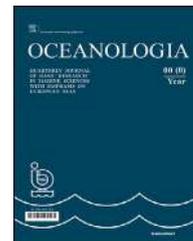


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ORIGINAL RESEARCH ARTICLE

The influence of biochemical parameters on primary production in the Gulf of Gdańsk region: A model study

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Abstract Understanding the changing levels of biochemical parameters and the factors that influence them throughout the seasons is crucial for comprehending the dynamics of marine ecosystems. It also helps us identify potential threats that could harm their condition, aiding decision-making processes related to their protection. This study focuses on examining the variations in nutrients (such as nitrates, phosphates, and silicates), dissolved oxygen, and phytoplankton within the Gulf of Gdańsk. Additionally, we analyze the primary production process at three representative locations. To achieve this, we used data from the *EcoFish* biochemical numerical model. To ensure the model's accuracy, we compared its results with in situ data from the ICES database. The comparison revealed high correlations and minimal errors. Furthermore, we investigated how limiting factors impact primary phytoplankton production and demonstrated how the intensity of spring diatom blooms influences the nature of cyanobacterial blooms in the summer.

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1. Introduction

Primary production in marine environments is associated with the process of photosynthesis, in which organisms such as phytoplankton (and other photosynthesizing organisms) use sunlight, water, and carbon dioxide to produce organic matter. Phytoplankton is a key component of the marine food web and plays an important role in shaping the ecosystem of the Gulf of Gdańsk (Verity and Smetacek, 1996). It serves as the primary source of food for many organisms, such as zooplankton (for example invertebrates) or small

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fish, which then are consumed by larger fish, birds, and marine mammals. Various factors, including water temperature, nutrient availability, and sunlight, influence primary production in the Gulf of Gdańsk. Its location at the mouth of the Vistula River (and other smaller rivers), which provides nutrient-rich freshwater, makes it a particularly productive area (Tomczak et al., 2016).

The Baltic Sea is exposed to a range of natural processes and anthropogenic stressors (von Storch, 2023). These include climate change, rising sea levels, coastal processes, excessive nutrient loads resulting in eutrophication, hypoxia, acidification, agriculture, fisheries, organic pollution, sunken munitions, marine litter, underwater noise and tourism (Reckermann et al., 2022; Szymczycha et al., 2019).

During the latest socioecological assessment, the Baltic Sea achieved a Baltic Health Index (BHI) score of 76 out of 100, indicating that its overall condition is suboptimal and achieving management objectives and associated targets requires significant effort (Blenckner et al., 2021). Regionally, the Gulf of Gdańsk achieved the lowest BHI score of 55 among all regions considered, mainly due to a low assessment in relation to contaminants, carbon storage, and lasting special places. Therefore, continuous monitoring of the state of the Gulf of Gdańsk and appropriate management of human maritime activities is particularly important to minimize their negative impact on the condition of its waters.

The project *Knowledge transfer platform FindFISH* (short: *FindFISH*) (Dzierzbicka-Głowacka et al., 2018) is perfectly suited to the implementation of the aforementioned tasks (monitoring and management of human activities). The project aimed to develop a user-friendly platform to provide fishermen and scientists with accessible knowledge and information regarding the Gulf of Gdańsk's physical and biological state. As part of the project, a *Fish Module* was designed to generate maps indicating the best environmental conditions for specific commercially caught fish species in the Gulf of Gdańsk, such as herring, sprat, and flounder. This tool enables targeted fishing, reducing unintended catch and minimizing pollution caused by fishing expeditions, thus promoting environmental protection.

The heart of *FindFISH* is the 3D prognostic ecohydrodynamic model *EcoFish*, developed within the project. The *EcoFish* model (www.findfish.pl) operates in real-time mode, creating 48-hour forecasts of hydrodynamic parameters (water temperature, salinity, sea currents, sea surface height) and biochemical parameters (nitrate, phosphate, silicate, chlorophyll *a*, phytoplankton and microzooplankton biomass, dissolved oxygen and dissolved organic carbon concentration).

