads of ammonium, nitrate, and phosphate reached 1029.4, 118.7 and 306 tons·year^{-1}, respectively. The share of the collector in Mechelinki in overall nutrient loads was 81.7%, 53%, and 78.6%, for ammonium, nitrate, and phosphate, respectively. The share of all small rivers was 10.5%, 12%, and 5.6% for ammonium, nitrate, and phosphate, respectively. These results were a clear signal for the decision makers that water quality in the bay should be improved primarily by reducing N and P emissions from WWTPs. The modernization of four sewage treatment plants (Dębogórze, Hel, Jastarnia, Swarzewo) took many years, starting from the 1990s. At present, the WWTPs effluents from three of them (Dębogórze, Hel, Jastarnia) are dumped to the bay, while from the fourth in Swarzewo is discharged beyond the Puck Bay, to the open sea (https://www.sws-swarzewo.pl/technologia/oczyszczalnia-jastarnia). After the expansion and modernization of the largest WWTP in Dębogórze, which was completed in June 2009, it meets the strictest requirements for the quality of treated sewage (TN<10 mg·dm^{-3}, TP<1.0 mg·dm^{-3}). This WWTP has a comprehensive sludge management system with a dewatered sewage sludge incinerator and its own ash landfill. Within this undertaking, a deep-water collector was constructed and that replaced the shore outlet in Mechelinki. WWTP in Dębogórze discharges the treated wastewater through deep-water collectors (positioned under the seabed) beyond the coastal zone of the bay, ca. 20 km offshore (https://www.pewik.gdynia.pl/o-spolce/podstawowe-informacje/ochrona-srodowiska/oczyszczalnia-sciekow). The outcome of water quality monitoring proved that between 2008 and 2019, suspended particulate matter in the coastal zone declined from 9.5 to 0.7 mg·dm^{-3}; biological oxygen demand (BOD_5) declined from 5.9 to 0.4 mgO_2·dm^{-3} (0.28 ml·l^{-1}), TN declined from 12.7 to 6.7 mgN·dm^{-3}, whereas TP dropped from 0.82 to 0.62 mgP·dm^{-3}. At the same time, in the area of the new sewage discharge, there has not been any increase in the subjected environmental parameters (Burska et al., 2022).

1.3.2. Declining anthropogenic pressure (nutrients) - riverine discharges

Although the Vistula is important in terms of its impact on the Puck Bay, we believe it is worth showing the outcome of modeling studies (MONERIS) focused on N and P emission not only into the Vistula but also to the Oder basin (Pastuszak et al., 2018b). These authors had access to the data for the Oder (N emission in 1880-2015; P emission in 1955-2015) for a much longer period than for the Vistula (N, P emission in 1995-2015), which gives a much broader picture of anthropogenic

pressure in Poland prior and after 1989. The year 1989 was a turning point, because it marked the beginning of the transition period, and Poland's economy has undergone a profound transformation from a centrally planned economy to a market economy (Ouanes and Thaker, 1997). This transition has led to major institutional and economic structural changes over the last decades. Reforms initiated in the early 1990s provided opportunities to revise and implement environmental management and legislation, and to achieve greater integration of environmental concerns into other policies (Jadczyszyn and Rutkowska, 2012). Pro-ecological actions covered various sectors of Polish economy, including agricultural sector, development of sewage system with continuous construction of new, as well as upgrading of the old, less-efficient WWTPs (Kowalkowski et al., 2012; Pastuszak and Witek, 2012; Pastuszak et al., 2012a,b, 2014, 2016, 2018a,b; Jarosiewicz et al., 2015; Burska et al., 2022).

The outcome of the above mentioned modeling studies (MONERIS) (Pastuszak et al., 2018b) showed that population growth and agricultural intensification in the nineteenth/twentieth century were responsible for respective 5.3-fold and 3.5-fold increase in N and P emission into the Oder basin. The emission maximum (135 000 tonsN·year^{-1}; 14 000 tonsP·year^{-1}) was observed at the turn of the 1980s/1990s. Available data allowed the authors to encounter the maximum of N and P emission into the Vistula basin (170 000 tonsN·year^{-1}; 14 200 tonsP·year^{-1}), which was found at the turn of the 1980s/1990s. In 1985-2015, N emission into Oder basin decreased from 135 000 to 94 000 tons·year^{-1}; P emission declined from 14 000 to 5000 tons·year^{-1}. In 1995-2015, N emission into the Vistula basin decreased from 170 000 to 140 000 tons·year^{-1}; P emission declined from 14 200 to 10 600 tons·year^{-1}. In both river basins, the declines of nutrient emission were mainly generated by groundwater, WWTPs, and overland flow; the relative shares of these nutrient emission pathways in overall nutrient emission were considerably changing over time. The authors further document that in the Vistula basin (1995-2015), three pathways, i.e., groundwater, tile drainage, and, to a lesser extent WWTPs, played a key role in N emission, and they were responsible for ca. 80% of overall N emission in both basins. Four pathways, i.e., erosion, overland flow, WWTPs, and urban areas, played a key role in P emission and accounted for ca. 80% of overall P emission into Vistula and Oder basin; contribution of WWTPs in P emission was considerably declining in both river basins. Contribution of a given nutrient emission paths must always be referred to natural (type of bedrock, soil type, lake area), and anthropogenic factors, which encompass regionally and temporarily different type and intensity of agricultural activity, spatially different structural changes in agriculture during the transition period, regionally and temporarily different investment in wastewater treatment plans. Both anthropogenic

and natural factors have great impact on nutrient emission and transport (Kowalkowski et al., 2012). Weather conditions have a huge impact on increased (floods) or reduced (droughts) N and P emissions. Particularly, nitrogen emission is susceptible to variable weather conditions and it is strongly enhanced by long-lasting wet periods (Kowalkowski et al., 2012; Pastuszak et al., 2012a,b, 2018b).

Agricultural systems leak N and P *via* three major routes: (i) upward, *via* crop uptake and *via* transfer of gaseous nitrogen compounds (NH_3, N_2, N_2O, NO_x) and phosphorus as atmospheric aerosols to the atmosphere (minor flux of P), (ii) laterally, *via* surface runoff, subsurface flow and tile drainage, and (iii) downwards, *via* leaching. The balance between these three different routes depends on farming system, nitrogen and phosphorus fertilizing history, climate, topography, soil type, and hydrology (Haycock et al., 1993; Oenema and Roest, 1998; Hooda et al., 2000, 2001; Honisch et al., 2002; Oenema et al., 2003, 2005; Salo and Turtola, 2006). Surface waters receive agricultural nitrogen *via*: (i) atmospheric deposition, (ii) surface runoff and erosion, (iii) subsurface flow and tile drainage, (iv) seepage of nitrate containing groundwater from agricultural land (Oenema and Roest, 1998). The pool of nutrients that enters the surface waters depends very much on N and P pathways from the soil surface and root zone to the surface recipient of water (Grizzetti et al., 2005; Kowalkowski et al., 2012).

Nitrate is the primary form of N leached into surface waters and groundwater; it is very soluble at concentrations found in soil, and moves freely throughout most soils. The widespread appearance of $N\text{-}NO_3$ in groundwater is a consequence of its high solubility, mobility, and easy displacement by water. In addition, it is well documented that nitrate leaching rates will be affected by rain, irrigation, tile drainage, and water table fluctuations during the growing season. Movement of nitrate with percolating water, through the unsaturated zone can be very slow, therefore there is significant time span between the enhanced emission and recorded elevated concentrations of N species in groundwater (from a year to 20 years, depending on situation) (Nixon, 1999; Hatfield and Follett, 2008).

Unlike nitrogen, the major proportion of phosphorus transported from agricultural soils is generally in sediment-bound form, the remaining percentage constitutes dissolved, molybdate reactive P (Probst, 1985; Misumura, 1989; Oenema and Roest, 1998). In most watersheds, P export occurs mainly in surface runoff rather than in subsurface flow. Generally, the concentrations of P in water percolating through the soil profile are small due to P fixation by P-deficient sub-soils. Exceptions occur in sandy, acid organic, or peaty soils with low P fixation or holding capacities, and in soils where the preferential flow of water can occur rapidly through macro-pores

and earthworm holes (Sharpley, 2006). Also unlike nitrogen, only a fraction of the phosphorus transported from agricultural land is directly bioavailable to aquatic biota. However, a substantial portion of particulate P may also be released into an algal-available form, especially when the particles have entered anoxic sediment surface.

The above-mentioned data and scientific comments clearly indicate that agriculture, in addition to WWTPs, is a significant source of N and P emissions to river basins, including the Vistula and Oder basins. Kundzewicz and Kozyra (2011) report that agriculture in Poland is at risk of an increase in the frequency of unfavorable climatic conditions affecting yields of agricultural crops from year to year. These authors further state that moisture deficiency during the growing season are becoming more frequent and more severe, and dramatic droughts are very likely to occur more often. In addition to the above-mentioned, the authors indicate other threats, e.g. heat waves, heavy rainfalls, floods and landslides, strong winds, pathogen development associated with warming. All these factors affect losses of nutrients from agricultural fields to the environment (Fotyma et al., 2012; Igras and Fotyma, 2012; Kowalkowski et al., 2012; Øygarden et al., 2014; Ockenden et al., 2016).

Nutrient emissions to river basins should not be understood as discharges to the Baltic Sea. Thanks largely to the natural course of the Vistula and Oder and their tributaries, over 91 000 tons of N and over 7600 tons of P are annually retained in the catchments of these rivers, thus do not reach the coastal zone (Pastuszak et al., 2018a; Stålnacke et al., 2015). The N and P loads reaching the coastal zone are calculated based on nutrient concentrations and water flows measured at the lowest monitoring stations on the rivers. There is commonly used flow normalization method that aims at removing the natural fluctuations in loads and concentrations caused by variability in water discharge or other weather-dependent variables. Simply speaking, the purpose of flow-normalization is to estimate the load at the "normal" water discharge. Such removal or reduction of irrelevant variation in the collected data can help to clarify the impact of human pressures on the environment, in this case, the impact on riverine loads of nutrients (for details - see Pastuszak et al., 2012a,b; 2018a,b).

Over the years 1988-2014, flow normalized TN loads carried by the Vistula River, feeding the Gulf of Gdańsk, declined from a maximum of 125 000 tonsN·year^{-1} in 1988 to ca. 74 000 tonsN·year^{-1} in the last two years of the study. Flow normalized N-NO_3 loads declined from 68 000 tonsN·year^{-1} in 1994 to ca. 40 000 tonsN·year^{-1} over the last three years of the study, whereas loads of N-NH_4 dropped from over 21 000 tonsN·year^{-1} in 1991 to slightly over 2000 tonsN·year^{-1} in 2014. TP discharged by the Vistula dropped from max. 7700 tonsP·year^{-1} in 1993 to ca. 5000 tonsP·year^{-1} in 2013-2014, whereas P-PO_4 loads dropped from 4000-4900 tonsP·year^{-1} in the 1990s to ca.

2000 tons$P \cdot year^{-1}$ in 2013-2014. Considerable declines in ammonium and phosphate loads must have been attributed to construction of a very large number of WWTPs and upgrading the less efficient ones (Pastuszak et al., 2012a,b, 2018a). Mainstone and Parr (2002) and Withers and Jarvie (2008) have documented that municipal wastewater is usually dominated by dissolved inorganic phosphorus and nitrogen, and that their concentrations depend on the efficiency of the sewage treatment.

Gustafsson et al. (2012), Schneider et al. (2015), and Kuliński et al. (2022) present an overview of historical changes in TN and TP waterborne inputs into the Baltic Sea, and they indicate that N, P loads increased dramatically during the last 150 years. The rate of increase is reported to become stronger after the Second World War and peaked around 1980s at about three (N) and seven (P) times higher than in 1850. However, as further stated, inputs have decreased significantly since the 1980s due to emission reduction measures (HELCOM, 2007, 2013a,b,c; Jadczyszyn and Rutkowska, 2012) and are presently at a level comparable to those around 1960s and 1950s in the case of nitrogen and phosphorus, respectively (Kuliński et al., 2022). The time variation of the waterborne loads of TN and TP delivered to the Baltic Sea as a whole is largely consistent with time variation of TN, TP loads delivered to the Baltic Sea by the Vistula and Oder rivers (Pastuszak et al., 2012a,b, 2018a). Since there are no statistically significant trends in annual discharges of river water to the Baltic Sea, the reductions in N and P loads are attributed to socioeconomic development, including the expansion of the wastewater treatment, and the reduction in atmospheric nitrogen deposition. These facts concern the entire Baltic Sea drainage basin and the observed effects are not climate-related (Gauss et al., 2021; Meier et al., 2022).

The declining anthropogenic pressure in the Gdańsk Basin is confirmed by HELCOM (2018) report, which evaluates average DIN concentration in surface waters (0-10 m) of the Baltic Sea during winter (December - February) for the assessment period 2011-2016. It arises from this documents that good status (DIN concentrations below threshold) was achieved in a few Polish and Swedish coastal areas (e.g. parts of the Gulf of Gdańsk - the Puck Bay area). Interestingly, the status of Kattegat, Kiel Bay and Gdańsk Basin are only slightly above the threshold values of eutrophication ratio (ER<1.2). “ER” stands for Eutrophication Ratio; it’s a numerical value used to assess the level of eutrophication in the Baltic Sea. ER is calculated by comparing the current concentration of a pollutant (like total phosphorus) to a threshold value (for details see - HELCOM, 2018).

The N and P loads discharged into the sea by rivers are the resultant of the water flow in a given river and the concentration of a given nutrient. The historical data indicate that annual cycles of water flows in the Vistula and Oder showed similar

patterns, with maxima during freshets in spring, and minima in summer (Fal et al., 2000). Owing to climate change, the well-established historical pattern has been significantly disturbed over the last decades. The spring maximum in water outflows in these rivers became shifted to February/April as in 2002, 2006, or even to June as in 2013 in the Oder River (Pastuszak et al., 2018a,b). The summers of 2001, 2010, and 2011 were exceptionally wet in both river basins and water flows were two/three times as high as the seasonal average. In June 2010, the record high flows were measured and they amounted to ca. 3200 m^3s^{-1} in the Vistula and 1400 m^3s^{-1} in the Oder. In both basins, the 2010 flood continued until January/February 2011 and caused very high N, P loads discharged by the Oder and Vistula (Pastuszak et al., 2018a,b). Short-term fluctuations in flow or isolated events may have limited impacts on estuarine biota; however, remedial engineering modification, resulting in longer-term persistent changes in flow regimes, can drive trophic shifts in estuaries, and that disrupts their structure and functioning (Potter et al., 2016).

1.4. Global anthropogenic pressure - climate change and global temperature increase

The majority of Earth's atmosphere is composed of a mixture of only a few gases i.e. nitrogen, oxygen, and argon. When combined, these three gases comprise more than 99.5% of all the gas molecules in the atmosphere. The gases that are most abundant within the atmosphere exhibit almost no effect on warming the earth and its atmosphere since they do not absorb visible or infrared radiation. However, there are minor gases which comprise only a small portion of the atmosphere (about 0.43% of all air molecules, most of which are water vapor 0.39%) that do absorb infrared radiation. These "trace" gases contribute substantially to warming of the Earth's surface and atmosphere due to their abilities to contain the infrared radiation emitted by the Earth. Since these trace gases influence the Earth in a manner somewhat similar to a greenhouse, they are referred to as Greenhouse Gases, or GHG (Jain, 1993; Pastuszak et al., 2021).

The processes responsible for adding carbon to and withdrawing it from the atmosphere are not understood well enough to predict future levels of CO_2 with great accuracy. These processes are a part of the global carbon cycle. Some of the processes that add carbon to the atmosphere or remove it, such as the combustion of fossil fuels and the establishment of tree plantations, are under direct human control. Other, such as the accumulation of carbon in the oceans or on land as a result of changes in global

climate (i.e. feedbacks between the global carbon cycle and climate), are not under direct human control, except through controlling rates of greenhouse gas emissions and, hence, climatic change (Prentice et al., 2001; Houghton, 2003; Schimel et al., 2015).

Carbon, in the form of carbon dioxide (CO_2), and methane (CH_4), form two of the most important greenhouse gases. Methane produces a larger greenhouse effect per volume as compared to carbon dioxide, but it exists in much lower concentrations and is more short-lived than carbon dioxide, making carbon dioxide the more important greenhouse gas of the two (Falkowski et al., 2000; Forster et al., 2007; Ciais et al., 2016). However, on a 20-year timescale, a mass of methane emitted, including indirect effects from stratospheric H_2O and tropospheric O_3, is about 85 times more powerful than an equal mass of carbon dioxide emitted at warming the Earth. However, on a 100-year timescale, it is projected to be only about 28-34 times more powerful, on the assumption the carbon dioxide will not be sequestered and will continue to warm the earth for decades after the methane is gone (Myhre et al., 2013).

Human activities over the past two centuries have significantly increased the amount of carbon in the atmosphere, mainly in the form of carbon dioxide. The increase was caused by modifying ecosystems' ability to extract carbon dioxide from the atmosphere and by emitting it directly, e.g., by burning fossil fuels and manufacturing concrete (Jain, 1993; Falkowski et al., 2000; Worrell et al., 2001; Ritchie et al., 2020) (Fig. 1.2). Enormous increase in the global consumption of fossil fuels resulted in a significant increase in emission of greenhouse gases to the atmosphere, and consequently in climate change (IPCC, 2021; Pastuszak et al., 2021). Carbon dioxide emissions globally increased from 2 Gton CO_2 in 1900 to over 37 GtonCO_2 in 2023 (Ritchie et al., 2020) (Fig. 1.2).

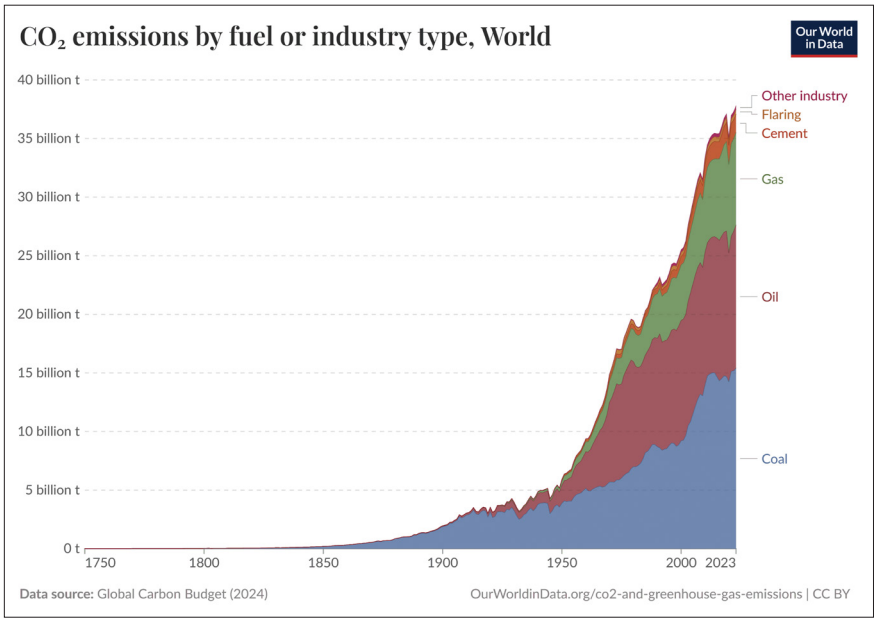

Fig. 1.2 Global carbon dioxide (CO_2) emissions by fuel type (source: Hannah Ritchie, Pablo Rosado, and Max Roser (2020) - "CO_2 emissions by fuel" Published online at OurWorldinData.org. Retrieved from: 'https://ourworldindata.org/emissions-by-fuel' [Online Resource]; Retrieved on 02 June 2025

(the USA meaning of a billion is a thousand million, or one followed by nine noughts (1,000,000,000); an European billion has 12 zeroes)

Global atmospheric CO_2 was relatively stable, fluctuating between 270 and 285 ppm until the 18th century. Since the Industrial Revolution, global CO_2 has been rapidly increasing, reaching 340 ppm in 1980, and 422.79 ppm in 2024 (Lindsey, 2024; Ritchie et al., 2024) (Fig. 1.3).

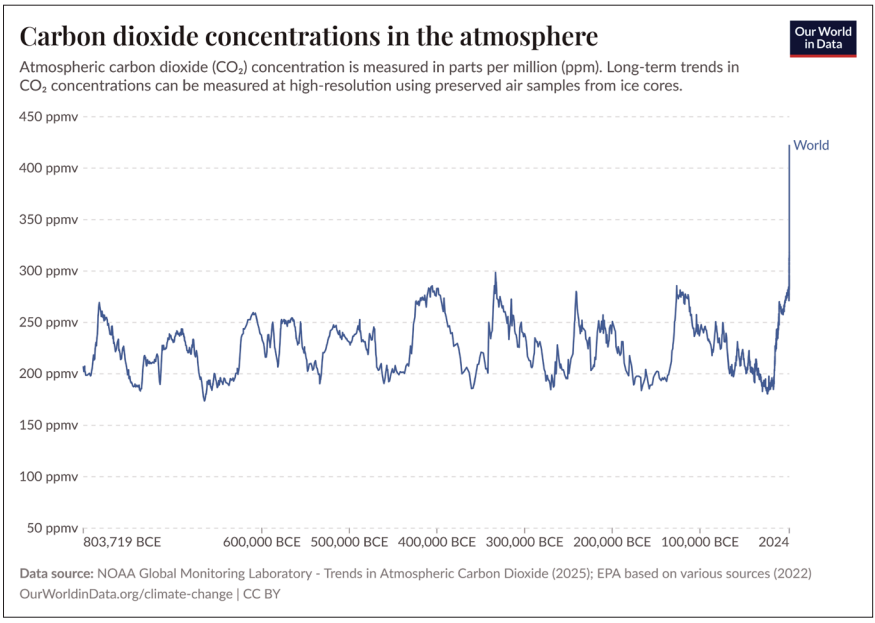

Fig. 1.3 Carbon dioxide concentrations in the atmosphere (source: "Data Page: Annual concentration of atmospheric carbon dioxide", part of the following publication: Hannah Ritchie, Pablo Rosado, and Veronika Samborska (2024) - "Climate Change". Data adapted from NOAA Global Monitoring Laboratory, United States Environmental Protection Agency. Retrieved from https://ourworldindata.org/grapher/co2-long-term-concentration [online resource]; Retrieved on 02 June 2025

Climate change, generated by human activities, mainly results from the energy imbalance in Earth's climate system, which in turn is caused by rising concentrations of heat-trapping gases (IPCC, 2021; Pastuszak et al., 2021; Ritchie et al., 2024). Human emissions of carbon dioxide and other greenhouse gases are the primary drivers of the global rise in temperatures starting from the 1980s/1990s (Fig. 1.4). The link between global temperatures and greenhouse gas concentrations - especially CO_2 - has been true throughout Earth's history (Ritchie et al., 2024; Samborska and Ritchie, 2025). In 2024, the world was around 1.5°C warmer than it was in pre-industrial times (Samborska and Ritchie, 2025) (Fig. 1.4). The warming has not been equally distributed across the world, and the Northern Hemisphere has warmed more than the Southern Hemisphere; temperature anomalies in the Northern Hemisphere are higher than the global ones (Figs. 1.4, 1.5; Ritchie et al., 2023a,b). Warming has been

especially strong at the poles; in some regions, temperatures have risen by more than 5°C (Ritchie et al., 2023a,b). About 93% of the energy imbalance accumulates in the ocean as increased ocean heat content, and estimates based on observations show rapid warming of Earth's oceans over the past few decades (Cheng et al., 2019).

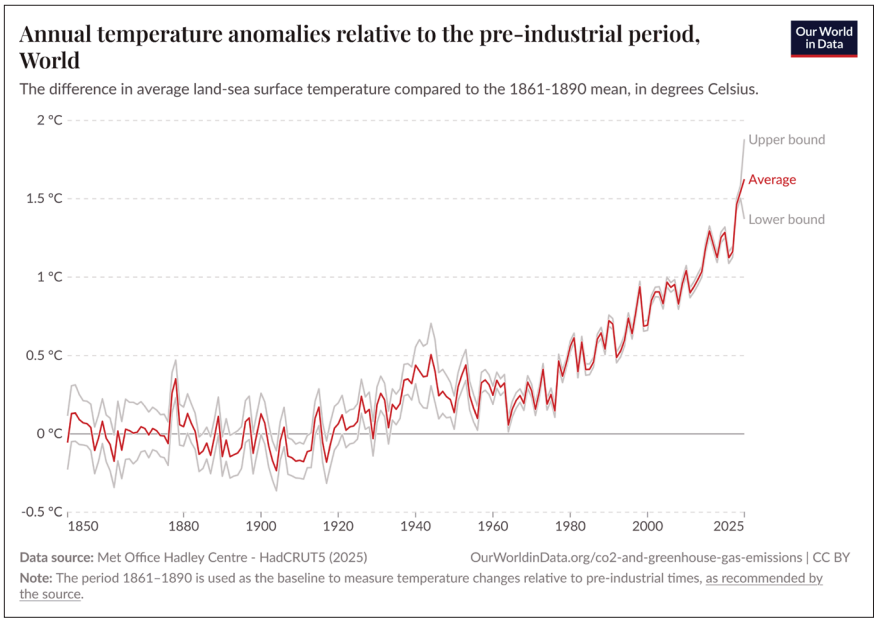

Fig. 1.4 Annual temperature anomalies relative to pre-industrial period, World; the difference in average land-sea surface temperature is compared to 1861-1890 mean {source: Hannah Ritchie, Pablo Rosado, and Max Roser (2023a) - "CO_2 and Greenhouse Gas Emissions" Published online at OurWorldinData.org. Retrieved from: 'https://ourworldindata.org/co$_2$-and-greenhouse-gas-emissions' [Online Resource]}; Retrieved on 02 June 2025

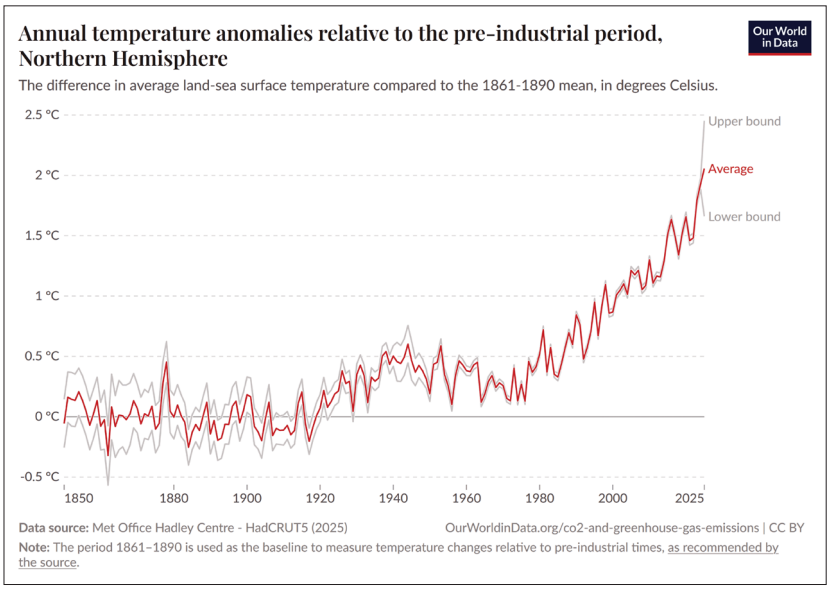

Fig. 1.5 Annual temperature anomalies relative to the pre-industrial period, Northern Hemisphere {(source: Hannah Ritchie, Pablo Rosado, and Max Roser (2023b) - "CO_2 and Greenhouse Gas Emissions" Published online at OurWorldinData.org. Retrieved from: 'https://ourworldindata.org/co2-and-greenhouse-gas-emissions' [Online Resource]}; Retrieved on 02 June 2025

1.4.1. Climate change - increase in air and water temperature in Poland

Knowing that water temperature is correlated with air temperature (AT) (Ziernicka-Wojtaszek and Krużel, 2016; Kubiak-Wójcicka, 2020; Zhu et al., 2022; Stockmayer and Lehmann, 2023; Marosz et al., 2023), and having access to a number of works describing long-term changes in AT in Poland, we decided to present some of the findings here. Marosz et al. (2023) showed the graph with average annual AT in Poland in 1951-2021; it is evident that a significant increase in AT took place in the late 1980's, similarly to considerable increase in water temperature in the open Gulf of Gdańsk starting from the late 1980s (Fig. 1.6; see next section). Marosz et al. (2023) further report that over the years 1951-2021 the AT in Poland has increased on average by 0.28°C·decade^{-1}, which gives a total change in this period exceeding 2°C. These authors divided each year into four seasons and concluded that the highest AT increase was observed in winter season (0.36°C·decade^{-1}), slightly lower in spring (0.35°C·decade^{-1}), and significantly lower in autumn (0.18°C·decade^{-1}).