The hydrodynamic part of the *EcoFish* model was described in separate papers (Janecki et al., 2021, 2022), along with the analysis of the variability of the physical parameters, confirming a very good agreement between the model results and environmental data. In this work, we focus on the biochemical part of the *EcoFish* model. The following chapters present the results for the biochemical parameters, their variability, and a comparison with *in situ* data from the ICES database.

One of the three groups of phytoplankton implemented in the *EcoFish* model is cyanobacteria. Cyanobacteria are prokaryotes but have historically been grouped with eukary-

otic "algae" and at varying times have been referred to as "blue-greens" or "blue-green algae" (Carmichael, 2008; O'Neil et al., 2012). This name does not reflect any relationship between cyanobacteria and other organisms called algae. Cyanobacteria are a distinct group of bacteria that perform oxygenic photosynthesis, and it is only the chloroplast in eukaryotic algae to which the cyanobacteria are related (Sato, 2021).

Although we are aware of the updated classification of cyanobacteria, for the purposes of our study, we have chosen to treat cyanobacteria as a component of phytoplankton as it was traditionally understood. This decision is motivated by the need to maintain consistency with previous studies and the existing literature, ensuring comparability and facilitating model-based analyses. By acknowledging the revised systematic position of cyanobacteria while using the term "phytoplankton" within the scope of our research, we aim to strike a balance between the historical perspective and the contemporary scientific understanding.

The purpose of the paper is not only to prove, that the *EcoFish* model provides reliable results on biochemical variables for the Gulf of Gdańsk. By analyzing the variability of nutrients (nitrates, phosphates and silicates), dissolved oxygen and phytoplankton in the Gulf of Gdańsk, we wanted to describe their impact on the pattern and intensity of the primary production. The rich nutrient deposition from rivers can significantly alter the biomass distribution of all phytoplankton groups.

The analysis of the seasonal variability dynamics of the primary production process is extremely important in the context of the conducted research, as it is a process directly related to the production and consumption of oxygen in the waters of the Gulf of Gdańsk. Dissolved oxygen concentration is one of the four parameters (along with temperature, salinity, and depth) that constitute an input variable crucial for the *Fish Module*.

2. Material and methods

2.1. Study area

The *EcoFish* model domain encompasses an enlarged area of the Gulf of Gdańsk (Figure 1). It is one of the most important coastal areas in the southern part of the Baltic Sea, with unique oceanographic and hydrological conditions. The western part of the Gulf of Gdańsk can be divided into a shallow part called the Puck Bay, and further west into the semiclosed Puck Lagoon (Majewski, 1972). The Vistula, which is the largest river flowing into the gulf and carrying nutrients and other substances originating from industry and other human activities, has a significant impact on the hydrology of the Gulf of Gdańsk (Voss et al., 2005; Witek et al., 1997). The Gulf of Gdańsk also contains the largest Polish ports, such as Gdańsk and Gdynia, which have a significant impact on its environment due to pollution, maritime transport, and fishing (HELCOM, 2010).

2.2. *In situ* data

To verify whether the *EcoFish* model accurately reproduces the variability of biochemical parameters in the Gulf of

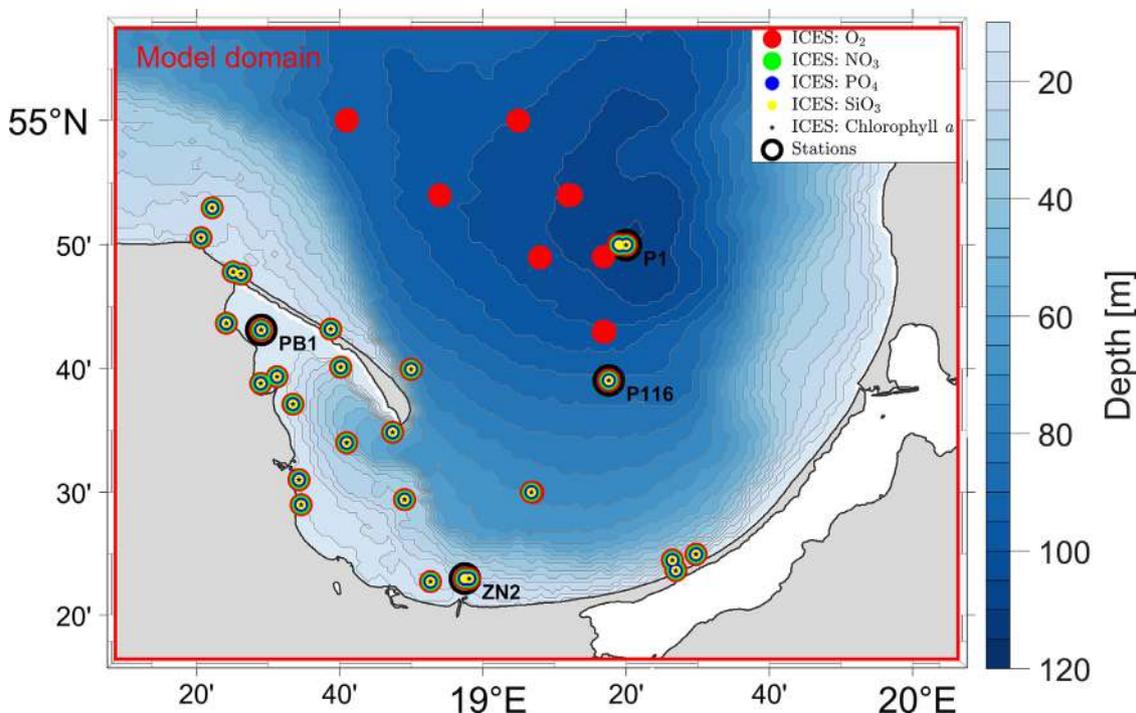


Figure 1 The *EcoFish* model domain with bathymetry, the location of environmental data from the ICES database, and the stations where primary production was investigated.

Gdańsk, the International Council for the Exploration of the Sea¹ (ICES) database was used. The ICES database for the years 2017–2020 contained 3329 measurements of oxygen (O_2), 2370 measurements of nitrate (NO_3), 2592 measurements of phosphate (PO_4), 2610 measurements of silicate (SiO_3), and 972 measurements of chlorophyll *a*. Most of the data originated from the shallow waters in the Puck Bay area and the southern part of the Gulf of Gdańsk. Only a small fraction (mainly for oxygen concentration) was located at greater depths in the open sea (Figure 1).

2.3. The *EcoFish* model

2.3.1. Configuration

The *EcoFish* model is a three-dimensional, numerical prognostic model of the Gulf of Gdańsk ecosystem with a horizontal resolution of 575 m, which was developed as part of the *FindFISH* project. The model is divided into 26 vertical levels, each with a thickness of 5 m. The *EcoFish* model consists of:

- Hydrodynamic component – this is an ocean model based on the Parallel Ocean Program (POP) code, which has been described and validated (for water temperature and salinity) in a separate article (Janecki et al., 2021);
- Biochemical component – this is an NPZD-type biochemical model, which is described and validated in this paper;
- *Fish Module* – this is an additional element created within the *FindFISH* project, which, based on data from the hydrodynamic and biochemical components, allows

for the creation of maps of optimal environmental conditions for the habitat of fish (sprat, herring, and flounder) commercially caught in the Gulf of Gdańsk region.

In addition to the three main components in which simulations are conducted, the *EcoFish* model includes dedicated modules for processing input and output data, data assimilation modules (for surface temperature and chlorophyll *a*), and a module coordinating the model in the operational mode. Its task is to control the components, handle errors, and transmit data between modules.

2.3.2. Water – water border

The *EcoFish* model domain is connected with the Baltic Sea from the north and northwest, which creates the need to provide the model with boundary conditions (open boundary). These forcings are transmitted to the *EcoFish* model using the results from the 3D CEMBS model with a horizontal resolution of 2 km (Dzierzbicka-Głowacka et al., 2013a,b).