Ziernicka-Wojtaszek and Krużel (2016) report that the AT increase in Poland in 1981-2019 amounted to 0.33°C·decade^{-1}, and it was by 0.08°C·decade^{-1} higher than that reported by Marosz et al. (2023). This difference may be caused by the fact that Ziernicka-Wojtaszek and Krużel (2016) took into account shorter period (1981-2019), without much cooler three earlier decades (Marosz et al., 2023). Increase in AT in the Vistula catchment (nearly half of the territory of Poland) is also reported by Kubiak-Wójcicka (2020), and it is between 0.27 and 0.45°C·decade^{-1}, depending on location.

The reported increase in AT in Poland resulted in increase also in water temperature in Polish rivers, including those directly or indirectly feeding the Puck Bay (0.26-0.31°C·decade^{-1}) (Ptak et al., 2016; Zhu et al., 2022), as well as in Polish lowland lakes (0.39°C·decade^{-1}) (Ptak et al., 2019). The average annual warming trend in Reda River directly feeding the Puck Bay reached 0.21°C·decade^{-1} (Zhu et al., 2022). Zhu et al. (2022) made a reconstruction of long-term river water temperature (RWT) from 125 water gauges in 70 Polish rivers for the period 1966-2020. The outcome of the studies showed clear warming trend in the past 55 years, with the warming rate ranging between 0.08 and 0.44°C·decade^{-1}, depending on the region. The seasonal trends of RWT showed that summer was warming fastest, followed by spring, and then by autumn and winter. Long-term increases in RWT were correlated with increases in air temperature. The average annual warming rates in the Vistula River (at the lowermost gauge) feeding the Gulf of Gdańsk reached 0.24°C·decade^{-1}; spring and summer warming trends in the Vistula reached 0.32 and 0.31°C·decade^{-1}, respectively. According to Ptak et al. (2022), the mean increase in water temperature in the Vistula River over the years 1971-2017 was 0.31C·decade-^{1}.

1.4.2. Climate change - water temperature increase in the Baltic Sea, the Puck Bay included

The Baltic Sea has been one of the fastest-warming semi-enclosed seas in the world over the last decades, yielding critical consequences on physical and biogeochemical conditions and on marine ecosystems (Kniebusch et al. 2019; Dutheil et al. 2022). The annual mean temperature trends during 1876-2018 indicate that air temperature has increased more in the Baltic Sea region than globally (HELCOM, 2021). During the recent decade, record breaking heat waves have hit the Baltic region, with an increasing trend of warm spell duration (Huth et al., 2000).

Studies of long-term climate variability (1958-2009) and the related impact on the Baltic Sea area revealed that observed changes in the warming trend are associated

with changes in large-scale atmospheric circulation over the North Atlantic (Lehmann et al., 2011). These authors prove that (i) the number and pathways of deep cyclones changed considerably in line with an eastward shift of the North Atlantic Oscillation (NAO) centers of action, (ii) there was a seasonal shift of strong wind events from autumn to winter and early spring. Stockmayer and Lehmann (2023) indicate that: (i) variability of sea surface temperature (SST) closely follows that of air temperature (AT) in the Baltic region, and that inter-annual variations of SST are significantly correlated with the North Atlantic Oscillation (NAO) in most parts of the sea in winter, (ii) the entire water column of the Baltic Sea has warmed over the period 1950-2020, and that the trend is strongest in the surface layer, which warmed by 0.3-0.4C·decade^{-1}, and was noticeably stronger since the mid-1980s. Kniebusch et al. (2019) are of the opinion that the strongest SST trends since 1980s can be explained by the superposition of global warming and a shift from the cold to the warm phase of the Atlantic Multidecadal Oscillation.

Pastuszak et al. (2021) documented that over the years 1946-2019 the increase in water temperature in 0-20 m layer in the Bornholm Basin (western part of the Baltic Sea) amounts to approx. 3°C, or ca. 0.4C·decade^{-1}. The sea surface (0-20 m) temperature increase was also observed in the open Gulf of Gdańsk (Fig. 1.6). The division of the entire period 1946-2023 into two sub-periods i.e. 1946-1987 and 1988-2023 shows that the late 1980s could have been a turning point in warming trend in the Gulf of Gdańsk, and most probably in its coastal subregion, the Puck Bay.

Between 1972-1990 and 2020, the average annual water temperature in OPB and PL increased by 2.89°C and 2.24°C, respectively (Chapter 2) and these numbers follow the available long-term AT increase in the Puck Lagoon. Between 1950/51 and 2019/20 AT in the Puck Lagoon increased from -0.3°C to ca. 2.4°C (Girjatowicz and Świątek, 2021).

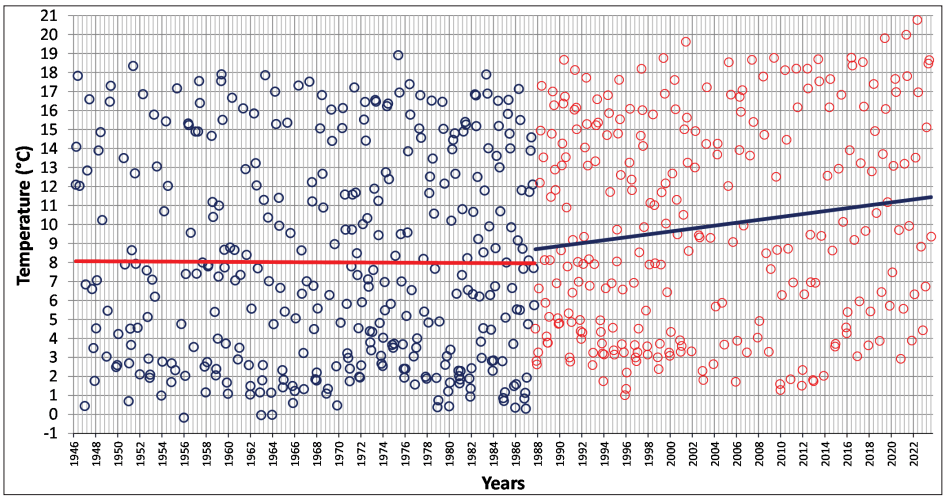

Fig. 1.6 Average monthly values of water temperature in the layer 0-20 m in two sub-periods i.e. 1946-1987 and 1988-2023, and the regression lines at station G2 (open Gulf of Gdańsk) (source: graphs based on the NMFRI data)

1.4.3. Climate change - ice cover in the Baltic Sea and the Puck Bay

The AT has a large influence on its spatial distribution and ridging and/or rafting. Due to increase in AT during the last century, winters have become milder, the ice season shorter and the maximum ice extent has decreased by about 30%. Indices based on the total winter ice volume show a decreasing trend in the period 1985-2015 (more than 10%·decade^{-1}) in many regions. Since the late 1980s, the winter season (Dec-Mar) in the Baltic Sea area has tended to be warmer, with less ice coverage and higher sea surface temperatures, particularly pronounced in the northern parts of the Baltic Sea (HELCOM, 2011, 2015, 2021).

Historical research covering the years 1946/47-1990/1991 shows that in the entire basin of the Gulf of Gdańsk, ice appeared first in the northwestern part of PL, which is mainly due to the bathymetry and sheltering of this basin. In PL, ice occurred in those years every winter, regardless of the severity of winters; the exception was the winter of 1974/75, when there was no ice. The average period of ice presence in PL was 60-80 days, whereas in OPB it ranged from 10 to 50 days (Szefler, 1993). Indices based on the total winter ice volume show a decreasing trend in the period 1985-2015 (more than 10%·decade^{-1}) in many Baltic regions (HELCOM, 2021).

Girjatowicz and Świątek (2021) studied the relationship between AT change and ice conditions in three lagoons: Szczecin, Vistula, and Puck, characterized by

relatively weak water dynamics, as the strongest movement of water masses in these regions is due to wind-induced wave motion; the lagoons are characterized by very weak water currents and lack of tides. Between 1950/51 and 2019/20 the number of days with ice in the Puck Lagoon decreased from 90 days to 30 days, whereas AT increased from -0.3°C to ca. 2.4°C. No ice occurred in the Puck Lagoon during the winters of 1974/75, 2007/08, 2014/15, and 2019/20.

1.5. Large scale Baltic circulation - indirect impact on the Puck Bay

The Baltic Sea is a shallow brackish sea, on the one hand supplied by rivers, on the other hand exposed to water exchange between the Baltic Proper and the North Sea. In general, there is an outflow of low saline water in the surface layer, while compensation current transports higher saline water in the deep layer into the Baltic Sea. The mean Baltic Sea salinity is strongly related to large-scale atmospheric variability and the accumulated freshwater inflow (Elken and Matthäus, 2006; Meier et al., 2006; Lass and Matthäus, 2008). This fact has a decisive effect on structure of the water column, which is two-layered, characterized by limited vertical mixing of water, which in turn causes the Baltic Sea is characterized by its natural predisposition to oxygen deficiency in the near-bottom layer.

Water exchange with the North Sea through the Sound and the Belt Sea is highly variable in direction and magnitude (Mohrholz, 2018). To have a significant impact on the deep water conditions in the central Baltic an inflow event must transport large amounts of saline and well oxygenated water into the western Baltic. The deep water of the Baltic Proper is replaced *via* episodic inflows of larger volumes (100-200 km^3) of highly saline (17-25 PSU - Practical Salinity Units) and oxygen-rich water; these are termed major Baltic inflows. Most major inflows occur between October and February (Elken and Matthäus, 2006; Lass and Matthäus, 2008; Hansson and Viktorsson, 2020).

Long-term salinity fluctuations in the bottom layer, but also in the 0-50 m layer, as seen in Fig. 1.7, are a reflection of the influence of saline water inflows from the North Sea. The visible significant decrease in salinity in 1980-2000 is the result of a long period of stagnation in the studied area, due to decline in major inflows (Elken and Matthäus, 2006; Lass and Matthäus, 2008; Mohrholz, 2018; Hansson and Viktorsson, 2020). Consequently, ventilation of stagnating bottom waters has considerably weakened thereby worsening oxygenation of near bottom waters in deep basins of the Baltic Sea. During stagnation, there is a decrease in oxygen content, but also the

appearance of increased phosphate and ammonium concentrations. Therefore, upwelled waters reaching the OPB may have different characteristics depending on the situation in the Gulf of Gdańsk. The incidental appearance of water with parameters significantly different from the parameters at adjacent measured levels, i.e. high salinity, low oxygen content, and high concentrations of nutrients, was observed in 2020, which proves the inflows of water from the Gulf of Gdańsk, and therefore the indirect impact of this water body on the abiotic parameters in the Puck Bay (Chapter 2).

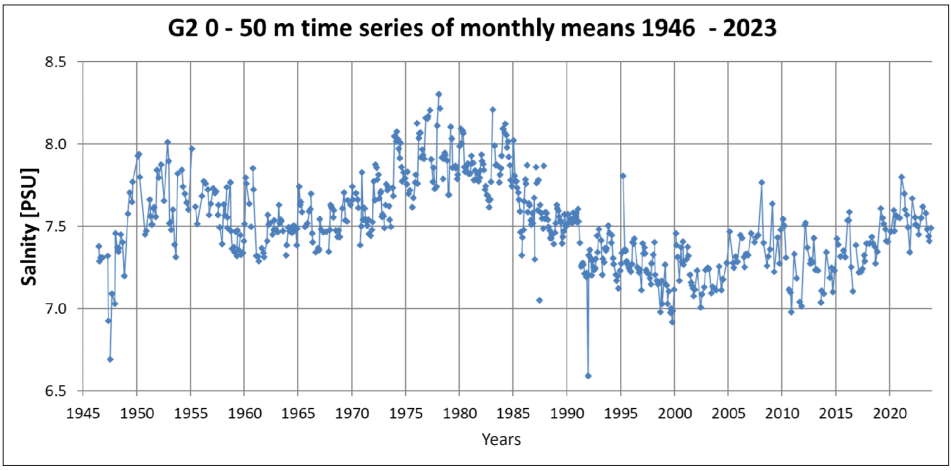

Fig. 1.7 Average monthly values of salinity (PSU) in 0-50 m layer on G2 station (deepest part of the Gulf of Gdańsk) in 1945-2023 (source: based on the MIR→NMFRI data)

1.6. Summary

- The content of this Chapter provides an important background for understanding the complexity of the Puck Bay region studied by us in 2020 and 2023. In our opinion, this will allow for a clearer understanding of the scientific meanders contained in Chapters 2 and 3. Based on international literature, in Chapter 1 we comment on the great economic importance of coastal regions on the one hand, and the negative impact of humans on the functioning of coastal ecosystems on the other hand. We emphasize the natural value of the Puck Bay, and provide actions at the national and international level aimed at broadly understood protection of the natural environment and resources of the bay.
- The division of anthropogenic stressors into local (WWTPs, riverine discharges of N and P) and global (climate change) makes us aware that all remedial actions

must have the same dimension, i.e. local and global. In order to bring closer the global problem, which translates into the local dimension, we decided to show a few graphs showing the increase in air temperature and consequently water temperature on the global scale.

- We present Polish studies showing the degree of increase in air temperature in Poland over the last few decades, and bring closer the fact of a similar increase in water temperature in the Puck Bay, Polish rivers and lakes. We also write that water exchange with the North Sea through the Sound and the Belt Sea is highly variable in direction and magnitude, and this may affect the hydrochemical parameters of water entering the Puck Bay on the way of upwelling between the open Gulf of Gdańsk and OPB.

1.7. References

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2

LONG-TERM CHANGES OF ABIOTIC PARAMETERS IN THE PUCK BAY

Marianna Pastuszak, Tycjan Wodzinowski, Mariusz Zalewski

2. LONG-TERM CHANGES OF ABIOTIC PARAMETERS IN THE PUCK BAY

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2.1. Study area - general overview

The Puck Bay is a subregion of the western part of the Gulf of Gdańsk, separated from the deepwater regions of the Gdańsk Basin by the Hel Peninsula (Nowacki, 1993a). A line connecting the Hel Peninsula Headland with Cape Orłowski is assumed the eastern border of the Puck Bay (Korzeniewski, 1993; Fig. 2.1). The Puck Bay consists of two parts: (i) much shallower western part (max. depth 9.4 m), which is the second-order estuary that meets all the features of the lagoon, therefore it is officially called the Puck Lagoon (PL), and (ii) the eastern part, which is much deeper (max. depth 55 m) and has direct contact with the open Gulf of Gdańsk and it is called the Outer Puck Bay (OPB) (Cyberski, 1993; Nowacki, 1993a). The transition zone between these two parts of the bay (overall length 11.7 km) is formed by 8.6 km long Rybitwia Shoal which faces Rewa Headland, the latter with a variable length, depending on the water level. Both forms are separated by a strait, which is about 1.8 km wide (Cyberski, 1993; Fig. 2.1). The same division of the Puck Bay is adopted in the documents of the Water Framework Directive (WFD) (http://geoportal.pgi.gov.pl/css/powiaty/prawo/ue_ramowa_dyrektywa_wodna).

The land use structure of the Puck Bay catchment area is as follows: agricultural land - 46.5%, forests and natural ecosystems - 41.3%, anthropogenically transformed areas -10.6%, inland marshes - 0.9%, and water reservoirs - 0.7%. In agricultural land structure, arable land predominates, and it is followed by meadows and pastures occupying mainly coastal lowlands and proglacial valleys, as well as river valleys. In anthropogenically transformed areas, the largest share is compact urban development, stretching mainly along the coast as well as in proglacial valleys and the edge zones (Cieśliński et al., 2022).

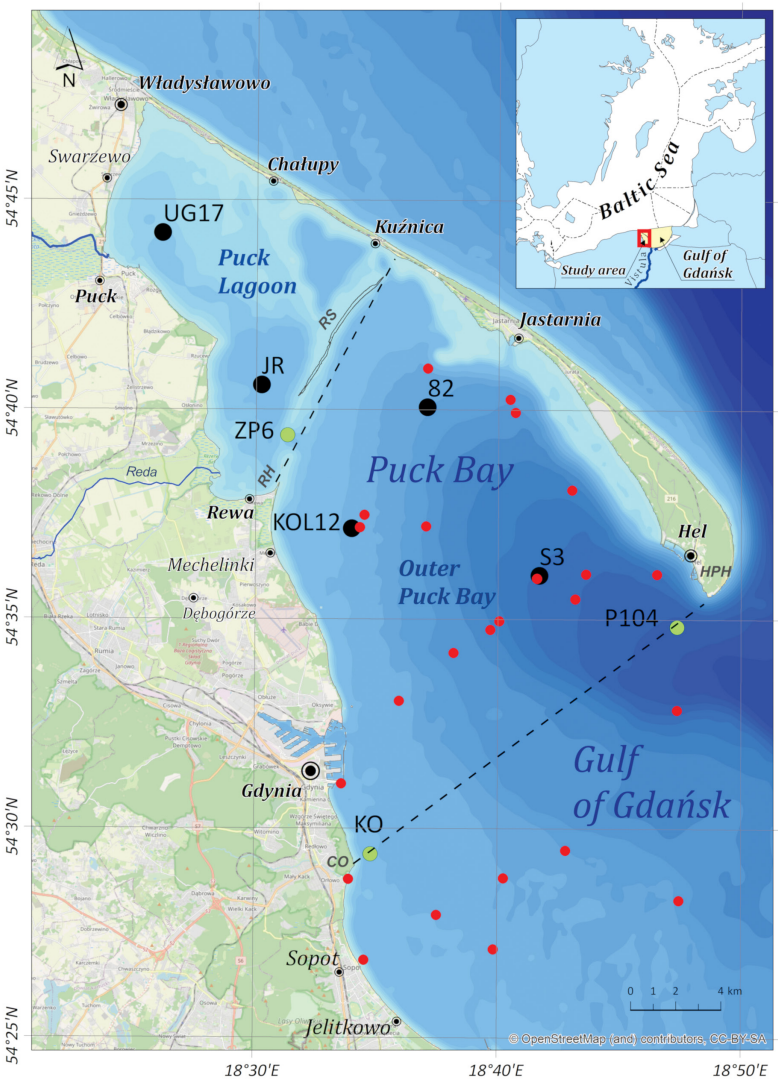

Fig. 2.1 The study area; black dots indicate obligatory stations at which abiotic and biotic parameters were determined in 12 monthly cruises performed in 2020, and in 6 monthly cruises (June-November) in 2023; red dots indicate sampling sites (source of biotic parameters only) during various scientific projects conducted by NMFRI in 1987-2018 (24 stations); green dots stand for the State Environmental Monitoring sampling stations (source of biotic parameters only) (KO, P104 and ZP6 - monitored since 2002); CO - Cape Orłowski, HPH - Hel Peninsula Headland, RS - Rybitwia Shoal, RH - Rewa Headland (source: map drawn by Lena Szymanek, NMFRI)

The OPB has an area of 256.5 km^2, and volume of 5.26 km^3, and this accounts for 70% of the area and 94% of the volume of the entire Puck Bay. Average annual flow of all watercourses in the Puck Bay catchment area is 6.871 m^3s^{-1}, of which the Reda River flow constitutes 72%. Much smaller PL (102.7 km^2) is supplied with water discharged from over 75% of the catchment area. Average annual inflow of all watercourses to the Puck Bay is 0.217 km^3. The hydrological regime of the entire Puck Bay is shaped by (i) water inflow from the catchment area of the bay (908.8 km^2), (ii) direct contact and exchange of water with the open Gulf of Gdańsk, (iii) the exchange of mass and energy with the atmosphere (precipitation, evaporation) (Nowacki, 1993a; Cyberski, 1993).

2.2. Methods of abiotic parameters determination (temperature, salinity, dissolved oxygen, nutrients, Secchi depth)

Studies carried out in the Puck Bay in 2020 and in 2023 were based on monthly (January-December, 2020, and June-November, 2023) sampling/measurements at two stations (UG17 and JR) located in PL and three (S3, 82 and KOL12) in OPB (Fig. 2.1).

Measurements of temperature (T) and salinity (S) on the depth profiles were made using the CastAway CTD probe (https://www.sontek.com/media/pdfs/castaway-ctd-web.pdf) (UNESCO, 1981; HELCOM, 2017a). Water samples for determination of dissolved oxygen content (O_2) and nutrient concentrations were taken with the Ruttner sampler. Water for oxygen content determination was collected from the depths: 0-1; 10; 20; 40 m, and 1 m above the bottom, and Winkler method was applied for determination of this parameter (Grasshoff, 1976; HELCOM, 2017b).

Nutrient concentrations [$N\text{-}NO_3$ - nitrate, $N\text{-}NO_2$ - nitrite, $N\text{-}NH_4$ - ammonium, TN total nitrogen, $P\text{-}PO_4$ - phosphate (also called DIP - dissolved inorganic phosphorus), TP total phosphorus, and $Si\text{-}SiO_4$ - silicate] were determined in water samples taken from the depths: 0-1; 2.5; 5; 10; 15; 20; 40 m, and 1 m above the bottom. Sum of $N\text{-}NO_3$, $N\text{-}NO_2$ and $N\text{-}NH_4$ gives dissolved inorganic nitrogen (DIN). Water for nutrient determinations was stored in 500 ml plastic bottles; chemical analyzes were performed in the laboratory onshore on the same day. Analytical procedures followed the standard methods recommended for the Baltic Sea by the BMP (Baltic Monitoring Program). TN and TP were determined from unfiltered water samples using persulfate oxidation at an autoclave temperature of ca. 120°C for 30 minutes (HELCOM, 1988; UNESCO, 1983; Grasshoff, 1976). Organic nitrogen (Norg.) and other forms

of phosphorus (P-other), commented in the paper, are the differences between TN and DIN (Norg.=TN-DIN), and between TP and DIP (P-other =TP-DIP).

During the research, the Secchi depth was measured (HELCOM, 2017c).

Historical data commented in the monograph were collected in 1981-1991 (nitrate, ammonium, phosphate, oxygen content) (Bolałek et al., 1993), and in 1972-1990 (temperature) (Nowacki, 1993b). The historical strategy of water sampling was the same as in 2020 and 2023 but the equipment was different, as Nansen bottles equipped with reversing thermometers were used then (Bolałek et al., 1993; Nowacki, 1993b). The applied analytical methods for determination of nutrients, and oxygen content were the same as those used by us in 2020 and 2023 (HELCOM, 1988; UNESCO, 1983; Grasshoff, 1976). The historical, as well as 2020 and 2023 average monthly values, were calculated for the entire water column at individual sampled stations, and then for the combined stations in PL and OPB (Bolałek et al., 1993; Nowacki, 1993a,b).

2.3. Abiotic parameters in the Puck Bay in 2020 and 2023 with reference to available historical data

Abiotic parameters are the foundation that determines the development of biological life in water bodies. The widely observed long-term changes of these parameters are currently not only local e.g. local problems with eutrophication, but global, with the main anthropogenic stressor i.e. climate change and air and water temperature increase (Chapter 1). Keeping this fact in mind, we were convinced that comprehensive, large-scale approach in explaining complexity of anthropogenic stressors observed in the Puck Bay deserves a separate chapter, and that is why Chapter 1 opens this monograph. In our opinion, such an approach left a clearer space for commenting on environmental data collected in 2020 and 2023, even if for obvious reasons they are referred to available historical data. In Chapter 2, we provide bulk of information that contributes to understanding the long-term variability of a given abiotic parameter, but also shows the degree of complexity of the ecosystem functioning, driven by internal, as well as external forcing. It was unavoidable to show some elements of the dependencies between abiotic and biotic parameters in Chapter 2, but the full spectrum of long-term changes in biotic parameters, referred to external and internal driving forces, is presented in Chapter 3.

The graphical presentation of the studied abiotic parameters in the Puck Bay in 2020 and in June-November 2023 (Fig. 2.2A,B) allows for quick detection of many

dependencies such as: (i) frequent inflows of high-salinity water in the bottom layer of the deepest station S3, due to upwelling, and the associated increase in salinity, decrease in oxygen content, and increase in nutrient concentrations, (ii) seasonal increase in temperature and formation of thermocline causing uneven vertical distribution of nutrient concentrations, and resulting in a uneven decrease in oxygen content throughout water column, (iii) differences between the nutrient concentrations in OPB (stations S3, 82, KOL12) and PL (stations JR, UG17), (iv) depletion of some nutrients, particularly P-PO_4 at shallow stations in 2020. The proposed graphical presentation also allows following the depth at particular stations in PL and OPB.