2.3.3. Atmosphere forcing

At the water-atmosphere boundary, the *EcoFish* model is driven by meteorological forcing. These forcings are derived from the UM (Unified Model)², developed at the Interdisciplinary Centre for Mathematical and Computational Modelling of the University of Warsaw (ICM UW). Some of the obtained parameters (wind speed, air temperature, specific humidity, atmospheric pressure, precipitation, radiation) are directly used as forcings after interpolation onto the *EcoFish* model grid. The missing parameters are calcu-

¹ <https://data.ices.dk>.

² www.meteo.pl.

Table 1 Rivers mouths' locations included within the *EcoFish* model domain and mean runoff.

	Source	River name	Longitude	Latitude	Mean runoff [m ³ s ⁻¹]
1	HYPE	Vistula	18.95	54.35	1064
2	HYPE	Bold Vistula	18.78	54.37	2.05
3	HYPE	Still Vistula	18.66	54.41	6.06
4	HYPE	Oliwski Stream	18.60	54.42	0.31
5	HYPE	Kamienny Stream	18.56	54.46	0.45
6	HYPE	Kacza	18.56	54.48	0.29
7	HYPE	Sewage Canal	18.51	54.61	0.21
8	SWAT	Zagórska Stream	18.47	54.63	0.11
9	SWAT	Reda	18.47	54.64	0.48
10	SWAT	Mrzezino Canal	18.46	54.66	0.20
11	SWAT	Gizdepka	18.46	54.66	0.30
12	SWAT	Żelistrzewo Canal	18.45	54.70	0.17
13	SWAT	Plutnica	18.39	54.72	0.91

lated by the atmospheric data module, which is an integral part of the *EcoFish* model.

2.3.4. Land-water linkage

In the *EcoFish* model, 13 rivers that flow into the Gulf of Gdańsk are taken into account (Table 1). Information about the volume of freshwater (runoff) and nutrients deposition for six rivers whose mouths are located in the area of the Puck Commune comes from the SWAT model (Kalinowska et al., 2020, 2018; Wielgat et al., 2021). SWAT was developed as part of the *Integrated Information-Predictive Service WaterPUCK* project (Dybowski et al., 2019; Dzierzbicka-Głowacka et al., 2019, 2022). The remaining seven rivers use runoff data from the Hydrological Predictions for the Environment (HYPE) model (Arheimer et al., 2012; Donnelly et al., 2016). Data on the amount of nutrient deposition in the HYPE model were available only in the form of monthly averages for the period 1980–2010. As a result of the HELCOM directives, the actual amounts of these substances entering the Baltic Sea from the territory of the Republic of Poland have been significantly reduced over the past 30 years (Pastuszak et al., 2018). The use of 30-year averages would lead to overestimation and distortion of the actual flow. Therefore, nutrient deposition for HYPE rivers was set based on the work of Pastuszak et al. (2018). Nitrate concentrations were established at 0.9 mg dm⁻³, ammonia at 0.07 mg dm⁻³, phosphate at 0.07 mg dm⁻³, and silicate at 1.1 mg dm⁻³. Concentrations were linked to daily volumes of freshwater introduced by these rivers, obtaining a satisfactory estimate of deposition (Dybowski et al., 2020).

2.3.5. NPZD-type biochemical model

The implementation of environmental variables in the *EcoFish* model was carried out by determining the source and sink functions for four types of nutrients (phosphates – PO₄, nitrates – NO₃, ammonia – NH₄, and silicates – SiO₃), three groups of phytoplankton and microzooplankton. There are two things that the general equation of turbulent diffusion with an advection component does in the *EcoFish* model (Equation (1)). First, it describes the dynam-

ics of changes in concentrations. Second, it serves as the link where the transfer of forcings between the hydrodynamic and biochemical components takes place.

$$\frac{\partial S}{\partial t} + (V + w_s) \cdot \nabla S = \frac{\partial}{\partial z} \left(K_z \frac{\partial S}{\partial z} \right) + \sum_{i=1}^2 \frac{\partial}{\partial x_i} \left(K_{x_i} \frac{\partial S}{\partial x_i} \right) + F_s \quad (1)$$

where S is each model variable, V (u , v , w) is the velocity vector, w_s is the sinking velocity of pelagic detritus, K_z , K_{x_i} , are vertical and horizontal turbulent diffusion coefficients and F_s is the biogeochemical source-sink term which describes possible sources and losses of the diffusing substance in the space being studied.

The source code of the biochemical part was filled with interrelated dependencies describing the variability of the primary production of phytoplankton biomass, as well as the concentration of chlorophyll a , microzooplankton biomass, nutrients concentrations (phosphates, nitrates, ammonia and silicates), dissolved oxygen, pelagic and benthic detritus (for NO₃ and PO₄). Source and sink functions were determined based on knowledge of the biological and chemical processes that occur in the marine environment and their mutual relationships (Dzierzbicka-Głowacka et al., 2013b; Moore et al., 2001).

The biochemical component of the *EcoFish* model requires information about the state and physical conditions of the ecosystem it represents. Therefore, it depends on the hydrodynamic component and operates in the same domain (Figure 1).

3. Results

In the following chapters, we present monthly average concentrations of dissolved oxygen (O₂), nitrate (NO₃), phosphate (PO₄), silicate (SiO₃), and phytoplankton (as chlorophyll a) for a four-year period from January 1, 2017 to December 31, 2020.

Furthermore, each biochemical variable was validated by comparing it with the available measurements from the ICES database (Figure 1). Basic statistical measures were deter-

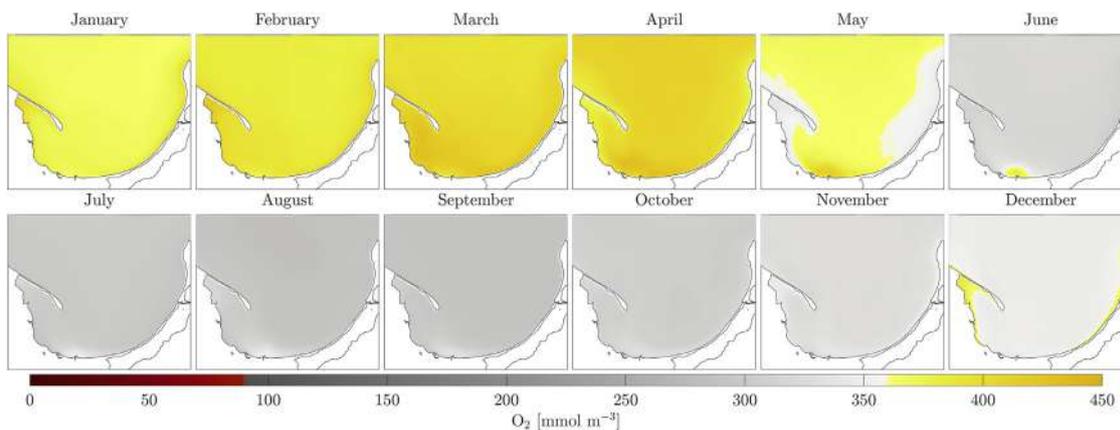


Figure 2 Average monthly concentrations of dissolved oxygen (O_2) in the surface layer for the period 2017–2020.

mined: means, standard deviations (STD), Pearson's correlation coefficients (r) and root mean square errors (RMSE).

In the *EcoFish* model, all depth levels have a thickness of 5 meters. However, the ICES data had non-uniform sampling density in the water column (e.g., 0 m, 1 m, 2.5 m, 4 m, 5 m, 10 m, 20 m). This resulted in several ICES measurements that differed from each other but corresponded to the same *EcoFish* model value, or an ICES measurement was taken from a depth at the boundary of two adjacent model levels. This could cause unnatural distortion of the validation results. To eliminate the negative impact of the non-uniform data density, interpolation (and extrapolation) between *EcoFish* model levels with a step of 0.1 m was applied. Among the available methods of interpolation and extrapolation, the third-order simplified Hermite polynomial method (PCHIP) was chosen, which interpolates both the function and its first derivative.