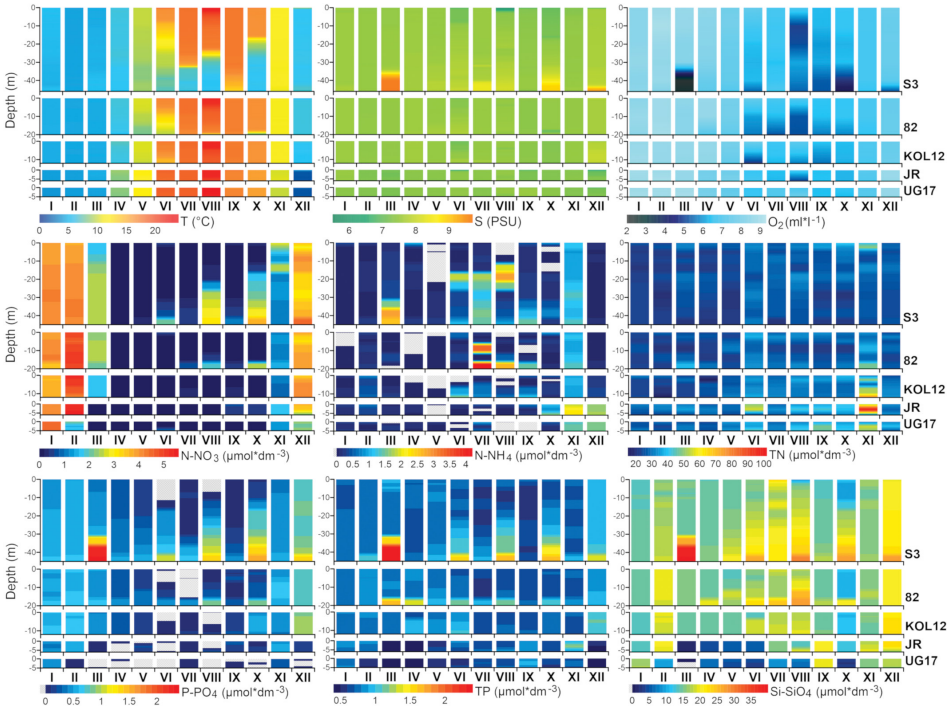

Fig. 2.2A Vertical, spatial, and seasonal changes of temperature (T), salinity (S), oxygen content (O_2), concentrations of nitrate (N-NO_3), ammonium (N-NH_4), total nitrogen (TN), phosphate (P-PO_4), total phosphorus (TP), silicate (Si-SiO_4) in the Outer Puck Bay (S3, 82, KOL12) and the Puck Lagoon (JR, UG17) in January-December 2020

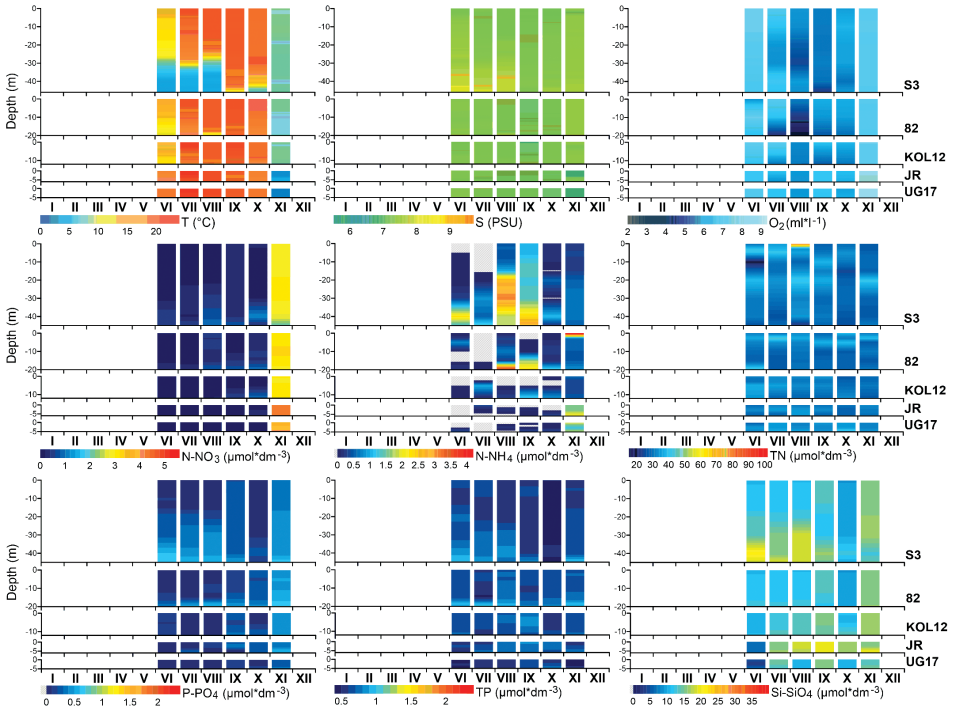

Fig. 2.2B Vertical, spatial, and seasonal changes of temperature (T), salinity (S), oxygen content (O_2), concentrations of nitrate ($N\text{-}NO_3$), ammonium ($N\text{-}NH_4$), total nitrogen (TN), phosphate ($P\text{-}PO_4$), total phosphorus (TP), silicate ($Si\text{-}SiO_4$) in the Outer Puck Bay (S3, 82, KOL12) and the Puck Lagoon (JR, UG17) in June-November 2023

2.3.1. Temperature

The annual average T in 2020 in PL was equal to 11.52°C, whereas in 1972-1990 it amounted to 9.28°C (difference 2.24°C). The annual average T in 2020 in OPB reached 10.60°C, whereas in 1972-1990 it was equal to 7.71°C (difference 2.89°C) (Fig. 2.3; Nowacki, 1993b). The greatest difference between monthly historical and 2020 averages in PL reached 4.66°C in June 2020, and 4.82°C in November 2020, whereas in OPB the greatest T difference (4.57°C), similarly to PL, was noted in June 2020. In 2023, average monthly T values in July and September-October in PL were higher, whereas in November 2023 lower than in 2020, the latter even slightly lower than T historical (1972-1990; Nowacki, 1993b). In PL, the seasonal well-marked T

maximum in 2020 was recorded in August, whereas in 2023 it was observed in July. In OPB, the seasonal T maximum in 2020 was recorded in August-September, whereas in 2023 it was observed in September, with much higher T also in October 2023 than in October 2020.

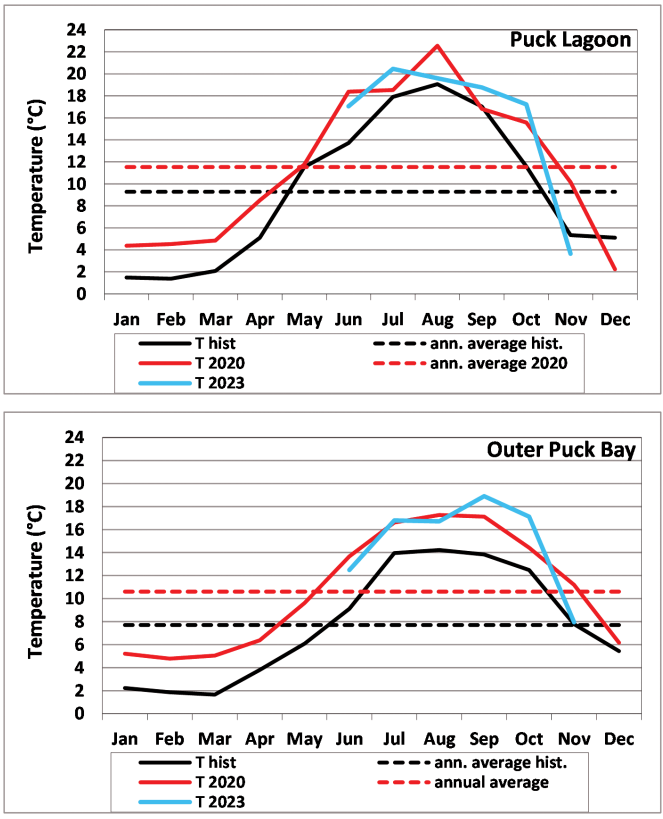

Fig. 2.3 Monthly and annual averages of water temperature (T) in the Puck Lagoon (JR, UG17) and the Outer Puck Bay (S3, 82, KOL12) in 1972-1990 (hist), 2020, and 2023 (source of historical data: Nowacki, 1993b)

In 2023, in majority of cases the monthly temperature values were either similar or higher than those measured in 2020 (November 2023 was exceptional, with seasonal T drop occurring earlier than in 2020). This fact indicates that the increase in water temperature in PL and OPB, observed throughout 2020, was not incidental, but it is a repeated response of the system to strengthening global warming. The

observed significant temperature changes did not occur in the same months in 2020 and 2023. In 2020 and 2023, the periods between June and October were marked by sudden and considerable water temperature changes in shallow PL, most probably as a response to heat waves (Zschenderlein et al., 2019; Tomczyk and Bednorz, 2023). Jędruszkiewicz et al. (2024) focused on heat waves in Poland and they found out that over the past few decades, Central and Southern Poland have experienced a considerable rise in maximum temperatures, which has led to an increase in the number of hot days. This increase, as the authors state, is particularly prominent during the summer months (June, July and August) but also in May and September, which extends the hot season. Although heat waves have become more frequent and persistent since 2006, their mean intensity has remained unchanged. Ghazi et al. (2023) carried out modeling studies focused on projection of climate change impact on extreme temperature and precipitation in Central Poland and the outcome showed that compared to the historical reference period (1990-2014), Central Poland will experience an increase in temperature and precipitation by the end of the twenty-first century. By the end of the twenty-first century the mean annual temperature and mean annual precipitation totals are said to increase by 1-4.8°C and 2-7.5%, respectively; the average number of hot, very hot days, and extremely hot days, tropical nights, and extremely high daily precipitation are said to increase. IMWM (2021) presents air temperature values, calculated for the basic physio-geographical units of Poland. These units spread from the north to the south and they are as follows: the Coast belt and the Southern-Baltic Coastlands belt, the lake districts belt, the lowlands belt, the uplands belt, the Podkarpacie, the Carpathians, and the Sudetes. In addition, the lowlands belt and the lake districts were divided into western and eastern parts along the 19°E meridian. Such a division, as the authors explain, allows showing possible differences related to the thermal regionalization of Poland. In 2021, the warmest regions of Poland were the Coast belt and the Southern-Baltic Coastlands belt, where the area average temperature reached 9.0°C. Interestingly, the same approach made in 2022 (IMWM, 2022) showed that the Coast belt and the Southern-Baltic Coastlands belt were not the warmest in Poland, but air temperature was there by 0.5°C higher than in 2021.

2.3.2. Salinity

In 2020, the annual average salinity value in PL reached 7.30 PSU and it was by 0.21 PSU lower than in OPB (Fig. 2.4). Nowacki (1993b) gives the average annual salinity values of surface waters calculated for the period 1965-1974 and they

amount to 7.31 PSU in PL and 7.65 PSU in OPB. It can be assumed that the salinity value calculated for surface waters in PL is representative for the entire water column, because it is a very shallow well-mixed region. The historical (1965-1974) average annual salinity in PL is almost identical to the value measured in 2020 (Nowacki, 1993b; Fig. 2.4). The decline in salinity in PL in March and December 2020 (Fig. 2.4) was most probably related to seasonally variable runoffs of Reda River, with highest outflows usually in spring and autumn (Szymczak and Piekarek-Jankowska, 2007). In 2023, S was declining in PL from ca. 7.25 PSU in June 2023 to ca. 6.93 in November 2023, whereas in OPB it was declining from ca. 7.36 in June 2023 to 7.13 PSU in September 2023, and then increasing to 7.4 PSU in October 2023, getting very close to the value observed in 2020.

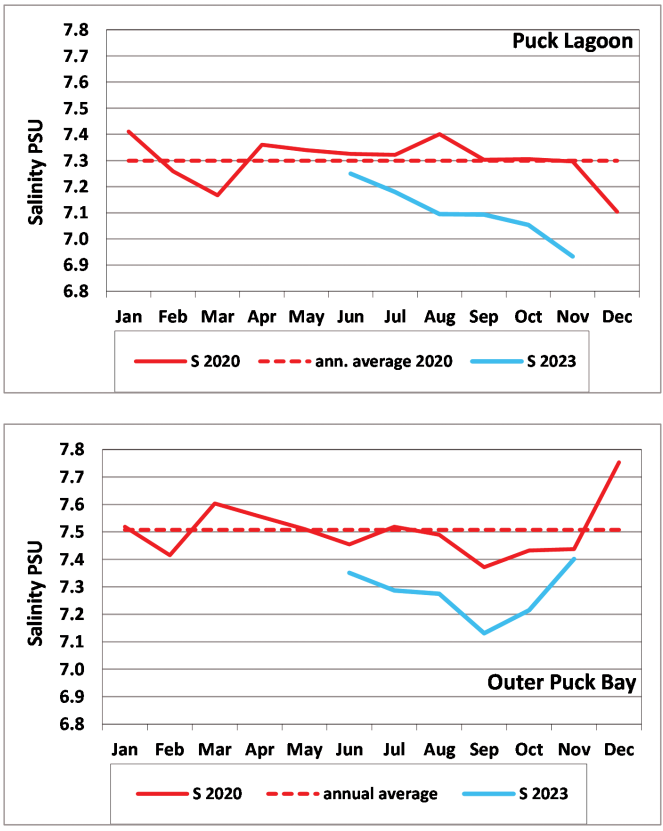

Fig. 2.4 Monthly and annual average of salinity in the Puck Lagoon (JR, UG17) and the Outer Puck Bay (S3, 82, KOL12) in 2020 and 2023

In 2023, monthly S values in PL and OPB were lower than in 2020; the difference reached over 0.3 PSU in PL in November 2023, and ca. 0.2 PSU in OPB in September 2023. Chlost and Cieśliński (2022) calculated the water balance for the entire Puck Bay and the outcome shows that 38% of inflowing water originates from the land, 32% - from the open Gulf of Gdańsk fed by the Vistula River, and 30% from precipitation. Water losses from the Puck Bay include outflow (46%) and evaporation (54%). Salinity in the Puck Bay is the resultant of the interaction of sea and land waters. Salinity in OPB remains under impact of the surface and bottom inflow of more salty waters from the Gulf of Gdańsk. Fresh waters, mainly from the Vistula River, additionally influence the surface layer in this subregion. In PL, salinity is primarily determined by the intensity of water exchange with OPB (Nowacki, 1993b; Jędrasik and Cieślikiewicz, 2022). Salinity distributions in OPB indicate a constant or relatively frequently repeated phenomenon of upwelling, which is favored by certain wind directions and strength and by the bottom topography characterized by the presence of a trough that shallows towards the Rybitwia Shoal (Nowacki et al., 2009; Fig. 2.1).

Incidents of considerable upwelled water fluxes to the Puck Bay from the open Gulf of Gdańsk occurred in March, October, and December 2020, resulting in short-term but a significant increase in salinity and nutrient concentrations, and decrease in oxygen content in the near bottom layer at the deepest S3 station (Fig. 2.2A). The bottom topography, plus a natural barrier formed by Rybitwia Shoal and Rewa Headland significantly limit water, thus salt and nutrients exchange between OPB and PL. That explains the average annual salinity in 2020 by 0.21 PSU lower in PL than in OPB (Fig. 2.4). The salinity, as well as nutrient and oxygen content gradients in the water column of the deepest station S3 did not indicate upwelling in June-November 2023 (Fig. 2.2B). This fact may partly explain lower S in the entire Puck Bay in June-November 2023 as compared with data gathered in 2020. There are two more facts that may help explain the commented decrease in salinity in 2023. In January-May 2023, monthly Vistula water runoffs were by ca. 600 m^3s^{-1} larger than in relevant months 2020 (Fig. 2.5). A long, five-month period, with high Vistula water runoff in 2023, if followed by favorable wind direction inducing water dynamics, could have had a delayed effect on salinity in the months that followed. We also cannot rule out that the reason for the lower salinity in both PL and OPB in 2023 was the cessation of brine effluent discharge, which took place in July 2021. The brine was a by-product of the construction of underground gas storage caverns in salt deposits (Robakiewicz, 2016; Zaborska et al., 2019).

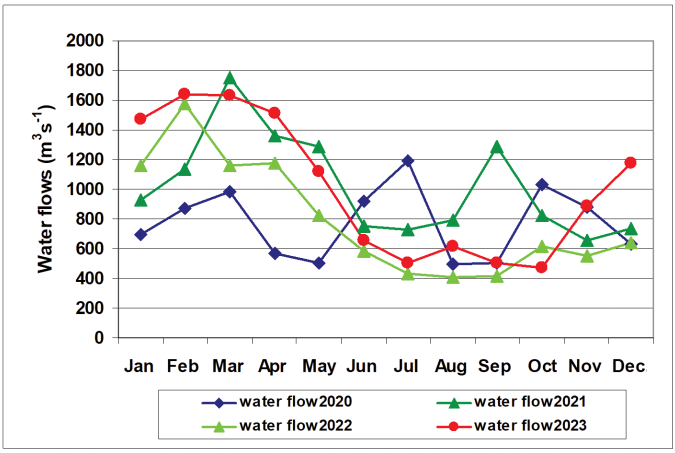

Fig. 2.5 Vistula water flows measured at the lowermost monitoring station (Tczew) in 2020-2023 (source of data: access to monitoring data provided by the Institute of Meteorology and Water Management - National Research Institute)

The salinity dynamics in the Baltic Sea is governed by net precipitation, river runoff, surface outflow of brackish Baltic Sea water, and the compensating deep inflow of highly saline water from the Kattegat, which is strongly controlled by the prevailing atmospheric forcing conditions (Meier and Kauker, 2003; Lehmann et al., 2022; Meier et al., 2022). Lehmann et al. (2022) prove that although 30-year variability in salinity was found for surface and bottom salinity there is no clear long-term trend of the mean salinity of the Baltic Sea. However, at regional scales as the authors state, in addition to the interaction with the open Baltic Sea, the salinity regime of estuaries and lagoons is closely related to the local water balance components, including river runoff, precipitation, and evaporation. Under changing climatic conditions, affecting the above mentioned water balance components, development of the salinity regime at regional scales may have various basic-specific features that might diverge from corresponding trends in the open Baltic Sea.

2.3.3. Oxygen content

The annual average of oxygen content in 2020 in PL was equal to 7.72 $ml \cdot l^{-1}$, whereas in 1981-1991 it amounted to 7.41 $ml \cdot l^{-1}$ (difference 0.31 $ml \cdot l^{-1}$). In OPB, average annual content reached 7.34 $ml \cdot l^{-1}$ in 2020, and 7.45 $ml \cdot l^{-1}$ in 1981-1991 (difference

0.11 $ml \cdot l^{-1}$) (Fig. 2.6; Bolałek et al., 1993). In February 2020, in both subregions the dissolved oxygen content was by 1-1.5 $ml \cdot l^{-1}$ higher than in 1981-1991 (conversion of $ml \cdot l^{-1}$ into $mg \cdot l^{-1}$ or $\mu mol \cdot l^{-1}$; https://www.ices.dk/data/tools/Pages/Unit-conversions.aspx). In April-June in OPB the oxygen content in 2020 was by 0.6-1.5 $ml \cdot l^{-1}$ lower than in 1981-1991. In the late summer/early autumn, the oxygen content minimum in 2020 and 1981-1991 was at comparable level in OPB, whereas in PL the historical records were lower than those in 2020. In both subregions, the oxygen content in June-November 2023 is interwoven with 2020 and historical values, maintaining the general seasonal trend. The fact that the decrease in T coexists with the increase in oxygen content in PL in November 2023 is noteworthy. The winter months in 1981-1991, 2020, and 2023 were characterized by seasonal maximum oxygen content, which was higher in PL than in OPB (even by over 1 $ml \cdot l^{-1}$) (Fig. 2.6).

Comparison of monthly averages of oxygen content in OPB and PL in 1981-1991 and 2020 (Fig. 2.6) shows some shifts in seasonal patterns as well as differences in peak heights, particularly observed in spring. Historically, favorable conditions for the phytoplankton bloom onset, i.e. water temperature and light, appeared in April 1981-1991 (Renk, 1993) but not in January-February, as observed in 2020 (Fig. 2.3; see Chapter 3). Historically, the winter months were a time of accumulation of nutrients, whose concentrations were significantly higher than in 2020 (see next section; Bolałek at al., 1993), thus constituted high resources for intensive spring photosynthesis process. Intensive photosynthesis on the one hand constitutes a natural source of oxygen, on the other hand leads to significant nutrient declines, or nutrient depletion and limitation of phytoplankton growth (see next section). In 1981-1991, 2020, and 2023, the spring maximum of oxygen content was followed by the summer minimum, with the latter values being well below the annual averages. The seasonal decline in oxygen content must have been related to seasonal increase in water temperature (Fig. 2.3) and oxygen consumption in the processes of organic matter mineralization. Despite long-term increase in water temperature (Fig. 2.3), oxygen content in PL in August 2020 was by ca. 0.8 $ml \cdot l^{-1}$ higher than in the same month in 1981-1991 (Fig. 2.6), and that may have resulted from a significant phytoplankton biomass decline (Chapter 3), thus less oxygen needed for mineralization of organic matter. A significant increase in oxygen content in 1981-1991, 2020, and 2023 was observed in November-December, and that is mainly due to drop in seasonal water temperature favoring an increase in atmospheric oxygen solubility (Figs. 2.2A,B, 2.3, 2.6; Bolałek at al., 1993).

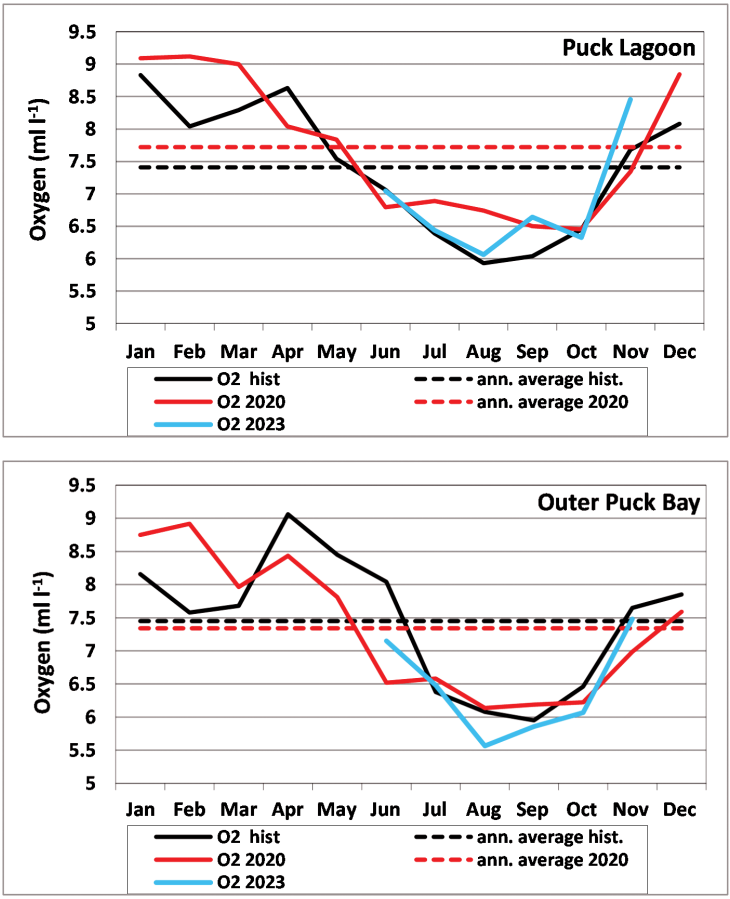

Fig. 2.6 Monthly and annual averages of oxygen content in the Puck Lagoon (JR, UG17) and the Outer Puck Bay (S3, 82, KOL12) in 1981-1991 (hist), 2020, and 2023 (source of historical data: Bolałek et al., 1993)

Deep waters of the open Gulf of Gdańsk, characterized by oxygen depletion (Hansson and Viktorsson, 2020; Janecki et al., 2023) occasionally intrude to the Puck Bay, but periods of low oxygen content occurring at the deepest station S3 are rather short (Fig. 2.2A). Thermal stratification of water column was very clear at deeper stations of the Puck Bay in summer 2020 and 2023 (Fig. 2.2A) and that fact also caused temporary declines of oxygen content, but the shallow well mixed coastal region did not suffer from oxygen depletion in 1981-1991, 2020, or in June-November 2023 (Figs. 2.2B, 2.6; Bolałek et al., 1993).

Hinrichsen et al. (2011) have documented the main mechanisms responsible for variations in oxygen content in the Baltic Sea over the last few decades, and they are as follows: (i) changed frequency and magnitude of major inflows of the North Sea waters (Meier and Kauker, 2003; Mohrholz et al., 2015), which have been identified as the most crucial process for the renewal of oxygen-depleted deep water masses in the Baltic Sea, (ii) increased oxygen consumption by enhanced degradation of suspended organic matter by bacteria caused by the progressive increase in water temperature, (iii) decreased oxygen solubility in water masses due to climate warming. Over the last decades, oxygen content in the Baltic Sea was decreasing (Hansson and Viktorsson, 2020) and the maximum negative trends up to 1 $ml \cdot l^{-1}$ per decade was found in the halocline of Bornholm and Gotland Basin (Lehmann et al., 2022).

2.3.4. Nutrients - nitrate, ammonium, phosphate

In 2020, the average annual concentration of $N\text{-}NO_3$ in PL was 1.13 $\mu mol \cdot dm^{-3}$, whereas in 1981-1991 it reached 3.68 $\mu mol \cdot dm^{-3}$ (difference 2.56 $\mu mol \cdot dm^{-3}$). The average annual concentration of nitrate in OPB was 1.48 $\mu mol \cdot dm^{-3}$ in 2020, and 3.41 $\mu mol \cdot dm^{-3}$ in 1981-1991 (difference 1.93 $\mu mol \cdot dm^{-3}$). In both subregions in 1981-1991, monthly average nitrate concentrations were higher than in 2020 and in June-November 2023; the maximum difference reached ca. 8-9 $\mu mol \cdot dm^{-3}$ in March 2020 and in November-December 2020 in PL, and ca. 6 $\mu mol \cdot dm^{-3}$ in March 2020 in OPB (Fig. 2.7A; Bolałek et al., 1993). Historical data show that between January and March there was generally increase in nitrate concentrations to reach a maximum in March, particularly well pronounced in PL. This maximum was followed by a steep decline in concentrations in both subregions until seasonal minimum was reached. In 1981-1991, seasonal $N\text{-}NO_3$ minimum was not falling below 0.5 $\mu mol \cdot dm^{-3}$ and low concentrations were measured from April until July in PL, and from May until August in OPB. Quite different $N\text{-}NO_3$ annual pattern was observed in 2020, with a steep decline in concentrations in February/March in PL, and in March-April in OPB (one-two months earlier than three decades earlier), and with absent sharp winter increase in concentrations in both subregions. In 2020, nitrate depletion or occasional values not exceeding 0.4 $\mu mol \cdot dm^{-3}$ were observed for eight months in PL and for six months in OPB; identical situation was observed in 2023, with nitrate depletion from June (earlier measurements were not conducted) till October. Nitrate concentrations in November 2023 were considerably higher than in November 2020, and that pattern followed T, O_2 patterns (Figs. 2.3, 2.6, 2.7A).

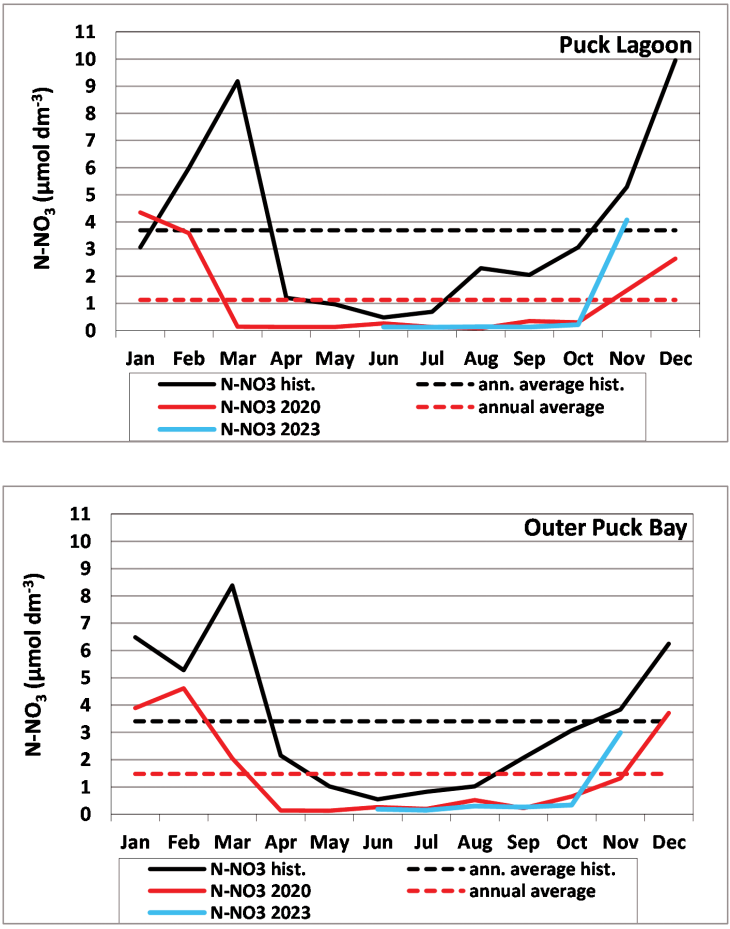

Fig. 2.7A Monthly and annual averages of nitrate concentrations in the Puck Lagoon (JR, UG17) and the Outer Puck Bay (S3, 82, KOL12) in 1981-1991 (hist), 2020, and June-November 2023 (source of historical data: Bolałek et al., 1993)

In both studied subregions, nitrite concentrations remained in the range of 0.00-0.04 µmol·dm^{-3} in March-October 2020 and in the range 0.20-0.33 µmol·dm^{-3} in the remaining months of the year. They were omitted in the graphical presentation (Fig. 2.2A,B), but included in DIN calculations (see the text that follows), and taken into account in statistical analysis (see Chapter 3).

In 2020, the average annual concentration of $N\text{-}NH_4$ in PL was 0.47 µmol·dm^{-3}, whereas in 1981-1991 it reached 2.70 µmol·dm^{-3} (difference 2.30 µmol·dm^{-3}). The

average annual ammonium concentration in OPB was equal to 0.37 μmol·dm^{-3} in 2020 and 2.00 μmol·dm^{-3} in 1981-1991 (difference 1.63 μmol·dm^{-3}) (Fig. 2.7B; Bolałek et al., 1993). With the exception of July in OPB, monthly ammonium concentrations were considerably higher in 1981-1991 than in 2020 or in June-November 2023, and the maximum difference reached ca. 5 μmol·dm^{-3} in February 2020 in PL. In 1981-1991, very high N-NH_4 concentrations were observed in January-March. Historical winter ammonium maximum was by ca. 2 μmol·dm^{-3} higher in PL than in OPB. In 1981-1991, winter ammonium maximum in both subregions was followed by considerable decline in concentrations to reach minimum values of ca. 0.7-1 μmol·dm^{-3} in June-July, and that minimum was followed by a sharp increase in autumn/winter. In 2020, ammonium depletion or occasional values not exceeding 0.5 μmol·dm^{-3} were observed for nine months in PL and six months in OPB. Monthly average ammonium concentrations in June-November 2023 remained very close to values observed in 2020, and that concerns PL and OPB. Huge drop in winter ammonium concentrations in OPB and PL in 2020, as compared with values found in 1981-1991, may arise not only from significantly decreased N anthropogenic loads (Pastuszak et al., 2018; Chapter 1), but also from its increasing uptake by phytoplankton in 2020, favored by earlier start of vegetation season (Chapter 3).

In 2020, the average annual concentration of P-PO_4 in PL was 0.14 μmol·dm^{-3}, whereas in 1981-1991 it reached 0.97 μmol·dm^{-3} (difference 0.83 μmol·dm^{-3}). The average annual phosphate concentration in OPB was equal to 0.38 μmol·dm^{-3} in 2020, and 0.84 μmol·dm^{-3} in 1981-1991 (difference 0.46 μmol·dm^{-3}) (Fig. 2.7C; Bolałek et al., 1993). In both subregions monthly phosphate concentrations were considerably higher in 1981-1991 than in 2020 or in June-November 2023, and the maximum difference reached ca. 1.6 μmol·dm^{-3} in PL in March 2020. In 1981-1991, P-PO_4 concentrations were changing from 1.7 μmol·dm^{-3} to ca. 0.3 in PL, and from ca. 1.5 μmol·dm^{-3} to ca. 0.4 μmol·dm^{-3} in OPB. In 2020, average annual phosphate concentrations were by 0.24 μmol·dm^{-3} higher in OPB than in PL; for seven months PL was characterized either by P-PO_4 depletion or concentrations well below 0.2 μmol·dm^{-3}. Monthly average phosphate concentrations in June-November 2023 remained very close to values observed in 2020, and that concerns PL and OPB; there was one exception i.e. October 2023, when P-PO_4 remained low, and the seasonal increase started in November 2023, but not in October, as seen in 2020. In 2023, the P-PO_4 pattern followed T and O_2 patterns (Figs. 2.3, 2.6, 2.7C).

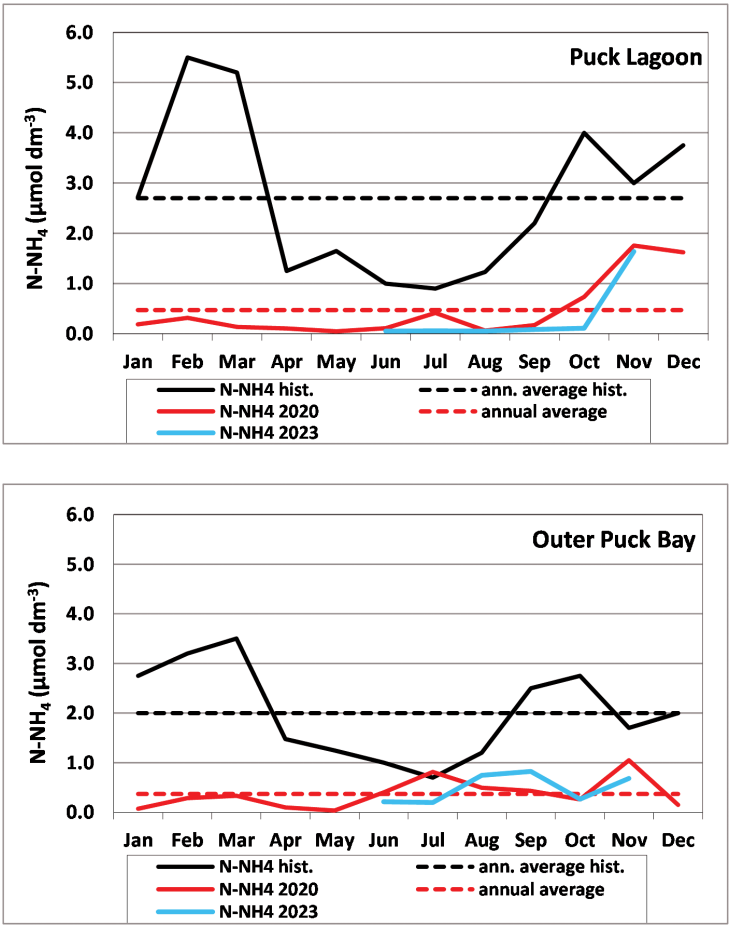

Fig. 2.7B Monthly and annual averages of ammonium concentrations in the Puck Lagoon (JR, UG17) and the Outer Puck Bay (S3, 82, KOL12) in 1981-1991 (hist), 2020, and June-November 2023 (source of historical data: Bolałek et al., 1993)

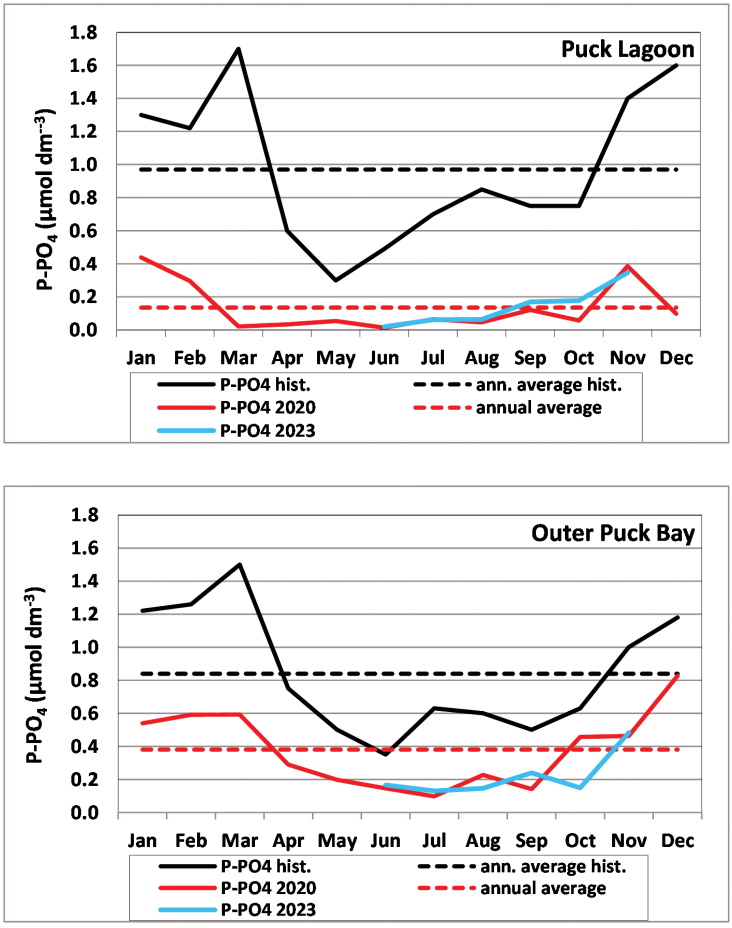

Fig. 2.7C Monthly and annual averages of phosphate concentrations in the Puck Lagoon (JR, UG17) and the Outer Puck Bay (S3, 82, KOL12) in 1981-1991 (hist), 2020, and June-November 2023 (source of historical data: Bolałek et al., 1993)

2.3.5. Nutrients - silicate, total phosphorus, total nitrogen

Average annual silicate concentration was 11.18 μmol·dm^{-3} in PL and 16.56 μmol·dm^{-3} in OPB (Fig. 2.8A). In PL, a very significant decrease in silicate concentrations, from ca. 15 μmol·dm^{-3} in February to ca. 1 μmol·dm^{-3} in March 2020, was observed. That minimum was followed by uneven increase in concentrations with the maximum value in September 2020 (ca. 20 μmol·dm^{-3}), which was followed by a decrease to approx. 8 μmol·dm^{-3} in October 2020, and then an increase to approx. 18 μmol·dm^{-3} in December 2020. Silicate concentrations in OPB showed much smaller seasonal fluctuations than in PL, with the minimum at the level of ca. 13 μmol·dm^{-3} in October and maximum of ca. 22 μmol·dm^{-3} in December 2020. The annual patterns of silicate and TP concentrations in PL were similar (Figs. 2.8A,B). In June-November 2023, silicate concentrations in PL and OPB to some extent followed the patterns observed in 2020.

In 2020, the average annual TP concentrations reached 0.64 μmol·dm^{-3} in PL and 0.79 μmol·dm^{-3} in OPB (Fig. 2.8B). In PL, TP concentrations showed a sharp decrease from approx. 0.78 μmol·dm^{-3} in January 2020 to ca. 0.45 μmol·dm^{-3} in March/April 2020. That sharp decrease was followed by an increase, and then a maximum of ca. 0.84 μmol·dm^{-3} in September 2020. That maximum was followed by a sharp decrease to 0.63 μmol·dm^{-3} in October 2020, and by a next increase to ca. 0.83 μmol·dm^{-3} in November 2020, and again by a decrease down to ca. 0.45 μmol·dm^{-3} in December 2020. TP monthly concentrations in OPB had a fluctuating character, with values above the annual average in March-June 2020 and December 2020, and with values below that annual average in July-September 2020 and in November 2020. It seems, that 2023 patterns of monthly TP concentrations in PL and OPB would fit better the ones from 2020 if they were shifted by one month towards the left (Fig. 2.8B). The sharp declines in silicate and TP concentrations in shallow PL closely follow the seasonal maxima of diatom biomass in 2020 (see Chapter 3).

The average annual concentration of TN in PL was at the level of 34.31 μmol·dm^{-3}, whereas in OPB - at the level of 27.89 μmol·dm^{-3} (Fig. 2.8C). Throughout the entire 2020, monthly TN concentrations were higher in PL than in OPB. In both sub-regions, TN values started to increase from the winter minimum of ca. 23-30 μmol·dm^{-3} to reach the first peak in June (approx. 32 μmol·dm^{-3} in OPB and approx. 41 μmol·dm^{-3} in PL), and the second one in November 2020 (approx. 37 μmol·dm^{-3} in OPB and approx. 54 μmol·dm^{-3} in PL). Patterns of TN monthly concentrations in June-November 2023 in PL and OPB are quite different than those of 2020. They do not show fluctuations, but instead they show rather flattened concentrations changing between ca. 30

µmol·dm^{-3} in June 2023 and 32 µmol·dm^{-3} in November 2023 in PL, and from ca. 32 µmol·dm^{-3} in June 2023 to ca. 29 µmol·dm^{-3} in November 2023 in OPB (Fig. 2.8C).

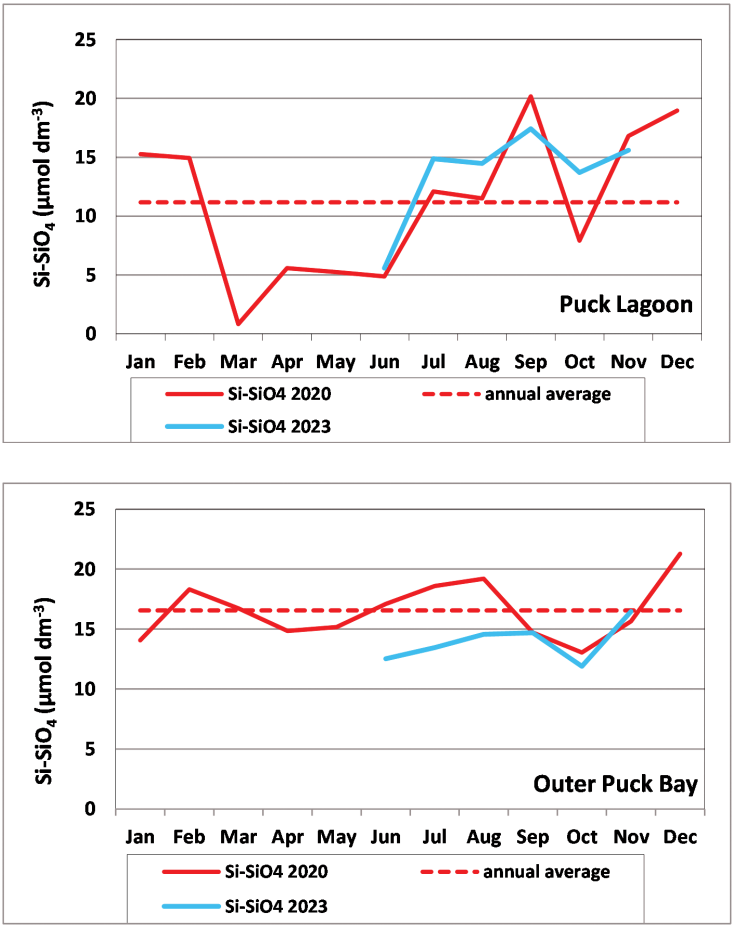

Fig. 2.8A Monthly and annual averages of silicate concentrations (no historical data) in the Puck Lagoon (JR, UG17) and the Outer Puck Bay (S3, 82, KOL12) in 2020, and June-November 2023

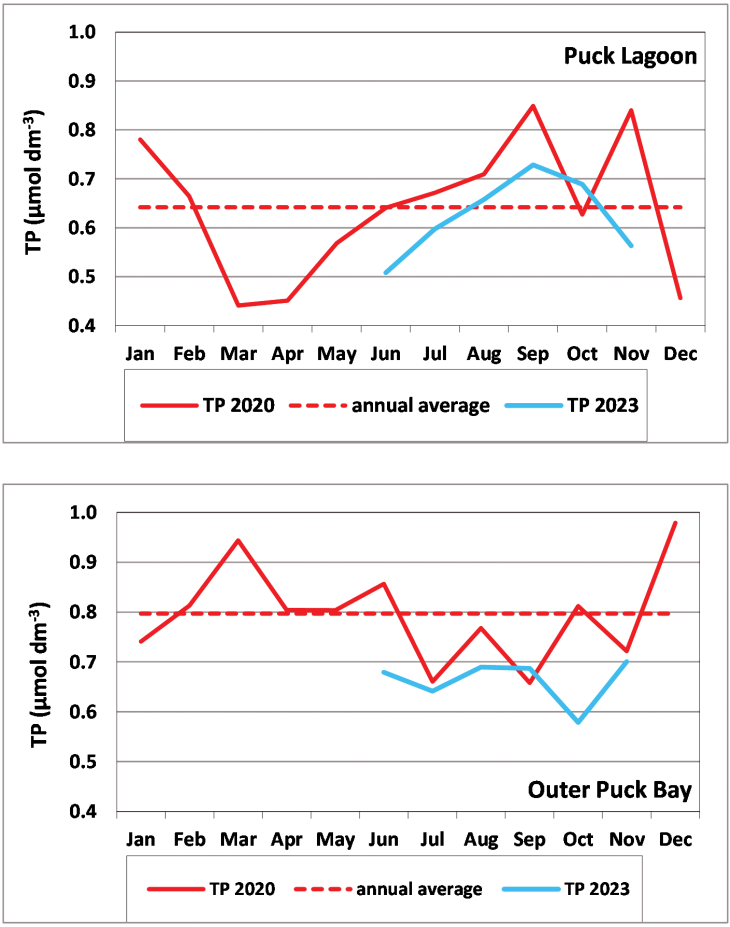

Fig. 2.8B Monthly and annual averages of total phosphorus concentrations (no historical data) in the Puck Lagoon (JR, UG17) and the Outer Puck Bay (S3, 82, KOL12) in 2020, and June-November 2023

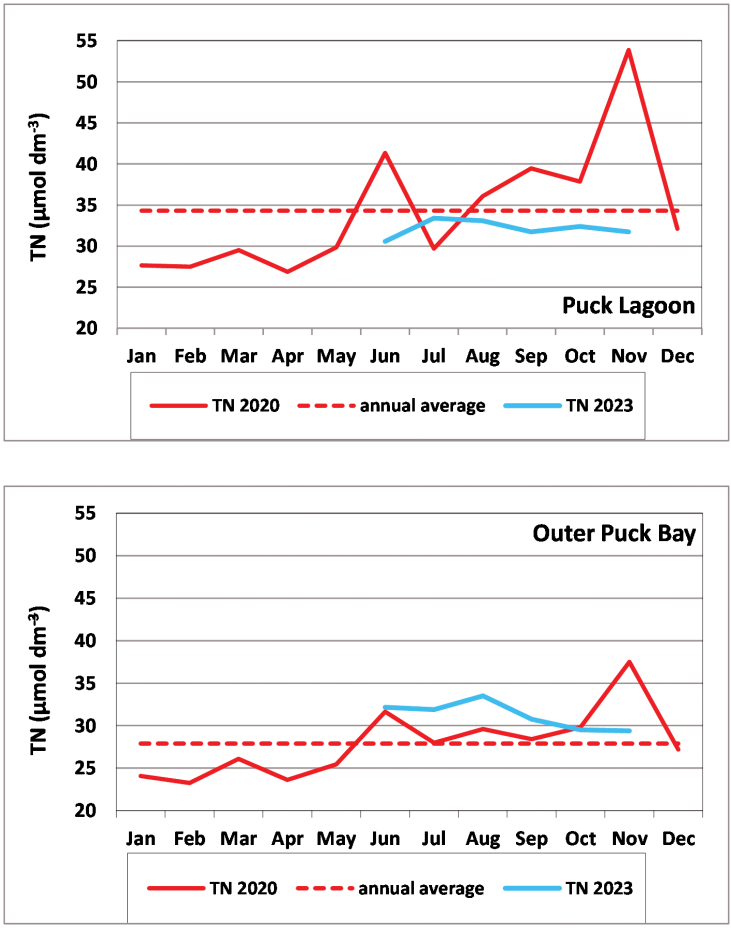

Fig. 2.8C Monthly and annual averages of total nitrogen concentrations (no historical data) in the Puck Lagoon (JR, UG17) and the Outer Puck Bay (S3, 82, KOL12) in 2020, and June-November 2023

2.3.6. Secchi depth

In PL, there were four months in 2020 (January, February, April, November) when the reading of the apparent transparency of the water was not possible because the water was transparent to the bottom. In 2023, Secchi depth in PL was either the same (January), higher as in August and October, much higher as in September, or lower as in July and November in comparison with relevant data of 2020 (Fig. 2.9).

Monthly Secchi depth in OPB in 2020 was changing from very high values in winter months, exceeding even 10 m, to a minimum seen in June 2020 (ca. 3.8 m). The Secchi depth readings in OPB in June-November 2020 and 2023 were in majority of cases comparable; July was exceptional with Secchi depth considerably lower in 2023 as compared with the value of 2020.

In 2020, Secchi depths in particular months, as well as their average annual values were much higher in OPB (6.8 m) than in PL (4.1 m). The historical data, covering the period 1975-1991 (Krężel, 1993), prove that the average annual Secchi depth in OPB, calculated based on average monthly values, was at the level of 5.4 m, thus by 1.4 m lower than in 2020. The historical monthly average Secchi depth varied from 3.7 m to 7.2 m, while in 2020 it was changing from ca. 3.5 m to ca. 10.5 m, with values over 8 m occurring in 5 months (Fig. 2.9).

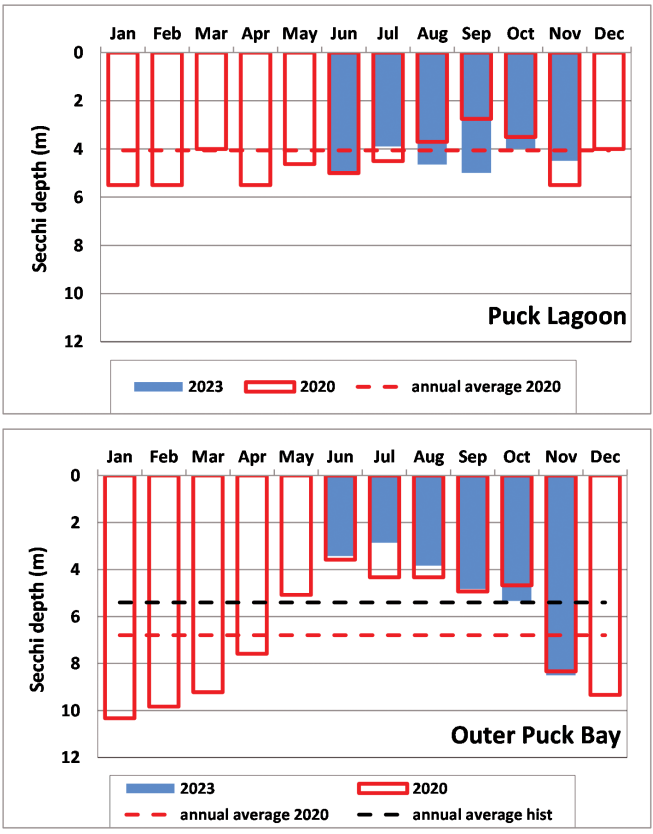

Fig. 2.9 Average monthly and annual Secchi depth in the Puck Lagoon (combined JR, UG17) and the Outer Puck Bay (combined S3, 82, KOL12) in 2020, in June-November 2023, and the average Secchi depth in OPB in 1975-1991 (hist) (source of historical data: Krężel, 1993)

2.4. Nutrient concentrations - anthropogenic pressure and biogeochemical processes

Two very important sources of anthropogenic pressure in terms of nutrients were identified in the Puck Bay i.e. the local sewage treatment plants and the impact of the Vistula River (Cyberski et al., 1993; Burska et al., 2022; Kowalkowski et al., 2012; Pastuszak et al., 2018), and these are extensively commented in Chapter 1. Long-term changes in nutrient concentrations in aquatic reservoirs, the Baltic Sea included, are the result of time- and space-varying anthropogenic pressure (Schneider et al., 2015;

Lønborg and Markager, 2021; Kuliński et al., 2022), whereas their seasonal variability is driven by biogeochemical processes taking place in both water column and sediments. The most important biogeochemical processes include uptake by algae and bacteria (Magnien et al., 1992), remineralization (Vidal and Morguí, 1995), nitrification (Pakulski et al., 1995; Yool et al., 2007; Baer et al., 2014), denitrification (Seitzinger, 1988, 1994; Seitzinger and Giblin, 1996; Pastuszak et al., 2005; Allin et al., 2017), sorption/desorption (Anschutz et al., 1998), sedimentation and resuspension (Vidal, 1994, Conley and Johnstone, 1995), and burial in sediments (Boynton et al., 1995; Howarth et al., 1995; Nixon et al., 1996). Processes in sediments play a very important role in shallow coastal estuarine systems, because a substantial part of the nutrients taken up by phytoplankton, sinks down to the bottom, and is recycled there (Boynton and Kemp, 1985; Kemp et al., 1990; Baird et al., 1995; Cowan and Boynton, 1996; Cowan et al., 1996; Conley et al., 1997; Pastuszak et al., 2003, 2005). The taxonomic and size structure of phytoplankton communities influence many biogeochemical processes, especially by regulating the photosynthetic efficiency of carbon fixation, the transfer of organic matter to higher trophic levels, and its export to the deep ocean through sinking (Kiørboe, 1993; Guidi et al., 2016). The above mentioned processes are driven by a number of factors, variable in time and space, such as the quantity and quality of the organic material supplied to the bottom sediments, temperature, salinity, oxygen content, redox status in the sediments, macrofaunal activity, and physical parameters causing resuspension. The fate of sedimenting organic matter is a key driver for material fluxes affecting ecosystem functioning (Baird et al., 1995; Cowan and Boynton, 1996; Conley et al., 1997; Janas et al., 2019).

Maksymowska-Brossard and Piekarek-Jankowska (2001) carried out studies in the open Gulf of Gdańsk and the Puck Bay and proved that there was great seasonal variation in ammonium fluxes from the sediments, with the greatest release in summer and early autumn, when bottom water temperatures were highest. Ammonium fluxes were the most intense in sediments containing the silty-clay fraction occurring in the deepest parts of the studied region i.e. in OPB. As further stated, the ammonium fluxes strongly depend on the supply of organic matter and its quality, whereas the degradation of this matter strongly depends on water temperature and the redox potential. It can be expected that increase in water temperature, observed over the last few decades (Fig. 2.3; see Chapter 1), may accelerate release of ammonium from sedimented organic matter, whereas the declining phytoplankton biomass (Chapter 3) may influence the peak heights of the fluxes. Baer et al. (2014) studied the effect of temperature on rates of ammonium uptake and nitrification in the western coastal Arctic during winter, spring, and summer. The conclusion of these studies is

that as the Arctic coastal ecosystem continues to warm, ammonium assimilation may become increasingly important, relative to nitrification, although the magnitude of its assimilation may be still lower than nitrification. This suggests that future increases in temperature can have far-reaching impacts on global biogeochemical cycles. Although the Puck Bay is located in a different climatic zone, we are aware of the fact that due to increase in AT during the last century, winters have become milder, the ice season shorter and the maximum ice extent has decreased by about 30% (see Chapter 1). Huge differences in ammonium concentrations in the winter of 1981-1991 and 2020 in OPB and PL (Fig. 2.7B) may arise not only from significantly decreased N anthropogenic loads but also from increase in assimilation in 2020 favored by earlier phytoplankton bloom triggered by shrinking ice cover and increasing water temperatures over the past decades (Chapters 1, 3). Allin et al. (2017) focused on denitrification in the Baltic Sea, other very important biogeochemical process that is a spatially and temporally highly variable and largely depends on temperature and N concentrations in the water. The authors conclude that climate change will have strong effects on denitrification because increasing temperatures favor denitrification, whereas changes in precipitation and consequently changes in N discharge will alter the availability of nitrogen, with strong differences between river basins. This finding is confirmed by recent studies of Soana et al. (2024) who focused on climate change impact on nitrogen and phosphorus discharges by Italian Po River. The authors concluded that an extended seasonal window of warm temperatures and the persistence of low flow periods are likely to create favorable conditions for permanent nitrate removal *via* denitrification, resulting in a lower delivery of reactive nitrogen to the sea. The presented results of these authors show that climate change-driven warming may enhance nitrogen processing by increasing respiratory river metabolism, thereby reducing export from spring to early autumn, when the risk of eutrophication in coastal zones is higher.

2.5. Nutrient limitation of phytoplankton growth - the Puck Bay

The optimal DSi:DIN:DIP molar ratio (Redfield ratio) for marine phytoplankton is 16:16:1 (Redfield, 1934). Any deviation from the optimal Redfield ratio has an impact on primary production, biomass and species composition of phytoplankton, and consequently on the dynamics of the entire food chain. DIN, DIP and DSi measurements are often used to estimate which element is the limiting factor for phytoplankton growth. Primary production is suggested to be mainly N-limited if DIN:DIP is below 10, or P-limited if DIN:DIP is above 20 (HELCOM, 2009). If

an excess of phosphorus over nitrogen is supplied to marine waters, primary production in coastal areas may be limited by nitrogen. This creates favorable conditions for the development of potentially toxic species of N_2-fixing cyanobacteria. Rahm et al. (1996) presented an operational definition that assumes that the limiting role of silicon occurs when DSi:DIN ratio is in the range 0.5-1.5 per atom.

The Redfied ratio (Table 2.1) indicates that phytoplankton growth was limited by nitrogen throughout 2020 at station S3, and for 11 months at stations 82 and KOL12; P limitation was noted at KOL12 station in June 2020 (OPB). At JR station (PL), phytoplankton growth was limited by nitrogen for 7 months and by phosphorus for one month. A unique situation occurred at UG17 station (PL), where phosphorus played a limiting role for 8 months, nitrogen for two months, and silicon only in March, which coincided with the peak of spring phytoplankton (diatom) bloom (Table 2.1; Chapter 3). Throughout 2020, concentrations of silicate, similarly to phosphate, were much higher in OPB remaining under impact of transformed nutrient-rich Vistula waters (Figs. 2.7C, 2.8A). With limited water exchange between OPB and PL, and therefore limited supply of silicate from the OPB, Si became significantly depleted during the spring diatom bloom, even leading to a periodic limitation of their growth in March 2020, as observed at UG17 station where DSi:DIN ratio dropped to 0.42 (Table 2.1).

Si limitation of diatom growth was observed in the Baltic Sea and numerous coastal regions in the USA (Officer and Ryther, 1980; Conley and Malone, 1992; Rahm et al., 1996). Unlike nitrogen and phosphorus, the silicon is present as H_4SiO_4 in dissolved form and its source in aquatic systems is dominated by the chemical weathering of silicate minerals. The dissolved silica, released from these reactions reaches the ocean *via* rivers. Rivers are responsible for almost 80% of the Si entering the global ocean as dissolved silicate (DSi) [$DSi=Si(OH)_4$], a product of weathering of continental rock and the continental and oceanic crust (Tréguer et al., 1995; Gerard and Ranger, 2002; Humborg et al., 2006; Conley et al., 2008; Dűrr et al., 2011).

Table 2.1 Redfield ratio (DIN:DIP, DSi:DIN) at stations S3, 82, KOL12 (Outer Puck Bay), and JR, UG17 (Puck Lagoon) in particular months of 2020

Month /parameter	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Station S3												
N:P	8.47	8.12	3.62	1.23	1.00	3.29	6.50	4.24	6.67	2.69	7.06	4.70
Si:N	3.26	3.82	6.62	38.62	65.63	18.07	19.27	10.08	17.33	9.68	5.23	6.44
Station 82												
N:P	7.74	8.98	5.14	0.52	0.91	4.00	18.38	4.95	3.68	2.63	4.88	5.34
Si:N	3.48	3.56	5.89	104.9	80.59	34.78	11.70	19.59	26.11	15.78	6.06	5.27
Station KOL12												
N:P	6.93	9.27	4.69	0.77	0.93	39.87	11.64	8.04	4.83	0.88	5.26	4.76
Si:N	3.44	3.24	7.33	67.86	105.5	26.51	30.65	66.29	21.46	26.57	6.83	5.04
Station JR												
N:P	10.30	11.81	8.24	11.57	1.43	8.79	4.20	2.23	4.74	17.35	7.89	34.05
Si:N	2.95	3.20	5.17	14.27	35.07	24.13	39.71	76.40	20.60	7.14	4.48	4.03
Station UG 17												
N:P	11.98	31.89	30.43	5.32	exhausted P	exhausted P	20.04	exhausted P	4.11	33.55	11.83	82.34
Si:N	3.30	4.67	0.42	30.85	21.78	6.91	11.37	70.06	160.1	8.19	5.17	4.35

2.6. Importance of dissolved organic forms of N and P in aquatic ecosystems

Successful management of coastal waters requires (i) a comprehensive understanding of the presence of the various forms of C, N and P and their role in the functioning of aquatic ecosystems, and (ii) an estimate of their total exports to aquatic systems (Håkanson and Bryhn, 2008; Håkanson et al., 2010). While management strategies have traditionally focused on the reduction of DIN and DIP=P-PO_4, the importance of dissolved organic forms of C, N, and P [e.g., dissolved organic carbon (DOC), dissolved organic nitrogen (DON), dissolved organic phosphorus (DOP)] is becoming increasingly apparent. DON and DOP are recognized as a significant component in nutrient emissions to seas and oceans (Berman and Bronk, 2003; Dumont et al., 2005; Seitzinger et al., 2005; Korth et al., 2012). Moreover, the anthropogenic sources of DON may dominate in some regions of the world (Harrison et al., 2005). It has been shown that bacteria and phytoplankton are both able to use DIN and DON and that many organic N compounds are released into the DON pool and taken up from this pool by planktonic microbiota on timescales of hours to days (Berman and Bronk, 2003; Bronk et al., 2007). These authors further state that many components of the DON pool can play an active role in supplying N nutrition directly or indirectly to phytoplankton and bacteria (Jörgensen et al., 1999) and, in so doing, may

affect the species composition of the ambient microbial assemblage. Cyanobacteria, for example, utilize dissolved organic nitrogen (DON) originating from organism excretion and detritus decomposition, absorbing it in the form of amino acid amide (Glibert et al., 1991). DON is a mixture of compounds including: dissolved free and dissolved combined amino acids (DFAA and DCAA), nucleic acids (DNA, RNA), urea, amino sugars, and humic substances but most compounds still remain chemically uncharacterized (Bronk, 2002; Osburn et al., 2016). DON in the ocean can originate from autochthonous and allochthonous sources. The autochthonous DON can be produced within the water column by phytoplankton, N_2 fixers, bacteria, micro- and macrozooplankton, and viruses (Bronk and Steinberg, 2008; Sipler and Bronk, 2015). Wannicke et al. (2009) have shown that cyanobacteria *Nodularia* sp. excretes up to 50% of the fixed nitrogen as DON into the surrounding waters. Additional sources of DON, important in shallow coastal ecosystems, include release from macro-organism excretion, direct release from macroalgae, detrital particle release *via* dissolution, and release from sediments *via* digenesis (Stepanauskas et al., 1999). The allochthonous sources of DON include rivers, groundwater, and atmospheric inputs (Bronk and Steinberg, 2008; Sipler and Bronk, 2015). Studies carried out by Stepanauskas et al. (2000, 2002) showed that 8-72% of DON is potentially bioavailable in rivers draining into the Baltic Sea. DON frequently comprises the largest part (60-69%) of total dissolved N in rivers, estuaries and surface ocean waters (Bronk, 2002).

The following forms of P are recognized in its marine cycle: dissolved inorganic phosphorus ($P\text{-}PO_4$=DIP), particulate inorganic (PIP) and organic phosphorus (POP), and dissolved organic phosphorus (DOP) (Karl and Björkman, 2015). DOP accounts for at least 40% of the total dissolved phosphorus pool in estuaries or coastal lagoons (McKelvie, 2005; Monbet et al., 2007), and 70-90% in oligotrophic waters (Ruttenberg and Dyhrman, 2012). The transformations between the various pools have been described in several studies, e.g., Jauzein et al. (2010), White et al. (2012), Karl (2014), however, a complete understanding of the P cycle is lacking. DIP is consumed by phyto- and bacterioplankton and incorporated into biomass, forming POP, and following cell death and remineralization is partly released as DOP into the surrounding water. Algal cells lose phosphorus very rapidly (Lean and Nalewajko, 1976). Ten minutes after their death, inorganic phosphorus is released. After thirty minutes, 12% is released, and after 24 hours, 50-60% of the cell's total phosphorus pool is converted into phosphate and released, and then quickly absorbed by living algal cells (Pliński and Jóźwiak, 1999).

DOP acts as an additional P source to microbial organisms, especially when it dominates the dissolved P pool, as observed in oligotrophic regions of the ocean

(Cavender-Bares et al., 2001) and in marine ecosystems where DIP is seasonally depleted (Mather et al., 2008; Lomas et al., 2010). When DIP is depleted, a number of marine organisms, including dinoflagellates, coccolithophores diatoms, and bacteria are known to synthesize hydrolytic enzymes in order to access the DOP pool to derive their P requirement (Monaghan and Ruttenberg, 1999; Ruttenberg and Dyhrman, 2005). There are reports that cyanobacteria can utilize organic phosphate such as phosphomonoesters and phosphodiesters, and some are also capable of using salts of phytic and phosphonic acids. These organisms, when using esters, produce phosphatases (Whitton et al., 2005).

The study of Moschonas et al. (2017), conducted in a typical Scottish fjord, representative of near pristine coastal environments, demonstrated that DON was important in supporting phytoplankton throughout the annual production cycle. Moreover, organic N not only contributes to regenerated production and to the nutrition of the small phytoplankton fraction, but it can contribute substantially to new production of the larger phytoplankton in coastal waters. The research work of Korth et al. (2012), carried out at salinity gradient from the North Sea to the Baltic Sea also proved that DON is an important component of plankton nutrition and can fuel primary production. As the latter authors conclude, DON may contribute substantially to eutrophication in the Baltic Sea, especially when inorganic nitrogen sources are depleted; Berg et al. (2003) and Stepanauskas et al. (1999) drew the same conclusion.

DON frequently comprises the largest part (60-69%) of total dissolved N in rivers, estuaries and surface ocean waters (Bronk, 2002). Bacteria and phytoplankton are both able to use DIN and DON and many organic N compounds are released into the DON pool and taken up from this pool by planktonic microbiota on timescales of hours to days (Berman and Bronk, 2003; Bronk et al., 2007). DOP accounts for at least 40% of the total dissolved phosphorus pool in estuaries or coastal lagoons (McKelvie, 2005; Monbet et al., 2007), and 70-90% in oligotrophic waters (Ruttenberg and Dyhrman, 2012). DOP acts as an additional P source to microbial organisms, especially when it dominates the dissolved P pool, as observed in oligotrophic regions of the ocean (Cavender-Bares et al., 2001) and in marine ecosystems where DIP is seasonally depleted (Mather et al., 2008; Lomas et al., 2010).

The scarcity of DIN and DIP in the Puck Bay in 2020 was accompanied by very high share of Norg. in TN, exceeding 90% at deep station S3; concentrations of Norg. were higher in shallow PL than in much deeper OPB. The share of P-other in TP ranged from 46% (S3) to 87% (UG17), and on average was much higher in PL than in OPB (Fig. 2.10A,B; Table 2.2).

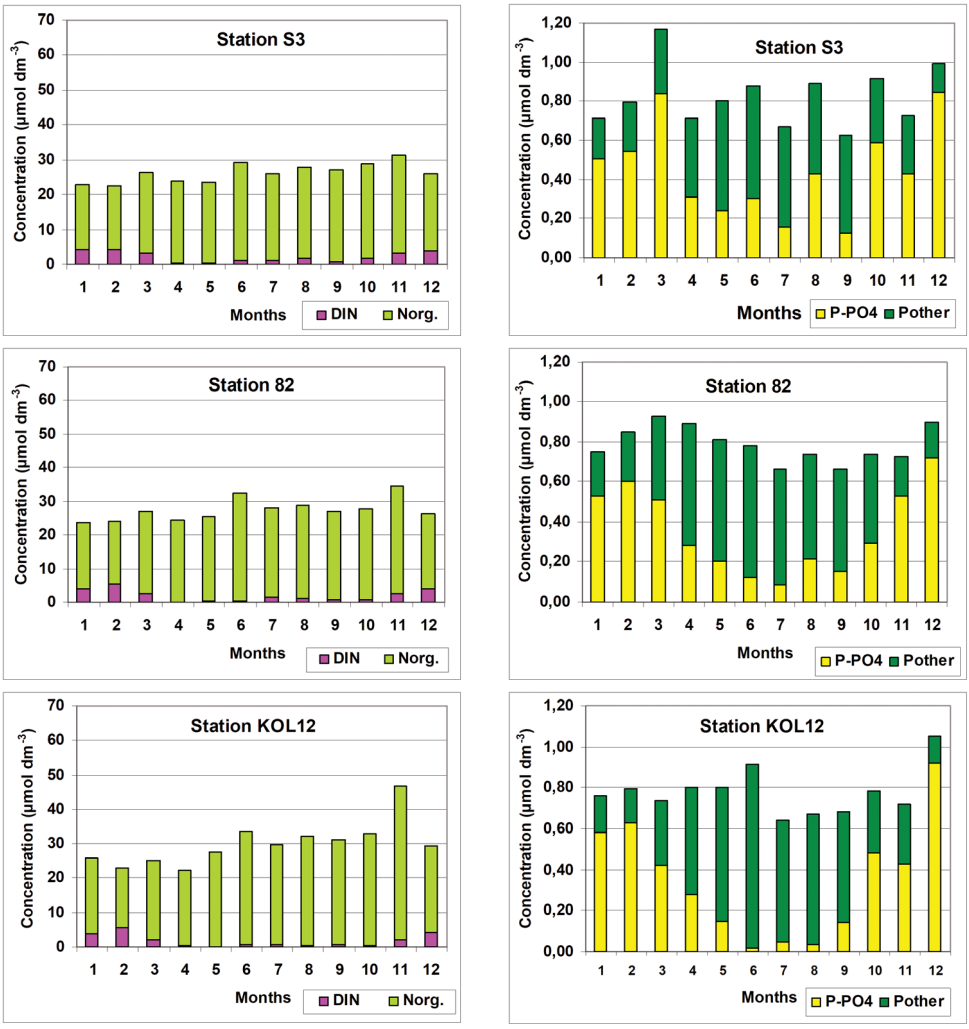

Fig. 2.10A. Seasonal changes of average monthly concentrations of dissolved inorganic nitrogen (DIN), organic nitrogen (Norg.), dissolved inorganic phosphorus ($P\text{-}PO_4$), other phosphorus (P-other) in water column in the Outer Puck Bay (stations S3, 82, KOL12) in 2020

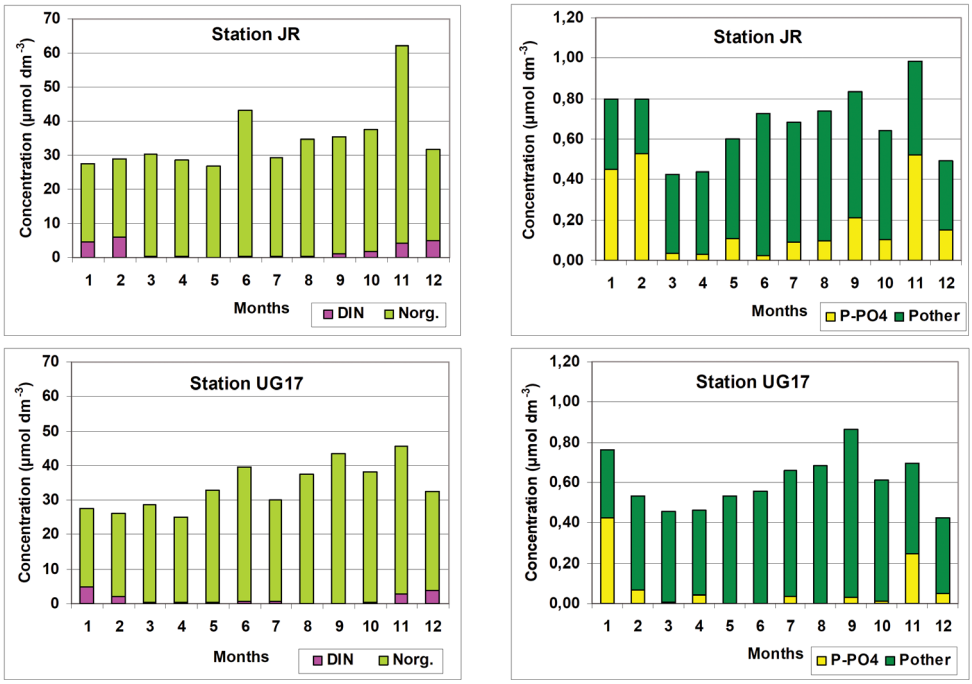

Fig. 2.10B. Seasonal changes of average monthly concentrations of dissolved inorganic nitrogen (DIN), organic nitrogen (Norg.), dissolved inorganic phosphorus ($P\text{-}PO_4$), other phosphorus (P-other) in water column in the Puck Lagoon (stations JR, UG17) in 2020

Table 2.2 Annual average concentrations of total nitrogen (TN), dissolved inorganic nitrogen (DIN), total phosphorus (TP), phosphate ($P\text{-}PO_4$), calculated for the entire water column, and the percentage of DIN in TN, and $P\text{-}PO_4$ in TP for the stations in the Outer Puck Bay (S3, 82, KOL12) and the Puck Lagoon (JR, UG17) in 2020

Station	TN [µmol·dm^{-3}]	DIN [µmol·dm^{-3}]	DIN share in TN [%]	TP [µmol·dm^{-3}]	$P\text{-}PO_4$ [µmol·dm^{-3}]	$P\text{-}PO_4$ share in TP [%]
S3	26.33	2.13	8.09	0.82	0.44	53.7
82	27.43	1.95	7.10	0.79	0.36	45.6
KOL12	29.92	1.78	5.9	0.78	0.34	43.6
JR	34.70	2.04	5.9	0.68	0.20	29.4
UG17	33.92	1.41	4.15	0.60	0.08	13.3

In our research of the Puck Bay, we did not conduct chemical determinations of individual organic forms of nitrogen or phosphorus. However, we have at our disposal the total amounts of organic nitrogen and so-called other forms of phosphorus, which include the above-mentioned specified organic forms of N and P in the sea. The importance of Norg. and P-other in terms of phytoplankton demand is statistically analyzed and described in Chapter 3.

2.7. Summary

- In 2020, average annual water temperature was by 2.89°C in OPB, and by 2.24°C in PL higher than relevant annual averages in 1972-1990. The level of water warming in the bay was comparable with long-term T increase in the open Baltic surface waters, and long-term air temperature increase in the region. That indirectly indicates that 2020 was not thermally exceptional, on a contrary it fell into the long-term trend. This conclusion is additionally supported by T values in the bay in June-November 2023; they either comply with values of 2020, or show seasonal maxima a bit shifted, thus suggesting impact of heat waves in different months in 2023, as compared with 2020.

- In 2023, monthly S values in PL and OPB were lower than in 2020; the difference reached over 0.3 PSU in PL in November 2023, and 0.2 PSU in OPB in September 2023. There are three possible reasons of the observed facts: (i) several upwellings were observed in 2020, but lack of upwellings was recorded in June-November 2023; upwellings are detected by elevated salinity readings, higher nutrient concentrations, and lower oxygen content; (ii) much higher and long-lasting Vistula River outflow in winter/spring in 2023 than in relevant period of 2020, (iii) the cessation of brine effluent discharge, which took place in July 2021; the brine was a by-product of the construction of underground gas storage caverns in salt deposits.

- The Puck Bay is a shallow well mixed coastal region and it did not suffer from oxygen depletion in 1981-1991, 2020, and in June-November 2023. Some shifts in annual patterns of oxygen content in 2020, 2023, as compared with the historical ones (1981-1991), are caused by water temperature increase and extended vegetative season.

- The construction/upgrading of local WWTPs and a significant decrease in nutrient discharges by the Vistula River, combined with changed seasonal nutrient demand, as well as turnover within the ecosystem due to a significant increase in water temperature, ultimately resulted in a significant decrease in nutrient concentrations in the Puck Bay in 2020 as referred to the data from 1981-1991. Between the given dates, the average annual concentrations of nitrate, ammonium, and phosphate in the bay declined from two to seven times. In 2020, there was observed rapid decline and depletion of nitrate from March/April to October in both sub-regions; rapid decline and depletion of phosphate from March to August only in PL; rapid decline and depletion of ammonium from March to October only in PL. There was no depletion of phosphate, and only short incidents of ammonium depletion in OPB, thus indicating impact of open Gulf of Gdańsk waters (transformed Vistula waters).

- Rapid nutrients exhaustion and variable in time and space limitation of phytoplankton growth was observed throughout 2020. Nitrogen (N) played a limiting role in OPB, while N, phosphorus (P), and silicon (Si) alternately in PL. At scarcity of inorganic N and P, Norg. and P-other could have supported phytoplankton growth in 2020, and these forms of N and P should be given attention in future studies on nutrients supplying the coastal region. Monitoring of riverine nutrient discharges should be given special attention, particularly in the light of climate change affecting nutrient emission to riverine systems, and then to the Baltic Sea.

- Repeated measurements of nitrate, phosphate, ammonium in June-November 2023 allow to state that the results obtained were almost identical to those in the same months in 2020. This further means that the depletion of these nutrients (except phosphate in OPB) during the growing season is a fact that should be taken into account when assessing the functioning of the entire ecosystem. Average annual concentrations of phosphate, total phosphorus, and silicate were considerably higher throughout 2020 in OPB than in PL, indicating the important role of the Vistula River in supplying the Puck Bay with P and Si. The lack of phosphate depletion in the OPB in 2020 and 2023 additionally confirms the important role of the Vistula River in supplying the bay with P.

- The historical (1975-1991) average Secchi depth in OPB was at the level of 5.4 m, thus by 1.4 m lower than in 2020. The historical monthly average Secchi depth varied from 3.7 m to 7.2 m, while in 2020 it was changing from ca. 3.5 m to ca. 10.5 m, with values over 8 m occurring in 5 months. In 2023, Secchi depth in PL was

either the same (January), higher - as in August and October, much higher - as in September, or lower as in July and November in comparison with relevant data of 2020. The Secchi depth readings in OPB in June-November 2020 and 2023 were in majority of cases comparable; July was exceptional with Secchi depth considerably lower in 2023 as compared with the value of 2020.

2.8. References

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3

LONG-TERM CHANGES OF PHYTOPLANKTON STRUCTURE AND DYNAMICS IN THE PUCK BAY

Lidia Nawrocka, Janina Kownacka, Mariusz Zalewski, Marianna Pastuszak, Joanna Całkiewicz

3. LONG-TERM CHANGES OF PHYTOPLANKTON STRUCTURE AND DYNAMICS IN THE PUCK BAY

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Marianna Pastuszak, Joanna Całkiewicz

3.1. Study area and methods of biotic parameters determination (chlorophyll *a*, phytoplankton)

The study area is described in detail in Chapter 2, so in this chapter, for the convenience of the reader, we repeated only the map showing the study area with all the sampling stations, including those where phytoplankton samples were collected and hereinafter scientifically analyzed (Fig. 3.1). Water samples for determination of chlorophyll *a* (Chl. *a*) concentrations, and the quantitative and qualitative composition of phytoplankton were collected with use of the Ruttner sampler. Water samples were collected from the following depths: 0-1; 2.5; 5; 7.5; 10; 15; and 20 m (depending on the depth of the station), and then integrated for two layers: 0-10 m and 10-20 m (or 0-bottom at shallow stations), as recommended by HELCOM (2017 a,b).

Water samples for the analysis of Chl. *a* concentrations were filtered on GF/F glass fiber filters with 0.7 μm pore size. After drying, filters along with collected material were frozen (-20°C), and then, prior to determination, they were extracted with ethanol at room temperature. Chl. *a* concentrations were measured by fluorescence emission method (HELCOM, 2017b), using the Turner Design fluorimeter.

In order to determine the quantitative and qualitative composition of phytoplankton, the integrated samples were preserved with acid Lugol solution, using 1 ml per 200 ml of seawater, following the recommendations provided by HELCOM COMBINE (HELCOM, 2017a) and UNESCO (Edler and Elbrächter, 2010).

Individual phytoplankton units (usually cells, but also filaments, colony, coenobia, chains - depending on the species) were determined, counted and measured using the inverted microscope (Olympus IX73, Olympus IMT2), following the Utermöhl method (Utermöhl, 1958). Phytoplankton biomass was estimated according to Olenina et al. (2006) and the updated appendix.

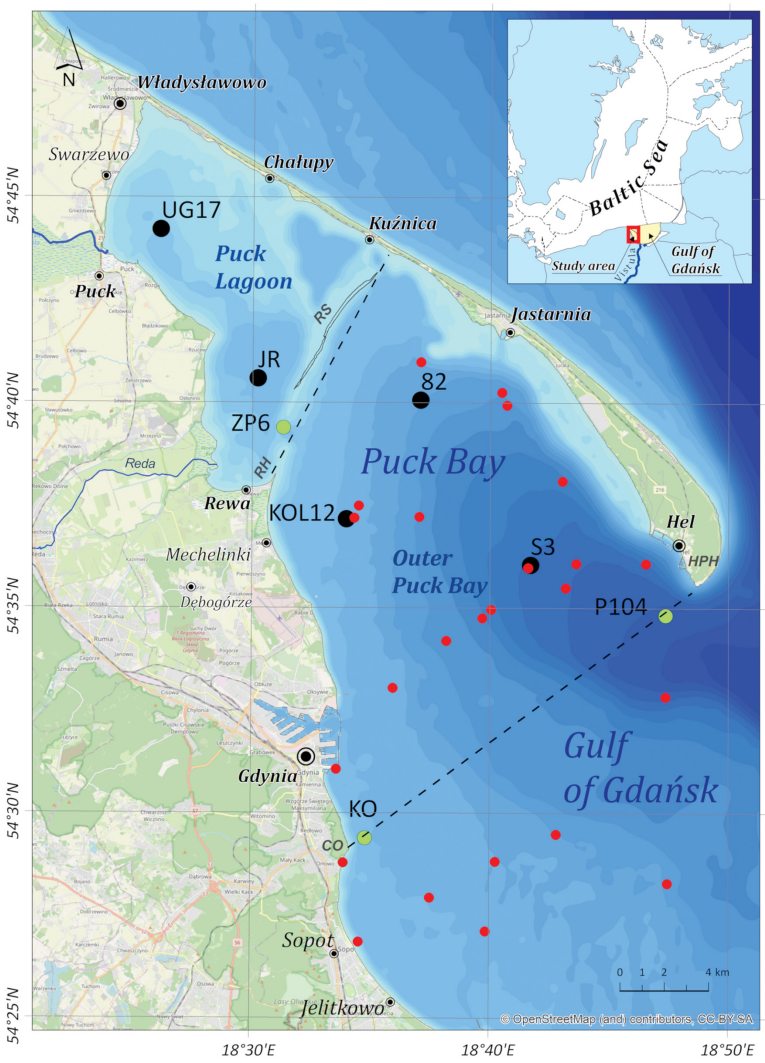

Fig. 3.1 The study area; black dots indicate obligatory stations at which abiotic and biotic parameters were determined in 12 monthly cruises performed in 2020, and in 6 monthly cruises (June-November) in 2023; red dots indicate sampling sites (source of biotic parameters only) in various scientific projects conducted by NMFRI in 1987-2018 (24 stations); green dots stand for the State Environmental Monitoring sampling stations (source of biotic parameters only) (KO, P104 and ZP6 - monitored since 2002); CO - Cape Orłowski, HPH - Hel Peninsula Headland, RS - Rybitwia Shoal, RH - Rewa Headland (source: map drawn by Lena Szymanek, NMFRI)

Phytoplankton taxa were determined to the lowest possible taxonomic level, in accordance with the applicable Latin nomenclature of the World Register of Marine Species (WoRMS) (https://www.marinespecies.org/aphia.php).

Long-term data series for biomass of 8 phytoplankton groups [Chlorophyta +Charophyta, Cryptophyta, Cyanobacteria, Euglenozoa, Myzozoa, *Mesodinium rubrum*, Ochrophyta, Others - consisting of Choanozoa, Haptophyta, *Ebria tripartita* (Schumann) Lemmermann, 1899 and non-identified flagellates] which were used for comparisons with the 2020 results, cover the period 2002-2018 for PL (State Environmental Monitoring station ZP6) and 1987-2015 for OPB (NMFRI data). As for these historical time intervals the long-term data in OPB were not available, we decided to combine available data from 17 stations located within the geographical area of OPB, and add 7 stations, which are in close vicinity, but beyond the area of OPB (NMFRI data); besides, we also used State Environmental Monitoring data from P104 and KO stations (Fig. 3.1). For the period 1987-2015, OPB should be understood as enlarged OPB, and this applies to the entire text hereafter.

The whole data set has been harmonized in order to ensure their comparability. All phytoplankton samples were collected according to the same method [integration from layer 0-10 (15) m]. All samples were preserved with Lugol solution and determined using an inverted microscope according to the Utermöhl method (Utermöhl, 1958). Phytoplankton biomass in samples collected prior to 2006 was estimated according to the method described by Edler (1979), whereas in samples collected after 2006, according to method by Olenina et al. (2006), comparable to the method of Edler (1979). Taxonomic harmonization consisted of updating the pre-2020 identifications to the nomenclature used in WoRMS (as of December 30, 2020) and aggregation to higher taxonomic units such as phylum, class or order.

The available historical data set has been divided into +/- decade periods. The first, covers the data collected prior to 2000 (it applies only to OPB; relevant data for PL are lacking). The second period covers the first decade of the 21st century, while the third includes available data from the second decade of the 21st century (2010-2015 in OPB, and 2010-2018 in PL).

The average monthly phytoplankton biomass during +/- decadal intervals of the period 1987-2018 was calculated in two steps: (i) monthly averages for each month in a given year, (ii) monthly averages for each month in the designated time intervals from the averages obtained in the first step. Average phytoplankton biomass for selected periods was calculated in three steps: (i) monthly averages for each month in a given year, (ii) annual average from monthly averages, (iii) time interval average from annual averages.

3.2. Biotic parameters in the Puck Bay in 2020 with reference to available historical data

3.2.1. Chlorophyll *a*

In 2020, average annual Chl. *a* concentrations were by ca. 0.8 $\mu g \cdot dm^{-3}$ higher in OPB than in PL (Fig. 3.2), with annual patterns being quite different in the subjected areas. In January-March 2020, Chl. *a* concentrations in PL were at the level of ca. 2 $\mu g \cdot dm^{-3}$, then they dropped to ca. 0.8 $\mu g \cdot dm^{-3}$ in April, and started to increase, with this tendency lasting till September maximum marked by the value ca. 1.3 $\mu g \cdot dm^{-3}$. In OPB, Chl. *a* concentrations were below 1 $\mu g \cdot dm^{-3}$ in January-February 2020, then they increased up to 3.4-4.3 $\mu g \cdot dm^{-3}$ in April-August 2020, and peaked in October to ca. 6.7 $\mu g \cdot dm^{-3}$. In November-December 2020, Chl. *a* concentrations were relatively high in PL, occasionally above 3 $\mu g \cdot dm^{-3}$, whereas in OPB they showed a sharp decline down to ca. 2 $\mu g \cdot dm^{-3}$ in November and to 1 $\mu g \cdot dm^{-3}$ in December 2020. It seems that the differences among Chl. *a* concentrations in the bay were mainly driven by nutrients, in practice by a very rapid decline in nitrate and phosphate concentrations in shallow PL, and exhaustion of these nutrients as early as in March 2020 (Fig. 2.7B,C). The decline in Chl. *a* concentrations in PL in April 2020 can be explained by scarcity of silicate and limitation of phytoplankton growth, which resulted in collapse of diatom bloom in PL (Fig. 2.8A and Table 2.1). In OPB, phosphate concentrations did not drop below 0.1 $\mu mol \cdot dm^{-3}$ throughout 2020, and average annual $P\text{-}PO_4$ concentration was at the level of 0.38 $\mu mol \cdot dm^{-3}$; nitrate showed depletion, but ammonium was present in low, but still higher concentration than in PL during vegetative period (Fig. 2.7A,B,C).

Looking at the changes in Chl. *a* concentrations from a historical perspective, we are able to conclude that in PL, the average annual concentration of Chl. *a* decreased from 5.49 $\mu g \cdot dm^{-3}$ in 2011-2016 (January-November) to 2.46 $\mu g \cdot dm^{-3}$ in 2020. In PL, the annual pattern of Chl. *a* concentrations in the compared periods showed not only much different monthly values but also shift of spring peak from the high historical value in February to hardly marked in March 2020, and shift of the summer peak from the historical (2011-2016) in August, to September peak in 2020. In OPB, long, although not always complete, annual data sets from the years 1967-1979, 1980-1999, 2000-2009, and 2011-2016 allow to notice the virtual disappearance of the spring Chl. *a* peak in 2020, and appearance of high Chl. *a* concentrations in October 2020, which was much higher than that in 1980-1999. In OPB, the historical spring values of Chl. *a* peaks were approximately 9.5-13 $\mu g \cdot dm^{-3}$, while in 2020 spring Chl. *a* concentrations

were flattened at the level of ca. 3-4 µg·dm^{-3}, and these were spread until August 2020. The available average annual Chl. *a* concentration in OPB in 1980-1999 was at the level of 4.24 µg·dm^{-3}, while in 2020 it reached 3.14 µg·dm^{-3} (Fig. 3.2).

The timing and intensity of spring blooms may have important consequences for the pelagic ecosystem, as stated by Townsend et al. (1994) and Platt et al. (2003). There are several authors who stress that the spring phytoplankton bloom: (i) accounts for a substantial part of the annual production in many temperate marine and freshwater systems, (ii) supports pelagic and benthic secondary production, and (iii) influences biogeochemical cycles (Howarth et al., 1995; Nixon et al., 1996; Nixon et al., 2009; Fulweiler and Nixon, 2009; Griffiths et al., 2017; Wasmund et al., 2017).

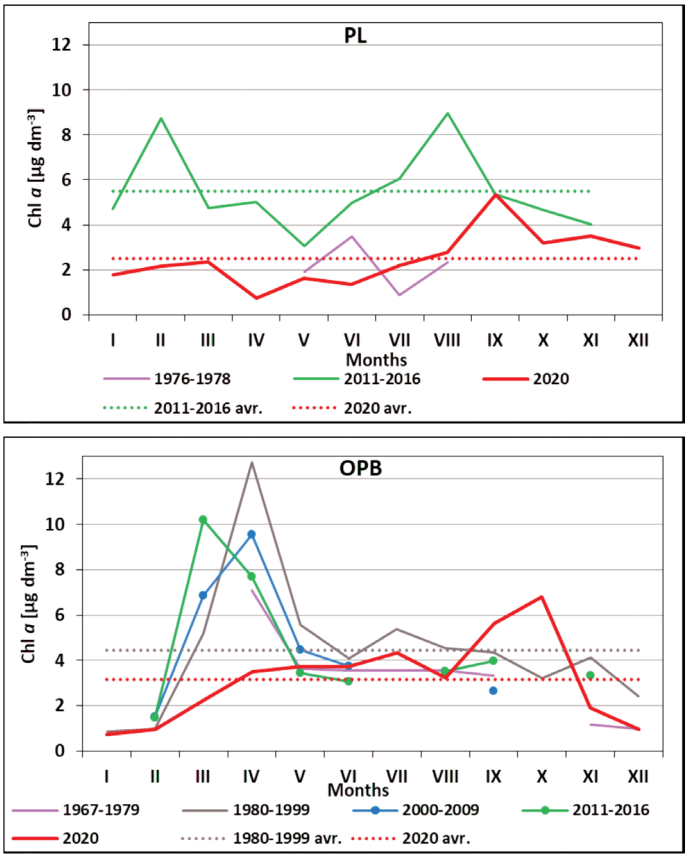

Fig. 3.2 Monthly and annual averages (only for 11-12 months data sets) of chlorophyll *a* concentrations in the 0-10 m layer in the Puck Lagoon and the Outer Puck Bay in 2020 and in the time intervals given in both graphs [source of historical data: Latała, 1993; Renk, 1993, 2000; Witek et al., 1993; State Environmental Monitoring (data from P104 and ZP6 stations)]

3.2.2. Quantitative and qualitative structure of phytoplankton in OPB and PL - analysis of long-term data

Quantitative and qualitative structure of the phytoplankton community in 2020 was referred to available historical data covering the following time intervals: 1987-1999, 2000-2009, 2010-2015 in OPB, and 2002-2009, 2010-2018 in PL (Fig. 3.3).

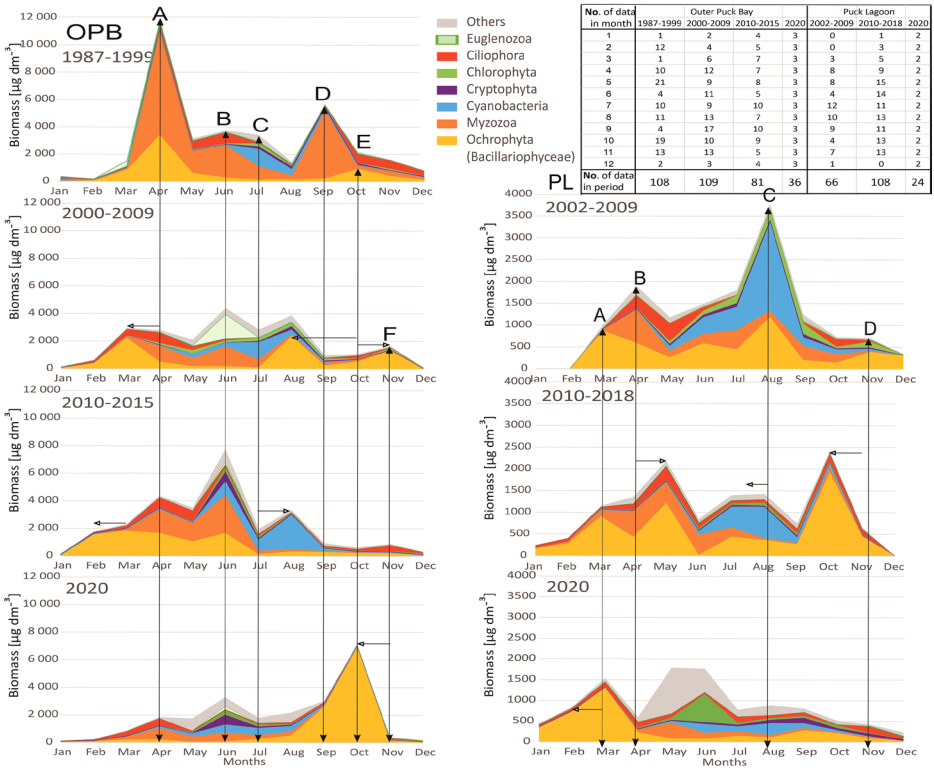

Fig. 3.3 Analysis of the dynamics of the average monthly phytoplankton biomass in the two subareas of the Puck Bay during +/- decadal intervals of the period 1987-2018 in comparison with the phytoplankton dynamics in 2020. Black vertical arrows (OPB: A - spring, B - early summer, C - summer, D - early autumn, E and F - autumn; PL: A - early spring, B - spring, C - summer, D - autumn) show time of phytoplankton biomass maxima in the earliest decade, whereas the horizontal arrows indicate time shifts in the appearance of these maxima in the periods that followed. The number of data used in each month and period is shown in the table (upper right corner). Please note different scales on the Y axis in OPB and PL (source of historical data: NMFRI, State Environmental Monitoring)

In OPB subarea, six distinct stages of phytoplankton development were distinguished in the annual cycle over the years 1987-2020 (Fig. 3.3; OPB - peaks A-F) and they indicate the most significant changes in phytoplankton dynamics that occurred during the study period.

The spring diatom bloom was shifted from April 1987-1999 to March 2000-2009, and then to February 2010-2015. Between 1987 and 2015, the height of diatoms spring peaks was very similar in the individual decades and was composed of small-celled taxa (*Thalassiosira levanderi* van Goor, 1924, *Pauliella taeniata* (Grunow) F.E. Round & P.W.Basson, 1997, *Chaetoceros* spp., *Skeletonema marinoi* Sarno & Zingone, 2005); only in 2020, it was not observed at all. The dynamics of diatom development in the remaining seasons looked different, depending on the period. In 1987-1999, there was also an autumn maximum (peak E), although much lower than the spring one and consisting of species with large cells (*Coscinodiscus* spp., *Actinocyclus* spp.). In 2000-2009, the above-mentioned autumn maximum was shifted to August, but in autumn, there appeared another, much lower peak F, composed mainly of the introduced species (*Chaetoceros pauciramosus* Z. Y. Chen, N. Lundholm, Ø. Moestrup, J. Kownacka & Y. Li, 2018), or those that expanded their range of occurrence (*Cerataulina pelagica* (Cleve) Hendey, 1937, *Dactyliosolen fragilissimus* (Bergon) Hasle, 1996, *Chaetoceros castracanei* Karsten, 1905). In 2010-2015, there was no late summer and autumn maximum of diatoms, while the spring bloom was extended until July, and its taxonomic composition was changing over the time (with the dominance of e.g. *Cyclotella* spp., *Synedra berolinensis* Lemmermann 1900). In 2020, a huge bloom of *D. fragilissimus* was recorded in September and October, i.e. two months earlier than in 2000-2009 (see also section 3.2.3).

The spring peak of dinoflagellates occurred in April throughout the study, but its height and species composition was changing. In 1987-1999, 7456 $\mu g \cdot dm^{-3}$ of dinoflagellates was mainly represented by *Peridiniella catenata* (Levander) Balech, 1977. In 2010-2015, 1776 $\mu g \cdot dm^{-3}$ of dinoflagellates consisted mainly of *Apocalathium* complex, while in 2020, both of these taxa occurred simultaneously, but in the amount of only 838 $\mu g \cdot dm^{-3}$.

Mixotrophic ciliate *Mesodinium rubrum* (Lohmann) Hamburger & Buddenbrock, 1911, changed time of its spring appearance from May-June in 1987-1999 to March-May in 2000-2020.

Diazotrophic cyanobacteria *Aphanizomenon* spp., *Dolichospermum* spp. and *Nodularia spumigena* Mertens ex Bornet & Flahault, 1888, extended time of their occurrence from June-August in 1987-1999 to May-September in subsequent periods. The average biomass of that potentially toxic, bloom-forming species fluctuated from

431 μg·dm^{-3} in 1987-1999, through 255 μg·dm^{-3} in 2000-2009, to the maximum value of 1346 μg·dm^{-3} in 2010-2015, and to the minimum value of 196 μg·dm^{-3} in 2020 (Fig. 3.3; OPB - peaks B, C).

In June 1987-1999, the phytoplankton community was represented mainly by *Mesodinium rubrum* and *Heterocapsa triquetra* (Ehrenberg) Stein, 1883 (3720 μg·dm^{-3}), while in the decades that followed, a community with high taxonomic diversity occurred, and the share of individual components [euglenids (*Eutreptiella gymnastica*, Throndsen 1969), cyanobacteria, green algae (*Pyramimonas*, *Tetraselmis*, *Carteria* and *Chlamydomonas*), diatoms, dinoflagellates, cryptophytes and small flagellates] ranged from 4 to 36%. The total biomass was the highest in 2010-2015 (7763 μg·dm^{-3}) and the lowest in 2020 (2269 μg·dm^{-3}) (Fig. 3.3, OPB, peak B).

The September maximum of phytoplankton biomass (5612 μg·dm^{-3}), observed only in 1987-1999, was caused by the introduction of dinoflagellate *Prorocentrum cordatum* (Ostenfeld) Dodge, 1975, recognized as invasive, non-indogenous species in the Baltic Sea.

In PL subarea, four phytoplankton biomass maxima can be distinguished (Fig. 3.3; PL). The first, appeared in March 2002-2009 and 87% of it was represented by small-celled diatoms (*Chaetoceros* spp., *Skeletonema marinoi*, *Talassiosira levanderi*); it was characterized by an increase in diatom biomass, from 878 μg·dm^{-3} in 2002-2009 to 912 μg·dm^{-3} in 2010-2018, and to 1300 μg·dm^{-3} in 2020. Although no data were available for January and February 2002-2009, a significant winter increase in diatom biomass, from 165 μg·dm^{-3} in 2010-2018 to 340 μg·dm^{-3} in 2020, is noteworthy.

The second, appeared in April 2002-2009 (1897 μg·dm^{-3}) (Fig. 3.3; PL-peak B), and apart from diatoms, it included dinoflagellates, *M. rubrum*, and about 10% of small flagellates; this late-spring maximum was shifted to May in 2010-2018 and it was characterized by similar taxonomic composition but slightly higher total biomass (2186 μg·dm^{-3}). In 2020, the late-spring maximum lasted until June and it was of different composition than in previous periods, with a dominance of fine (4-10 μm diam.) Prymnesiales (Haptophyta), unidentified flagellates (3-7 μm diam.), and *Pyramimonas* spp. (Chlorophyta).

The third, was the summer biomass maximum that appeared in August 2002-2009 (3779 μg·dm^{-3}) and July-August 2010-2018 (1399-1426 μg·dm^{-3}) (Fig. 3.3; PL-peak C); it was mainly composed of cyanobacteria (54%) and of large-celled diatoms (Centrales, *Coscinodiscus granii* Gough 1905) (32%); the average biomass of cyanobacteria decreased two times between these two sub-periods and the taxonomic composition also changed. In the first period the cyanobacteria *Microcystis aeruginosa* (Kützing) Kützing, 1846, *Microcystis wesenbergii* (Komárek) Komárek ex Komárek,

2006 and *Woronichinia* spp. dominated, and diazotrophic cyanobacteria constituted only 33% of the biomass of all cyanobacteria, while in the second period 80% of the cyanobacteria were diazotrophs: *Dolichospermum lemmermannii* (Richter) P.Wacklin, L.Hoffmann & J.Komárek, 2009, *N. spumigena* and *Aphanizomenon* spp. In 2020, cyanobacteria maximum did not occur and the occurrence of diazotrophic cyanobacteria (*Aphanizomenon* spp. and *N. spumigena*) was limited only to one station, where they constituted half of the cyanobacteria composition. In terms of percentage, small unidentified flagellates (3-7 μm in diameter), Cryptophyta and *Pyramimonas* spp. dominated the summer community.

The fourth, was the autumn maximum of phytoplankton biomass (Fig. 3.3; PL - peak D) which shifted from November 2002-2009 (710 $\mu g \cdot dm^{-3}$) to October 2010-2018 (2418 $\mu g \cdot dm^{-3}$) and its height increased three times in the latter period. It mainly consisted of diatoms (*Actinocyclus octonarius* Ehrenberg, 1837, *Coscinodiscus granii*, *S. marinoi*, *Chaetoceros* spp. and benthic large-celled species from the genera *Achnanthes, Amphora, Gyrosigma* and *Surirella*). In 2020, the autumn maximum of phytoplankton biomass (808 $\mu g \cdot dm^{-3}$) occurred already in September, and consisted mainly of diatoms, cryptophytes and cyanobacteria.

The average percentage share of the main phyla and average total phytoplankton biomass show the relevant quantitative and qualitative changes over the past decades (Fig. 3.4). Although the presented data series for OPB begins in 1987-1999, it is worth commenting data of Pliński (1993), who reported that in 1977-78 diatoms (69.3%), cyanobacteria (28.2%), and green algae (2.5%) dominated the percentage of the phytoplankton community in the Puck Bay; there were also present dinoflagellates, euglenids and Chrysophyceae, but their share in the total biomass was insignificant. In the late 1980s and 1990s, share of dinoflagellates in the total phytoplankton biomass significantly exceeded that of diatoms. Cryptophyta, *M. rubrum*, Euglenozoa and the Others group, mainly consisting of small flagellates in size range 2-15 μm, were also among new components of phytoplankton in 1987-1999 (OPB). In the decades that followed, the average phytoplankton biomass decreased from 2994 $\mu g \cdot dm^{-3}$ in 1987-1999 to 1799 $\mu g \cdot dm^{-3}$ in 2020, but the decline was not as gradual as in PL (Fig. 3.4). In OPB, the largest decrease in biomass between 1987-1999 and 2020 concerned euglenids, dinoflagellates, cryptophytes and *M. rubrum*, and it amounted to 95%, 84%, 57% and 57%, respectively. On the other hand, the biomass of diatoms and Others between 1987-1999 and 2020 increased by 32% and 50%, respectively. In PL, the average phytoplankton biomass showed its gradual decrease from 1445 $\mu g \cdot dm^{-3}$ in 2002-2009 to 1170 $\mu g \cdot dm^{-3}$ in 2010-2018, and finally to 889 $\mu g \cdot dm^{-3}$ in 2020. In PL, the changing environmental conditions had the strongest impact on cyanobacteria,

euglenids, dinoflagellates, diatoms and *M. rubrum*, whose respective biomass decreased by 80%, 70%, 67%, 39%, and 28% over the entire period of studies. In contrast, between the start and end of the study the biomass of Cryptophyta and Others (containing various types of flagellates) increased by 6% and 57%, respectively.

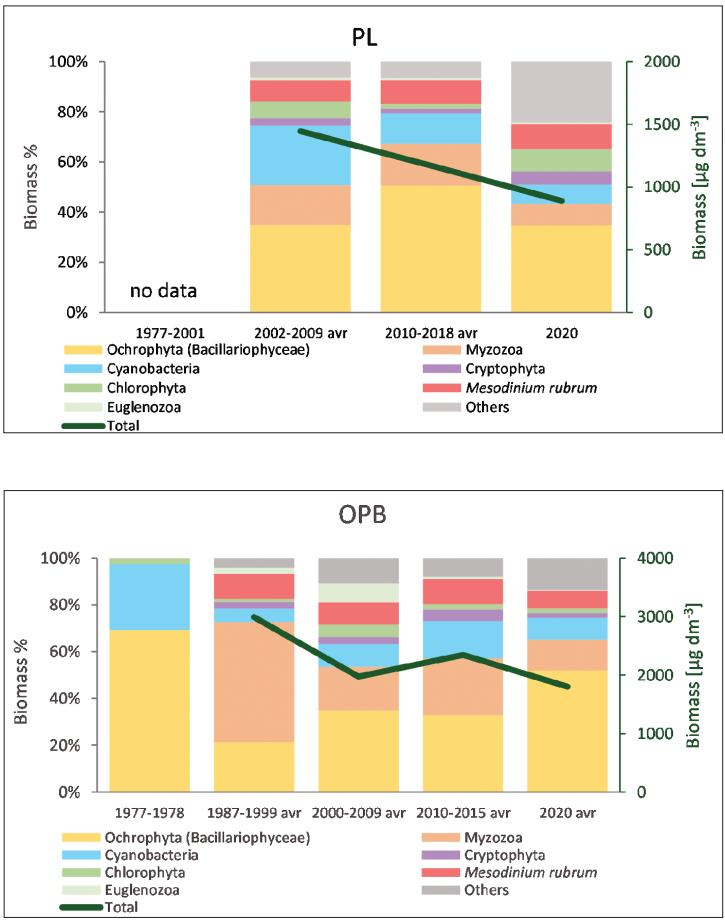

Fig. 3.4 Average percentage share of the main phyla (bars) and average total phytoplankton biomass (green line) in two subareas (PL, OPB) of the Puck Bay in the given periods [source of historical data: NMFRI; State Environmental Monitoring; 1977-1978 data from Pliński (1993)]

3.2.3. Quantitative and qualitative structure of phytoplankton in OPB and PL in 2020

In 2020, patterns of seasonal variability of phytoplankton biomass were different in the studied subregions (Fig. 3.5). In PL, the phytoplankton biomass maximum, occurred in March at UG 17 (ca. 2200 $\mu g \cdot dm^{-3}$) and it was represented mainly by Ochrophyta (Bacillariophyceae), and in June at JR (ca. 2600 $\mu g \cdot dm^{-3}$) and it was represented mainly by Charophyta. At all OPB stations the biomass maxima (6200-8000 $\mu g \cdot dm^{-3}$), represented mainly by Ochrophyta (Bacillariophyceae), were recorded in October, with slightly lower biomass records observed in 10-20 water layer (Fig. 3.5). In 2020, the quantitative and qualitative structure of the phytoplankton community was subject to significant variability over time, i.e. the seasonal succession of the main dominant groups, which is one of the characteristics of phytoplankton communities in the temperate climatic zone. The initial period of the growing season, from January to March 2020, was dominated by the winter-early-spring phytoplankton community, and that consisted of the cold-water diatoms *Chaetoceros* (mainly *C. wighamii* Brightwell, 1856, *C. holsaticus* F. Schütt, 1895, *C. ceratosporus* Ostenfeld, 1910) and *Skeletonema marinoi* at all stations of the Puck Bay, with maximum biomass in PL. *Conticribra guillardii* (Hasle) K. Stachura-Suchoples & D.M.Williams, 2009 and *Melosira moniliformis* (O.F. Müller) C. Agardh, 1824 were recorded only in PL, whereas *Thalassiosira baltica* (Grunow) Ostenfeld, 1901, *T. decipien*s (Grunow) E.G. Jørgensen, 1905, and *Actinocyclus octonarius* were observed mainly in OPB. At the stations where the proportion of diatoms was low, dinoflagellates (Myzozoa) as *Apocalathium* complex and *Heterocapsa rotundata* (Lohmann) G.Hansen, 1995, together with ciliates (Ciliophora) *Mesodinium rubrum* and *Strobilidium* spp., were present (Fig. 3.5).

In April (spring), a decrease in diatom biomass and an increase in the biomass of dinoflagellates, mainly *Peridiniella catenata* that occurred only in OPB, were observed. In PL, flagellates and ciliates (Fig. 3.5) replaced dinoflagellates.

In May (late spring), at all stations there were present the mixotrophic flagellates of the genera *Prymnesium* and *Chrysochromulina* (Haptophyta), capable of occurrence in bloom quantities, especially after warm winters. Their presence in the phytoplankton community was significant, in terms of both biomass, and abundance. Apart from haptophytes, the unidentified flagellates and dinoflagellates still had a significant share in the phytoplankton biomass, represented by *Heterocapsa triquetra* in PL, and by auto- and heterotrophic Gymnodiniales, as well as *Dinophysis norwegica* Claparède & Lachmann, 1859 and *D. acuminata* Claparède & Lachmann, 1859 in OPB.

The summer phytoplankton community was characterized by the coexistence of representatives of many phyla in even proportions (from a few to about 30% of the total phytoplankton biomass in each phylum), especially in OPB. Also in this part of the Puck Bay, there occurred the diazotrophic cyanobacteria *Aphanizomenon* spp., *Dolichospermum* spp. and *Nodularia spumigena*, known for creating summer blooms, but the 2020 bloom was rather moderate. Like all other phytoplankton groups, they accounted for up to 30% of phytoplankton biomass (130-540 $\mu g \cdot dm^{-3}$). In PL, the occurrence of diazotrophic cyanobacteria was limited only to the JR station. In terms of abundance, small flagellates at all stations dominated the summer community. The highest abundances, from June to August 2020, were also achieved by cryptophytes of the genus *Plagioselmis* and cyanobacteria with pico- and nano-sized cells (<2 μm) belonging to three orders: Chroococcales, Oscillatoriales and Synechococcales.

The end of August (late summer with thermal water stratification; Chapter 2) and the beginning of September were typically represented by the following diatom species: *Coscinodiscus granii*, *Coscinodiscus* sp., *Chaetoceros castracanei* Karsten, 1905, *C. danicus* Cleve 1889, *C. pauciramosus*. When the thermal stratification became weaker in September and the concentrations of nutrients in the water increased (Fig. 2.7A,B,C), other diatom species: *Dactyliosolen fragilissimus* and *Cerataulina pelagica*, began to appear.

In autumn (September and October), *D. fragilissimus* and *C. pelagica* developed into a huge autumn bloom, which occurred only at OPB stations. Average values of biomass were then four times higher than in spring and the highest throughout the year (maximum 7200 $\mu g \cdot dm^{-3}$). The abundance (maximum 6.8 M cells$\cdot dm^{-3}$) exceeded even the most numerous pico- and nanoplankton. Such huge bloom did not occur in PL, where the Bacillariophyceae class was represented by fine centric diatoms, belonging to the genera *Cyclotella* and *Thalasiossira*, accompanied by cyanobacteria, cryptophytes, charophytes, and ciliates.

In November (late autumn), the phytoplankton biomass decreased significantly, although the taxonomic structure was similar to that of October.

Winter was characterized by the lowest phytoplankton biomass and abundance during vegetation period. Phytoplankton community in PL, apart from diatoms and ciliates, consisted mainly of various flagellates, cryptophytes, euglenids and Choanozoa preferring low temperatures. On the other hand, in the area of OPB, diatoms with large cells of *Coscinodiscus* and *Actinocyclus* genera were accompanied by Cryptophyta and Ciliophora and dominated the taxonomic structure. At some stations, the structure of phytoplankton was very similar to that found in January 2020. With regard to the winter abundance, cryptophytes (*Teleaulax* and Cryptomonadales), which are cold

loving and sensitive to the concentration of nutrients, dominated at all stations in the Puck Bay, although their share was slightly higher in OPB (Fig. 3.5).

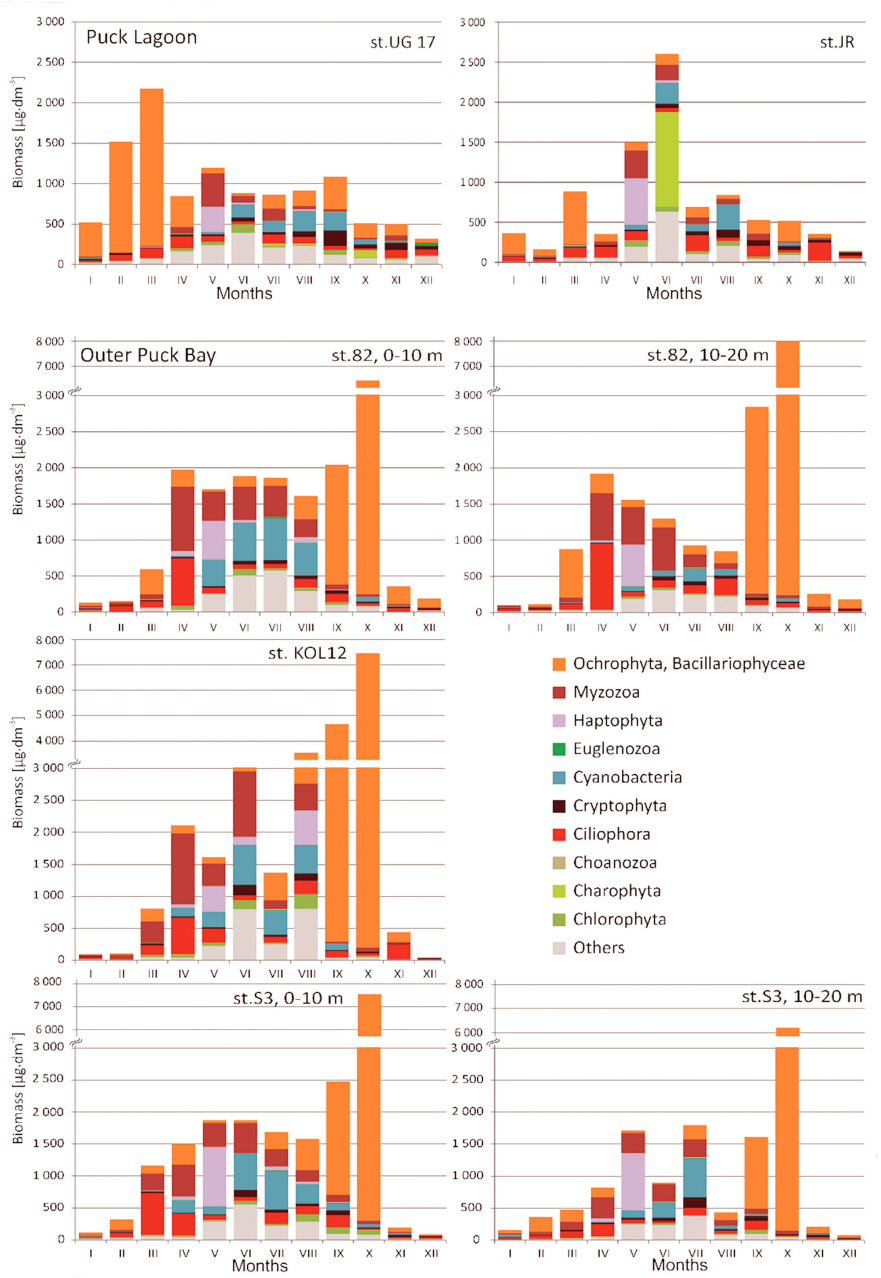

Fig. 3.5 Monthly phytoplankton biomass (µg·dm^{-3}) and its composition within the specified phyla at each sampling station in the Puck Lagoon and Outer Puck Bay in 2020

3.3. Statistical analyses and the outcome

The phytoplankton biomass data collected in the Puck Bay in 2020 were subjected to canonical correspondence analysis (CCA) using the cca function from the vegan package (Oksanen et al., 2019) in R (R Core Team, 2020) allowing identification of the most important environmental factors affecting phytoplankton biomass. CCA was applied to the already √√-transformed biomass data matrix of species (Hellinger transformation) to reduce the excessive influences of dominant species over rare ones. In the first step, we constructed the full model including all environmental factors. Final models were selected using the ordistep function for stepwise model selection. Variance Inflation Factors (VIF) for each of the constraints (variables) from the environmental matrix was also calculated for the final model, but we did not detect any collinearity between variables. Finally, we did permutation tests in constrained ordination to test the significance of models, variation explained by individual constrained axes and explanatory variables. The CCA was carried out for (i) autotrophic phyla (AU) represented by: Chlorophyta, Charophyta, Cyanobacteria, Myzozoa (AU only), and Bacillariophyceae, Haptophyta, Euglenozoa, Cryptophyta (AU only) and species *Mesodinium rubrum*, in each subarea separately, (ii) taxa identified in a given autotrophic phylum grouped to the genus or order level in each subarea separately. The following environmental variables were included in the analysis (i) abiotic factors influencing the quality of the environment in which the phytoplankton lives ("bottom up" effect): nitrate ($N\text{-}NO_3$), ammonium ($N\text{-}NH_4$), nitrite ($N\text{-}NO_2$), DIN, Norg., phosphate ($P\text{-}PO_4$), P-other, silicate ($Si\text{-}SiO_4$), salinity (S), (Secchi depth), water temperature (T), (ii) biomass of microzooplankton, i.e. heterotrophic protist determined during routine analysis of each phytoplankton sample (Myzozoa HT, Ciliophora HT, Cryptophyta HT, *Ebria tripartita* (J.Schumann) Lemmermann, 1899, Choanozoa) as a "top down" factor potentially affecting autotrophs.

The impact of the environmental factors on phytoplankton biomass in 2020 was assessed based on the results of CCA (Fig. 3.6). The most important factor influencing the biomass of autotrophic phyla in shallow PL was the temperature, explaining 73%, and silicate, explaining 27% of the total variability (Fig. 3.6a). In much deeper OPB, remaining under strong impact of the open Gulf of Gdańsk, P-other was indicated as the most important factor explaining 32% of the total variability of autotrophic biomass, followed by temperature (25%), and DIP (14%); the next factors were silicate, microzooplankton biomass, $N\text{-}NO_3$, and salinity, accounting for approximately 10%, 9%, 6%, and 4% of the total variability, respectively (Fig. 3.6a).

The CCA (Fig. 3.6) indicates that Norg. and P-other played an important role in

supporting phytoplankton development in the Puck Bay. P-other appeared as the most important factor in OPB. Cyanobacteria and mixotrophic Haptophyta were correlated with high concentrations of P-other as well as summer diatoms genera *Coscinodiscus*, *Diplopsalis* and *Cylindrotheca* together with flagellate *Pseudopedinella* (Ochrophyta). In PL, dinoflagellates: Peridiniales and *Gonyaulax* spp. preferred occurrence of P-other in the environment, whereas genera *Dissodinium* and *Prorocentrum* preferred Norg., both in OPB and in PL; Norg. together with relatively high temperature was of significant importance for diatoms occurring in late summer and forming autumn bloom (*Dactyliosolen fragilissimu*s, *Cerataulina pelagica* and *Coscinodiscus* spp.). The importance of P-other for diatoms is supported by a sharp drop in TP concentrations, represented nearly exclusively by P-other during the spring and autumn bloom of diatoms in PL (Figs. 2.8B, 2.10A,B). Diatoms need not only silicon, but also nitrogen and phosphorus for their growth (Giri et al., 2022).

Cyanobacteria and Chlorophyta in the entire region, and additionally Charophyta in PL, preferred higher temperatures, while Euglenozoa, *M. rubrum*, Bacillariophyceae and autotrophic Cryptophyta were more abundant at lower temperatures. Cryptophyta and Euglenozoa across the Puck Bay were associated with rather high concentrations of silicate in water (Figs. 2.2A,B, 2.8A, 3.6a). In OPB, higher concentrations of inorganic forms of N and P (Fig. 2.7A,B,C) were also of great importance for Euglenozoa and Cryptophyta, as well as for *M. rubrum;* P-other explained the variability of the mixotrophic Haptophyta, *Dinobryon* spp. and the autotrophic *Pseudopedinella* spp.. In PL, P-other and Norg. (Fig. 2.10B) were of significant importance for dinoflagellates and diatoms occurring in the summer and autumn seasons.

The highest biomasses of Bacillariophyceae occurred when the level of silicate concentrations significantly declined (Fig. 2.8A), possibly due to Si uptake in the development of the initial stage of blooms. In OPB, microzooplankton was strongly associated with the occurrence of autotrophic dinoflagellates such as *Apocalathium* complex, *P. catenata*, *Amylax triacantha* (Jörgensen) Sournia, 1984, which occurred in spring, as well as with spring diatoms (*Thalassiosira*, *Melosir*a, *Chaetoceros*, *S. marinoi*, *Diatoma tenuis* C.Agardh, 1812). On the other hand, the autumn bloom of *D. fragilissimus* was influenced by relatively high water temperature and high concentrations of Norg. (Figs. 2.3, 2.10A,B). The occurrence of diazotrophic cyanobacteria in OPB was mainly influenced by high temperature and low concentrations of $N\text{-}NO_2$, $N\text{-}NO_3$, and $P\text{-}PO_4$ (Figs. 2.3, 2.7A,C), while in PL, salinity and temperature (Figs. 2.3, 2.4) were of the greatest importance for the development of cyanobacteria.

Haptophyta, which are known to efficiently utilize nutrients at their low level (Suikkanen et al., 2013), were more abundant in the Puck Bay when dissolved

inorganic N, P and Si were in low concentrations, but P-other in high, followed by relatively high T (Figs. 2.3, 2.7A,B,C, 2.8A, and 2.10A,B). Due to mixotrophic way of nutrition, they can utilize phosphate from bacteria and picoplankton. Thanks to this, mixotrophic Haptophyta overbalance the autotrophs under P-limiting conditions (Dahl et al., 2005; Majaneva et al., 2012). Mixotrophic *Dinobryon* spp. and the autotrophic *Pseudopedinella* spp. in OPB are other examples strongly positively related to P-other (Fig. 3.6a,b). Because of the way of nutrition, Haptophyta are considered of low food-quality due to low energy efficiency (Suikkanen et al., 2013). In PL, P-other and Norg. were of significant importance for dinoflagellates and diatoms occurring in the summer and autumn seasons (Fig. 3.6b,c). In addition, the largest in 2020 autumn bloom of diatom *Dactyliosolen fragilissimus*, was correlated with high concentrations of Norg., followed by relatively high temperature (Figs. 2.3, 2.10B).

In order to detect significant monotonic trends in phytoplankton time series data in both studied areas, non-parametric Seasonal Mann-Kendall test (MK-test; Hirsch and Slack, 1984; with use of VBA macro for M-K test of temporal trends, version 6.1 Jan 19, 2011, developed by Grimvall, A., Libiseller, C., and Wahlin, K. form the Department of Computer and Information Science Linköping University, Swedish Institute for the Marine Environment, Gothenburg University) was carried out for the total phytoplankton biomass and for individual phyla in selected time series data (2002-2020 for PL and 1987-2015 for OPB; the year 2020 could not be included in OPB analysis due to patchy series caused by lacking 2016-2019 data). Non-parametric Seasonal Mann-Kendall test (MK-test) revealed statistically significant increasing trends in the biomass of cyanobacteria in May and June in PL, and in June in OPB (Table 3.1). This confirms the increasing abundance of cyanobacteria in spring and early summer (Fig. 3.3, OPB). Statistically significant increasing trend was identified in July, September, and November for *Mesodinium rubrum* (PL). On the other hand, decreasing trends occurred for Euglenozoa biomass in the entire Puck Bay and for Chlorophyta in PL. Also for the total phytoplankton biomass in OPB in October, a downward trend was detected, but it applies only to the 1987-2015 series [Figs. 3.3 (OPB), and 3.4].

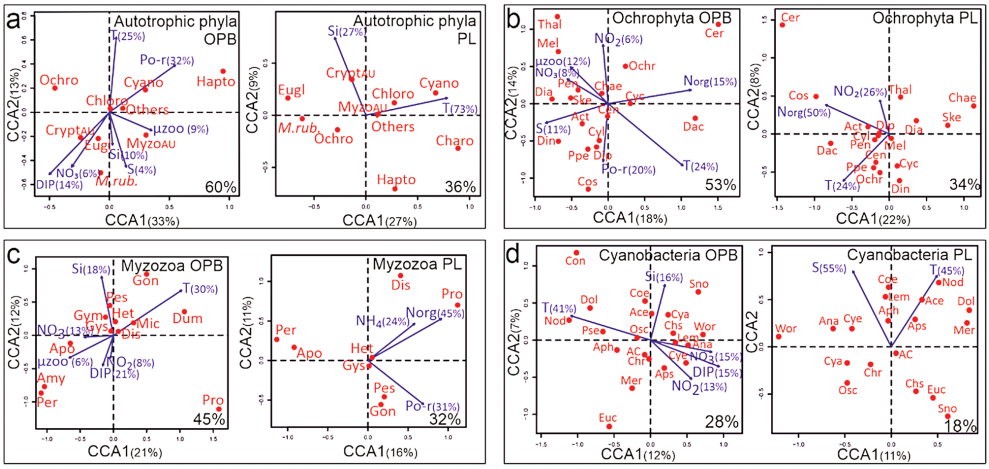

Fig. 3.6 Results for 8 separately calculated canonical correspondence analysis (CCA) of phytoplankton biomass data (autotrophic phyla - a, genera of the Ochrophyta - b, genera of Myzozoa - c, genera of Cyanobacteria - d) and corresponding environmental factors (vectors); *n*=24 for PL and *n*=60 for OPB. The percentage of species biomass variation, explained by all environmental variables, was placed in each lower right corner. The percentage of variation explained by a specific environmental variable was placed next to the appropriate vector. Variation explained by individual constrained axes was placed along the appropriate axis. All models, environmental variables and axes were statistically significant ($p<0.05$) (except for one axis - CCA2 in Cyanobacteria PL diagram). Abbreviations used: Ace=*Aphanothece*, Act=*Actinocyclus*, Act=*Aphanothece / Cyanodictyon*, Amy=*Amylax*, Ana=*Anathece*, Aph=*Aphanizomenon*, Aps=*Aphanocapsa*, Apo=*Apocalathium* complex, Cen=Centrales, Cer=*Cerataulina*, Chae=*Chaetoceros*, Charo=Charophyta, Chloro=Chlorophyta, Chr=*Chroococcus*, Chs=Chroococcales, Coe=*Coelomoron*, Con=*Cyanonephron*, Cos=*Coscinodiscus*, CryptAU=autotrophic Cryptophyta, Cya=*Cyanodictyon*, Cyano=Cyanobacteria, Cyc=*Cyclotella*, Cye=*Cyanophyceae*, Cyl=*Cylindrotheca*, Dac=*Dactyliosolen*, Dia=*Diatoma*, Din=*Dinobryon*, Dip=*Diploneis*, Dis=*Dinophysis*, Dol=*Dolichospermum*, Dum=*Dissodinium*, Euc=*Eucapsis*, Eugl=Euglenozoa, Gon=*Gonyaulax*, Gym=*Gymnodinium*, Gys=Gymnodiniales, Hapto=Haptophyta, Het=*Heterocapsa*, Lem=*Lemmermanniella*, *M.rub*=*Mesodinium rubrum*, Mel=*Melosira*, Mer=*Merismopedia*, Mic=*Micracanthodinium*, MyzoAU=autotrophic Myzozoa, Nod=*Nodularia*, Ochr=other Ochrophyta, Ochro=Ochrophyta, Osc=Oscillatoriales, Others=other autotrophs, Pen=Pennales, Per=*Peridiniella*, Pes=Peridiniales, Ppe=*Pseudopedinella*, Pro=*Prorocentrum*, Pse=*Pseudanabaena*, Ske=*Skeletonema*, Sno=*Snowella*, Thal=*Thalassiosira*, Wor=*Woronichinia*, µzoo=heterotrophic protist, Si=silicate, Po-r=P-other

Table 3.1 Results of Mann-Kendall tests of temporal trends in time series of phytoplankton biomass from OPB and PL areas in different testing periods

Response variable	Month	MK statistic	p-value (twosided)	Significance code	Slope (change/unit)	Median
PL 2002-2020						
Chlorophyta	7	-43	0,0186	-	-4,59159	34,22769
Ciliophora	7	27	0,0157	+	6,936183	35,01784
Ciliophora	9	34	0,0197	+	7,988821	69,56659
Ciliophora	11	34	0,0381	+	6,734823	120,0352
Euglenozoa	8	-23	0,0397	-	-1,15042	1,87115
Ochrophyta	9	48	0,0307	+	16,25457	215,5742
PL 2010-2020						
Cyanobacteria	5	23	0,0397	+	3,191345	11,23276
Cyanobacteria	6	31	0,0056	++	20,99925	60,39466
Euglenozoa	11	-25	0,0253	-	-0,77483	6,051652
OPB 1987-2015						
Cyanobacteria	6	29	0,0240	+	17,30607	283,4571
Euglenozoa	4	-53	0,0037	--	-0,6009	4,492189
Euglenozoa	8	-29	0,0240	-	-0,54525	3,688
Total	10	-31	0,0158	-	-65,7083	758,2838

3.4. Long-term changes of phytoplankton structure and dynamics in the Puck Bay and beyond

Marine phytoplankton constitutes the base of aquatic food webs and is of global importance because it affects the abundance and diversity of marine organisms, drives marine ecosystem functioning, and sets the upper limits to fishery yields (Botsford et al., 1997; Chassot et al., 2010). Phytoplankton is responsible for half of the global (land and sea) primary production (Field et al., 1998). In the light of the overview of studies of numerous researchers presented by Winder and Sommer (2012) it is evident that climate change affects phytoplankton both directly through physiology and indirectly by changing water column stratification and resource availability, mainly nutrients and light, or intensified grazing by heterotrophs. These modifications, as the above mentioned authors state, in turn (i) lead to a widespread advance in spring bloom timing of phytoplankton and changing bloom magnitudes, (ii) affect phytoplankton species composition and size structure, (iii) favor species traits best adapted to changing conditions, and, (iv) such shifts can have far-reaching consequences for ecosystem structure and functioning.

Recent studies show that climate change has multiple direct and indirect potentially synergistic effects that influence the Baltic Sea species, organism communities, and ecosystem functioning through physical and biogeochemical environmental characteristics of the sea (Viitasalo et al., 2015; Viitasalo and Bonsdorff, 2022; Reckermann et al., 2022). Effects of changes in ocean temperature and chemistry may alter the physiological functioning, behavior, and demographic traits of organisms, leading to shifts in the size structure, spatial range, and seasonal abundance of populations (Doney et al., 2012; Winder and Sommer, 2012), and initiate interactions in marine food webs (Lynam et al., 2017). Weiskopf et al. (2020) prove that impact of climate change is observed not only at the level of individuals, populations, and species, but also at the level of ecosystems.

Water temperature is a critical parameter for estuarine/coastal ecosystems as it has a direct impact on the growth rates, presence, and habitat of species (Vroom et al., 2017). Trombetta et al. (2019) state that water temperature is a key factor affecting phytoplankton bloom dynamics in shallow productive coastal waters, and stress that global warming can modify bloom phenology and change phytoplankton community structure, in turn affect the entire food web and ecosystem services. Harley et al. (2006) present the opinion that although potential shifts in distribution and abundance, driven directly by temperature, are reasonably well understood, the changes in ocean chemistry should be given more attention as they might be more important than changes in temperature for the performance and survival of many organisms. Winder and Sommer (2012), in their review paper on phytoplankton response to a changing climate, conclude that dynamics of phytoplankton cells are linked to annual fluctuations of temperature, water column mixing, resource availability, and consumption. Moreover, climate can modify these environmental factors and alter phytoplankton structure, seasonal dynamics, and taxonomic composition. Water temperature is a critical parameter because it has a decisive influence on the rate of chemical reactions, and therefore on physiological processes. The Van't Hoff equation has been widely utilized to explore the changes in state functions in a thermodynamic system. An increase in temperature by 10°C causes a 1.5- to 4-fold acceleration of physiological reaction rates. With this in mind, it is worth adding that changes in the metabolic activity of phytoplankton shape the abiotic structure of the environment (Paerl and Huisman, 2009).

As indicated by Anderson et al. (2022), temperature and nutrients concentrations are the most important abiotic drivers responsible for phytoplankton growth. These findings were earlier analyzed by Eppley (1972), who demonstrated that temperature can regulate growth and cellular metabolism, and by Sterner and Elser (2002) and Morel and

Price (2003), who showed nutrients impact on phytoplankton biomass by providing the elements needed to build cellular structures, and by enhancing enzymatically catalyzed pathways, like photosynthesis. The outcome of our statistical analysis (Fig. 3.6) is in good agreement with above statements, showing water temperature and various nutrients supply as factors determining the qualitative and quantitative changes in phytoplankton in the Puck Bay. Studies of Litchman et al. (2010), Aranguren-Gassis et al. (2019), Boyd (2019), and Anderson and Rynearson (2020) confirm the key role of temperature and nutrients availability in influencing microbial growth rate, imposing selective pressure on community diversity, shaping size distribution, and driving species succession. Anderson et al. (2022) showed in their experiment that the temperature-nutrient interaction altered the community dynamics of phytoplankton. At high nutrients concentrations, rising temperature acted as an enhancer, increasing phytoplankton community growth rates and total Chl. *a*, whereas at low supply of nutrients, warming acted as a stressor which suppressed growth rates and altered species proportions. Such relationships, i.e. low supply of nutrients and warming, could have been responsible for a decrease in phytoplankton biomass in the Puck Bay area over the last decades (Fig. 3.4).

Hjerne et al. (2019) showed that there was a general trend of earlier phytoplankton blooms by 1-2 weeks over the last 20 years of their studies in the Baltic region, and that fact was associated with more sunshine and less windy conditions. Changes in bloom timing, composition and magnitude can have dramatic effects on food web dynamics because of the phytoplankton role in energy transfers (Winder and Sommer, 2012; Suikkanen et al., 2013; Trombetta et al., 2019; Almén and Tamelander, 2020). Due to significant long-term water temperature increase in the Baltic Proper and its coastal regions, e.g. the Puck Bay, generated by climate change, the duration of phytoplankton growing season in the Baltic Sea changed from April-August (Latała, 1993; Renk, 1993, 2000) to March-November (Wasmund et al., 2019), or even to January-November, as it arises from our studies (Fig. 3.3).

A characteristic pattern of seasonal dynamics of phytoplankton biomass, showing two clear maxima i.e. spring max. in April, and autumn max. in September/October, slightly lower biomass in summer, and extremely low biomass in winter, was observed in 1960-1980 (Bralewska, 1992; Latała, 1993; Pliński, 1993; Renk, 1993; Witek et al., 1993). The same pattern of phytoplankton biomass was detected in 1987-1999 in OPB (Fig. 3.3). The research results presented in this monograph indicate that the dynamics of phytoplankton biomass was changing over time. The highest historical spring and autumn peaks of phytoplankton biomass became flattened, and the reduced biomass remained at a similar level throughout the entire growing season,

which became longer (Fig. 3.3; OPB 2000-2009). With the passage of time, there was further extension of the growing season, and the highest ever-recorded phytoplankton summer biomass was detected in 2010-2015 in OPB. In contrast, in 2020, there was a situation without spring bloom but with a gradual increase in phytoplankton biomass from February to October, when the autumn maximum appeared (Fig. 3.3; OPB 2020).

The historical periods of phytoplankton biomass studies (Fig. 3.3) do not match the periods of available historical data on Chl. *a* concentrations (Fig. 3.2; Latała, 1993; Renk, 1993, 2000; Witek et al., 1993), which makes direct comparisons impossible. Another issue is the lack of historical Chl. *a* concentration measurements in the winter months. Despite these limitations, it is clear that the historical spring peaks of Chl. *a* concentrations in OPB (Fig. 3.2) were ca. 3-4 times higher than the one observed in 2020; in 2020, the highest seasonal peak appeared in October. The annual distribution of Chl. *a* concentrations in the OPB in 2020 is fully consistent with the distribution of phytoplankton biomass in that year (Figs. 3.2, 3.3).

The relationship between Chl. *a* concentrations and phytoplankton biomass is not always as visible as in the case of OPB in 2020 (Fig. 3.2). In PL, the maximum of Chl.*a* concentrations occurred in September 2020, whereas the maximum of phytoplankton biomass was detected in October 2020. It is worth noting that in October 2020 the phytoplankton biomass was dominated by the presence of diatoms exclusively, while in September, in addition to the seasonally increasing diatom biomass, there were also present cryptophytes and cyanobacteria. Although Chl. *a* is commonly considered as an indicator of phytoplankton biomass, there are a number of factors that can distort this relationship. The reason for the lack of such a relationship may be because the share of Chl. *a* in a biomass unit differs among taxa (Wasmund et al., 1998; Pliński and Jóźwiak, 1999), it depends on light conditions (Cullen, 1982; Geider, 1987), and it is affected by variable nutrient resources (Cloern et al., 1995). Therefore, one of the HELCOM recommendations regarding water biomonitoring is to take into account biomass and species composition for the interpretation of variability of Chl. *a* concentrations (HELCOM, 2023).

High water temperature, calm weather conditions, availability of $P\text{-}PO_4$, and low N:P ratio create good conditions for development of diazotrophic cyanobacteria (Wasmund, 1997; Pliński and Jóźwiak, 1999; Wasmund et al., 2011; Suikkanen et al., 2013; Munkes et al., 2020). In the surveyed area, they are represented by potentially toxic genera *Aphanizomenon*, *Dolichospermum* and *Nodularia spumigena*, known to form large summer blooms in the Baltic Sea (Kownacka et al., 2020). Although water temperature was increasing over the last decades in the Baltic Sea, and in the

Puck Bay (Chapter 2), it seems that depletion of $P\text{-}PO_4$ in March-September 2020 in PL, and considerable decline in $P\text{-}PO_4$ in April-September 2020 in OPB (Fig. 2.7C) greatly reduced the development of cyanobacteria in the Puck Bay. Their summer maximum biomass dropped from 1236 $\mu g \cdot dm^{-3}$ in 1987-1999 to 571 $\mu g \cdot dm^{-3}$ in 2020 in OPB, and from 2032 $\mu g \cdot dm^{-3}$ in 2002-2009 to 284 $\mu g \cdot dm^{-3}$ in 2020 in PL (Fig. 3.7). Munkes et al. (2020) prove that too low phosphate concentrations can prevent any growth of diazotrophic cyanobacteria.

3.4.1. Diatoms to Dinoflagellates ratio

Hjerne et al. (2019) showed that high water temperatures were associated with earlier blooms of diatoms and dinoflagellates that dominate the spring bloom, and decreased diatom bloom magnitude. These findings partly follow our conclusions, with the differences that we observed two/three-month-shifts in phytoplankton blooms, and that a considerable decrease in magnitude of spring diatom bloom was observed only in OPB, with a simultaneous increase in the biomass of autumn diatoms (Fig. 3.3). Klais et al. (2011) argues that shifts in the dominant spring bloom algal groups can have significant effects on major elemental fluxes and functioning of the Baltic Sea ecosystem, but also in the vast shelves and estuaries at high latitudes, where ice-associated cold-water dinoflagellates successfully compete with diatoms.

Numerous publications (Wasmund and Uhlig, 2003; Alheit et al., 2004; Wasmund et al., 2011, 2017) show that temperature, salinity, oxygen, and nutrients have an immense influence on functioning of the entire Baltic ecosystem. Increasing water temperature and variable surface salinity (Lehmann et al., 2022; Chapter 2) triggered disturbance in water dynamics in the upper layer and that resulted in drastic decrease in spring diatoms biomass followed by parallel increase in dinoflagellates and total phytoplankton biomass in the Bornholm and Gotland Basin in 1988-1989 (Wasmund and Uhlig, 2003; Wasmund et al., 2011). The same phenomenon was observed in OPB in 1987-1999 (Fig. 3.3). The algal spring bloom in the Baltic Sea represents an anomaly from the winter-spring bloom patterns worldwide in terms of frequent and recurring dominance of dinoflagellates over diatoms (Klais et al., 2011; Wasmund et al., 2011). Studies of Klais et al. (2011) showed that in 1995-2004 the proportion of dinoflagellates increased relative to diatoms mostly in the northernmost basins of the Baltic Sea (Gulf of Bothnia, from 0.1 to 0.4 and in the Gulf of Finland, from 0.4 to 0.6), which are typically ice-covered areas (Tikanmäki et al., 2025). In the southern Baltic Proper and the Mecklenburg Bight, alternating oscillations

between dominance of diatoms (1980s and since 2000) and dinoflagellates (1990s) were observed. Alheit et al. (2004) and Wasmund et al. (2011) are of the opinion that the observed decline in diatom and increase in dinoflagellates biomass was related to higher stability of the water column in the winter-spring period due to increasing winter temperatures. The other reason of diatom biomass decline in the Baltic Sea lies in a decrease in silicon concentrations, mainly due to river damming (Humborg et al., 2006; Conley et al., 2008).

Our study showed a decline in diatom biomass only in PL, characterized by very dynamic variability of silicate concentrations (Chapter 2) and local limitation of diatom growth in March 2020 (Chapter 2). In OPB, silicate concentrations were much higher than in PL and their level was stable during the vegetation season (Chapter 2). In 1987-2020, a gradual increase in diatom biomass was detected from decade to decade in OPB, but in some sub-periods low diatom growth in spring was followed by a strong one in autumn (e.g. in 2020 in OPB), or quite high in summer (e.g. 2000-2015, Fig. 3.3). This is consistent with Wasmund et al. (2011) observations in the southern Baltic Proper. On the other hand, the occurrence of the regular, cyclical oscillations between diatom and dinoflagellate biomass peaks in the 10-year phases, as suggested by Wasmund et al. (2011), is not clearly confirmed in the case of research conducted in the Puck Bay. Over the last 30 years, a gradual increase in diatom biomass and a simultaneous decrease in dinoflagellate biomass were observed in the bay (Figs. 3.3 and 3.4). The highest values of the dinoflagellate biomass were found in OPB in 1987-1999, but the ratio of diatom to dinoflagellates biomasses was still at the level of 0.5-0.6 during the spring bloom, similarly to that in 2000-2009. The lowest diatom/dinoflagellates ratios 0.09, 0.02, 0.17, 0.24 were found in our study in OPB in 1993, 2001, 2010 and 2020, respectively, whereas the highest diatom/dinoflagellates ratios 0.72-0.96 occurred in 2008 and 2013-2015.

3.5. Non-indogenous species in the Puck Bay and beyond

Hereafter, we present documented examples of invasive non-indogenous species, and species that extended their range and appeared in the late 1990s and early 2000s (Fig. 3.3 OPB, peaks D, F) and could have contributed to changes in structure of the Puck Bay ecosystem.

In September 1997, dinoflagellate *Prorocentrum cordatum* originating from the North Sea appeared as the dominant species in the phytoplankton community in OPB (Witek and Pliński, 2000; Olenina et al., 2010). A red bloom of this toxic,

mixotrophic species was detected in one of the canals in Gdynia harbor. Since then, *P. cordatum* has been one of the autumn components of the phytoplankton community in the Puck Bay, although its red blooms have no longer been seen.

In October 2001, a strong dominance of the diatom *Dactyliosolen fragilissimus* in the Gulf of Gdańsk was recorded for the first time (Witek, 2010). This species, common in warm waters of medium and high salinity in the Kattegat, Skagerrak, Arkona Basin and Mecklenburg Bay, expanded eastwards up to the Curonian Lagoon (Łotocka, 2006; Witek, 2010; Olenina and Kownacka, 2010). It has settled in OPB and every few years it causes intense autumn phytoplankton blooms; in 2020, it formed the highest autumn diatom maximum observed since 1987 (Fig. 3.3).

Kownacka et al. (2013) and Chen et al. (2018) described the history of the appearance of the diatom *Chaetoceros pauciramosus* in OPB, whose characteristic cysts were recorded for the first time in autumn phytoplankton in 2003 near Sopot. This species has also settled in the Puck Bay as a permanent component modifying the autumn phytoplankton community.

During autumn 2007, an unusual increase in the potentially toxic haptophyta *Prymnesium polylepis* was observed throughout the Baltic Proper (Majaneva et al., 2012), including in the Gulf of Gdańsk. It persisted throughout the very mild, ice-free winter 2007/08 (Girjatowicz and Świątek, 2021) and formed a large bloom culminating in May 2008. Since then, after exceptionally warm winters, *P. polylepis* builds up a considerable biomass during the spring. Such event took place also during spring 2020 after the warmest winter in Poland since the mid-20th century (IMGW, 2022), and the share of *P. polylepis* in total phytoplankton biomass in May was between 25-50% depending on station (Fig. 3.5).

3.6. Key summary thoughts from international and our own research

Since we have limited data in the studied region, it seems sensible to use the knowledge of those who had access to much larger databases and a wider range of studies. Numerous authors are of the opinion that future trajectories of change in coastal ecosystems will largely depend on the extent of future greenhouse gas emissions and human activities in, and around coastal zones (Doney et al., 2012). However, critical knowledge gaps remain, particularly regarding the interactions among stressors and the nature of ecological tipping points. Addressing these gaps through further research will be necessary to improve projections of future impacts and support the conservation and resilience of these valuable ecosystems (Somero, 2012). In recent

publications (e.g. Reid et al., 2016; Scheffers et al., 2016; Oschlies, 2019; Heshmati, 2020; Li et al., 2020; Garcia-Soto et al., 2021; Meier et al., 2022; Guild et al., 2025), focused on climate change impacts on marine ecosystems, the authors confirm that coastal ecosystems are facing unprecedented challenges from climate change. Water warming, acidification, sea level rise, freshwater changes, and shifts in circulation and disturbance patterns, each imposing significant pressures, are manifesting these challenges. All these changes contribute to qualitative and quantitative ecosystem changes, already observed in various parts of the globe. Guild et al. (2025) emphasize that future research should prioritize expanding long-term monitoring efforts and improving assessment models that integrate the full suite and interaction of stressors in an ecosystem. Undertaken efforts can facilitate understanding of how coastal ecosystems will react to projected climate scenarios and help to identify and support the adaptive strategies necessary for their resilience. All the mentioned above authors are of the opinion that mitigating further degradation and fostering resilience in coastal ecosystems demands global reductions in both, the GHG emissions and coastal activities, which degrade natural environment, alongside innovative management strategies.

- The abiotic and biotic data, obtained by us in the Puck Bay throughout 2020 were compared with their available long-term historical counterparts, and the main goal was to estimate to what extent the changes in anthropogenic pressure (temperature and nutrients as the main driving forces identified in the studied region) influenced phytoplankton over the past 2-3 decades. Constantly rising air, and obviously water temperature over the last few decades, must have given an impetus for the earlier vegetation process, as observed in 2000-2009 in OPB and in 2010-2018 in PL. The phytoplankton and Chl. *a* data show that in 2020, the growing season started 2-3 months earlier than 2-3 decades earlier and lasted from January to November. Much earlier start of vegetation meant earlier demand for nutrients, thus disruption of their winter accumulation, which historically was typical for our climate zone.

- The available historical Chl. *a* concentrations in OPB in 1967-1979, 1980-1999, 2000-2009, and 2011-2016 in majority of cases do not cover the entire calendar year, but allow noticing that spring values of Chl. *a* peaks in 1980-1999, 2000-2009, 2011-2016 reached appox. 9.5-13 $\mu g \cdot dm^{-3}$, while in 2020 the spring peak was flattened at the level of ca. 3-4 $\mu g \cdot dm^{-3}$, and these values were spread until August 2020. The available average annual Chl. *a* concentration in 1980-1999 was at the level of 4.24 $\mu g \cdot dm^{-3}$, while in 2020 it reached 3.14 $\mu g \cdot dm^{-3}$. In PL, the average

annual concentration of Chl. *a* decreased from 5.49 μg·dm^{-3} recorded in 2011-2016 (January-November) to 2.46 μg·dm^{-3} observed in 2020.

- The profound changes in abiotic parameters must have been responsible for: (i) a decrease in average phytoplankton biomass in OPB (from 2994 μg·dm^{-3} in 1987-1999 to 1799 μg·dm^{-3} in 2020) and in PL (from 1445 μg·dm^{-3} in 2002-2009 to 889 μg·dm^{-3} in 2020). These changes were mainly caused by reduction of cyanobacteria and dinoflagellates biomass, (ii) increased importance of small flagellates in the size range of 2-15 μm, both unidentified and belonging to Haptophyta and Cryptophyta, (iii) generally unchanged average diatoms biomass, but with significantly altered periods of its appearance.

- Although the water temperature was increasing over the last decades in the Baltic Sea, and in the Puck Bay, it seems that depletion of P-PO_4 in March-September 2020 in PL, and considerable decline in P-PO_4 in April-September 2020 in OPB greatly reduced the development of cyanobacteria in the Puck Bay. Their summer maximum biomass dropped from 1236 μg·dm^{-3} in 1987-1999 to 571 μg·dm^{-3} in 2020 in OPB, and from 2032 μg·dm^{-3} in 2002-2009 to 284 μg·dm^{-3} in 2020 in PL.

- The observed decline in phytoplankton abundance and change in its seasonal dynamics and taxonomic composition indicate an improvement in the ecosystem condition in terms of limiting unfavorable phenomena caused by eutrophication; the improvement was mainly manifested by an increase in Secchi depth and a significant decrease in the intensity of cyanobacterial blooms in recent years. It should be noted, however, that because of the described changes and transformations in the environment, in 2020 we observed a phytoplankton community of rather lower value for consumers in comparison with phytoplankton community from the 1970s -1980s. That was due to the increase in the share of mixotrophic flagellates, which contribute to dispersing energy rather than transferring it to higher trophic levels.

- Our research shows that extensive changes have occurred in the studied Puck Bay ecosystem, both in terms of abiotic and biotic parameters. These changes may have serious consequences for the functioning of the entire ecosystem, up to its highest trophic levels.

3.7. References

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4

SUMMARY

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The Puck Bay, a semi-closed coastal part of the Gulf of Gdańsk, is a unique reservoir due to the preserved species richness of plants and animals inhabiting its bottom, the coexistence of various communities of benthic flora and fauna, and the presence of rare species of benthic plants and animals. This region, consisting of the Puck Lagoon (PL) and the Outer Puck Bay (OPB) is regarded as the most diverse and biologically valuable part of the Polish marine areas, and is a key site for a number of species that are not present along the open seacoast. It is, therefore, not surprising that this region is subject to legal protection under both national and international regulations (Chapter 1). The Puck Bay, similarly to other coastal water bodies is the transitional system, located at the interface between land and sea. It remains under local anthropogenic pressure [Waste Water Treatment Plants (WWTPs); riverine nitrogen (N) and phosphorus (P) emission from the bay catchment; indirect impact of the Vistula River carrying substantial loads of N and P to the Gulf of Gdańsk], but also under global anthropogenic pressure (climate change). The division of anthropogenic stressors into local and global makes us aware that all remedial actions must have the same dimension, i.e. local and global (Chapter 1).

The presented data show that profound changes of abiotic and biotic parameters have been observed in the Puck Bay over the past 2-3 decades (Chapter 2 and 3). Temperature and nutrients were indicated as the main driving forces that influenced phytoplankton dynamics (Chapter 3), therefore we focus on these parameters in the summary. Temporal and spatial variability of oxygen content and salinity are given attention in Chapter 2 exclusively. The increase in water temperature (due to climate change) in the bay was consistent with almost identical trend found in many regions of the Baltic Sea, the open Gulf of Gdańsk included. The presented studies prove that in 2020, average annual water temperature was by 2.89°C in OPB, and by 2.24°C in PL higher than relevant annual averages in 1972-1990. Either temperature values in the bay in June-November 2023 complied with values of 2020, or showed seasonal maxima a bit shifted, thus suggesting impact of heat waves in different months in 2023, as compared with 2020. The level of water warming in the bay was comparable with long-term temperature increase in the surface layer of the open Baltic Sea, and long-term air temperature increase in the region. These facts indirectly indicate that 2020 was not thermally exceptional, on a contrary it fell into the long-term trend (Chapter 2).

Nutrient concentrations and their variability in the bay were related not only to their seasonally variable uptake by phytoplankton and recycling within a given ecosystem, particularly under changed thermal conditions, but also to their considerably declining anthropogenic supply to the system (Chapter 1 and 2). Much earlier start of vegetation (Chapter 3) meant earlier demand for nutrients, thus disruption of their winter accumulation, which historically was typical for our climate zone (Chapter 2). Analysis of long -term data, point to the fact that in 2020, monthly as well as average annual concentrations of nitrate, ammonium, and phosphate were much higher in 1981-1991 than in 2020. It is also important that the annual patterns of these nutrients in 1981-1991 were significantly different from the relevant patterns in 2020. Historical data clearly show very high winter peaks of nitrate, ammonium, and phosphate concentrations in PL and OPB, followed by their sharp declines in spring, then remaining at a relatively high level during the growing season, and increasing again in autumn. Annual nutrient patterns in 2020 and 2023 (June-November) were completely different from those in 1981-1991. Firstly, in 2020, winter peaks of nitrate and phosphate were significantly lower than historical ones. Secondly, in 2020, nitrate depletion or occasional values not exceeding 0.4 $\mu mol \cdot dm^{-3}$, and ammonium depletion were observed for eight months in PL, and for six months in OPB; identical situation was observed in 2023, with nitrate and ammonium depletion from June (earlier studies were not conducted) until October. Thirdly, in 2020, for seven months, PL was characterized either by $P\text{-}PO_4$ depletion or concentrations well below 0.2 $\mu mol \cdot dm^{-3}$; identical situation was observed in 2023. Not only average annual concentrations of phosphate, but also concentrations of total phosphorus, and silicate were considerably higher throughout 2020 in OPB than in PL, indicating the important role of the Vistula River in supplying the Puck Bay with P and Si. The lack of phosphate depletion in the OPB in 2020 and 2023 additionally confirms the important role of the Vistula River in supplying the bay with P. We wish to explain that silicate, total nitrogen, and total phosphorus were not determined in 1981-1991; therefore, Chapter 2 presents the seasonal variability of monthly concentrations of these parameters in 2020 and in June-November 2023.

Calculations of the monthly Redfield ratio at individual PL and OPB stations investigated in 2020 allow to state that N played a limiting role in OPB, whereas N and P, as well as silicon (Si) alternately in PL. At scarcity of inorganic N and P, Norg. and P-other could have supported phytoplankton growth in 2020, and the latter forms of N and P and their important role in supporting phytoplankton growth is proven in international bibliography which is extensively referred to in the monograph (Chapter 2).

Rising water temperature resulted in extension of phytoplankton growing season (Chapter 2 and 3). The phytoplankton and Chl. *a* data show that in 2020, the growing season started 2-3 months earlier than 2-3 decades earlier, and lasted from January to November (Chapter 2). The available historical Chl. *a* concentrations in OPB in 1967-1979, 1980-1999, 2000-2009, and 2011-2016 in majority of cases do not cover the entire calendar year, but allow noticing that spring values of Chl. *a* peaks in 1980-1999, 2000-2009, 2011-2016 reached ca. 9.5-13 $\mu g \cdot dm^{-3}$, while in 2020 the spring peak was flattened at the level of ca. 3-4 $\mu g \cdot dm^{-3}$, and these values were spread until August 2020. The available average annual Chl. *a* concentration in 1980-1999 was at the level of 4.24 $\mu g \cdot dm^{-3}$, while in 2020 it reached 3.14 $\mu g \cdot dm^{-3}$. In PL, the average annual concentration of Chl. *a* decreased from 5.49 $\mu g \cdot dm^{-3}$ recorded in 2011-2016 (January-November) to 2.46 $\mu g \cdot dm^{-3}$ observed in 2020.

The profound changes in abiotic parameters must have been responsible for: (i) a decrease in average phytoplankton biomass in OPB (from 2994 $\mu g \cdot dm^{-3}$ in 1987-1999 to 1799 $\mu g \cdot dm^{-3}$ in 2020) and in PL (from 1445 $\mu g \cdot dm^{-3}$ in 2002-2009 to 889 $\mu g \cdot dm^{-3}$ in 2020). These changes were mainly caused by reduction of cyanobacteria and dinoflagellates biomass, (ii) increased importance of small flagellates in the size range of 2-15 μm, both unidentified and belonging to Haptophyta and Cryptophyta, (iii) generally unchanged average diatoms biomass, but with significantly altered periods of its appearance. Although the water temperature was increasing over the last decades in the Baltic Sea, and in the Puck Bay, it seems that depletion of $P\text{-}PO_4$ in March-September 2020 in PL, and considerable decrease in $P\text{-}PO_4$ in April-September 2020 in OPB greatly reduced the development of cyanobacteria in the Puck Bay. Their summer maximum biomass dropped from 1236 $\mu g \cdot dm^{-3}$ in 1987-1999 to 571 $\mu g \cdot dm^{-3}$ in 2020 in OPB, and from 2032 $\mu g \cdot dm^{-3}$ in 2002-2009 to 284 $\mu g \cdot dm^{-3}$ in 2020 in PL (Chapter 2 and 3).

The observed decline in phytoplankton abundance and change in its seasonal dynamics and taxonomic composition indicate an improvement in the ecosystem condition in terms of limiting unfavorable phenomena caused by eutrophication; the improvement was mainly manifested by an increase in Secchi depth and a significant decrease in the intensity of cyanobacterial blooms in recent years. It should be noted, however, that because of the described changes and transformations in the environment, in 2020 we observed a phytoplankton community of rather lower value for consumers in comparison with phytoplankton community from the 1970s /1980s. That was due to the increase in the share of mixotrophic flagellates, which contribute to dispersing energy rather than transferring it to higher trophic levels. It is worth emphasizing that the response of phytoplankton to the changing anthropogenic pressure over the past

few decades is discussed on a local scale (the Puck Bay), but with the broad reference to disturbances occurring in the Baltic ecosystems, as well as in ecosystems beyond the Baltic Sea (Chapter 2 and 3).

Our research shows that extensive changes have occurred in the studied Puck Bay ecosystem, both in terms of abiotic and biotic parameters. These changes may have serious consequences for the functioning of the entire ecosystem, up to its highest trophic levels. In the light of current knowledge, it is undeniable that all changes occurring in aquatic and terrestrial ecosystems must be related to global changes, i.e. climate change and the increase in air temperature and, consequently, water temperature. There are some authors, we refer to in the monograph, who emphasize that future research should prioritize expanding long-term monitoring efforts and improving assessment models that integrate the full suite and interaction of stressors in an ecosystem. Undertaken efforts can facilitate understanding of how coastal ecosystems will react to projected climate scenarios and help to identify and support the adaptive strategies necessary for their resilience.

We believe that the presented scientific material and drawn conclusions may be of interest to a number of decision-making organizations, including government organizations responsible for decisions regarding sewage treatment plants or emission of N and P from utilized agricultural areas to the river basins and then to the Baltic Sea. We also believe that the presented material may be of interest of local authorities responsible for the policy of sustainable use of water and natural resources, as well as sustainable tourism economy.

APPENDIX

Ref. all Chapters

ABBREVIATIONS AND ACRONYMS

AT	Air Temperature
BOD5	Biological Oxygen Demand
Chl. *a*	Chlorophyll *a*
CTD	Conductivity Temperature Depth
DCAA	Dissolved Combined Amino Acids
DFAA	Dissolved Free Amino Acids
DIN	Dissolved Inorganic Nitrogen
DIP	Dissolved Inorganic Phosphorus
DNA	Deoxyribonucleic Acid
DOC	Dissolved Organic Carbon
DOP	Dissolved Organic Phosphorus
DSi	Dissolved silica
ER	Eutrophication Ratio
GHG	Green House Gases
HAB	Harmful Algal Blooms
HELCOM	Helsinki Commission
IMWM	Institute of Meteorology and Water Management
IPCC	Intergovernmental Panel on Climate Change
MONERIS	Modeling Nutrient Emissions in River Systems
N	Nitrogen
Norg.	Organic Nitrogen
NAO	North Atlantic Oscillation
NMFRI	National Marine Fisheries Research Institute
OPB	Outer Puck Bay
P	Phosphorus
PIP	Particulate Inorganic Phosphorus
PL	Puck Lagoon

POP	Particulate Organic Phosphorus
P-other	Other Forms of Phosphorus
PSU	Practical Salinity Units
RNA	Ribonucleic Acid
RWT	River Water Temperature
S	Salinity
SST	Sea Surface Temperature
T	Temperature
TN	Total Nitrogen
TP	Total Phosphorus
UNESCO	United Nations Educational, Scientific and Cultural Organization
WFD	Water Framework Directive
WWTP	Waste Water Treatment Plant

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