3.1. Dissolved oxygen – O_2

Seasonal changes in water oxygenation are influenced by both climatic factors and primary production. Maximum concentrations of dissolved oxygen occur in the winter-spring season, with the combination of low water temperature and the beginning of the phytoplankton bloom period (Figure 2). The maximum monthly average concentration of dissolved oxygen in the surface layer of the *EcoFish* model (calculated for the entire domain area) occurred in March and April, and was $398.79 \text{ mmol m}^{-3}$ and $401.03 \text{ mmol m}^{-3}$, respectively. In the following months, as the temperature increases, the solubility decreases, and so the oxygen concentration in the water drops. However, there are areas where an increase in dissolved oxygen is noticeable as a result of intensive primary production. The minimum concentration of dissolved oxygen in the surface layer occurred in August with a mean value of $269.50 \text{ mmol m}^{-3}$. The average annual concentration of dissolved oxygen in the surface layer was $344.07 \text{ mmol m}^{-3}$ with a standard deviation of $40.33 \text{ mmol m}^{-3}$.

When examining the vertical profiles of mean monthly oxygen concentrations (Figure 3) at station P1 situated in the Gdańsk Deep area (Figure 1), it becomes apparent that there is a distinct variation as depth increases. In all months except summer months (May, June, July, and August), the

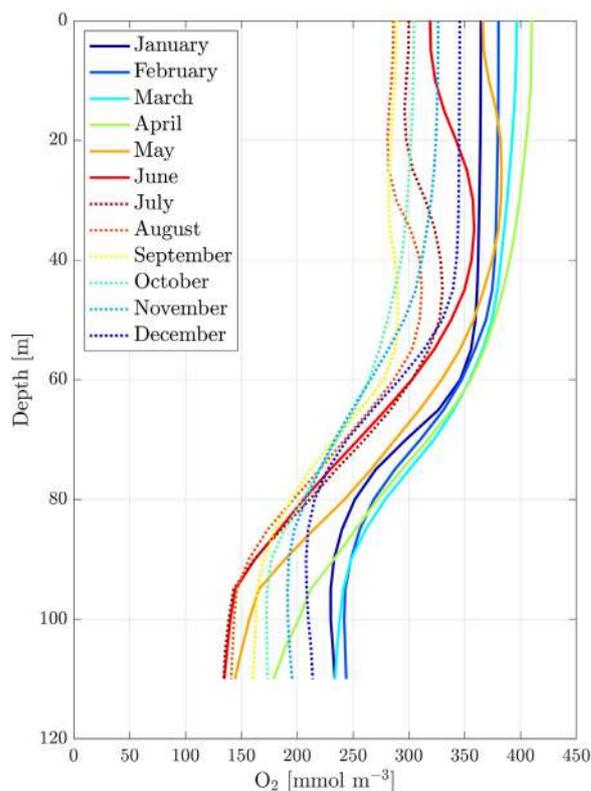


Figure 3 Vertical profiles of the mean monthly dissolved oxygen concentrations (O_2) for the period 2017–2020.

oxygen concentration remains constant (homogeneous) until a depth of approximately 40–50 meters. Then it begins to drop with increasing depth until it stabilizes at a depth of about 90 meters. In the winter months, this stable concentration at the greatest depths is higher (up to approximately 250 mmol m^{-3} in February). This is due to stronger vertical mixing, pushing the cold, oxygenated water from the surface to greater depths. In the summer, such strong vertical mixing does not occur, and the average oxygen concentration at greater depths drops to 150 mmol m^{-3} and below.

The concentration of dissolved oxygen is the most important modeled variable that needed to be verified for accu-

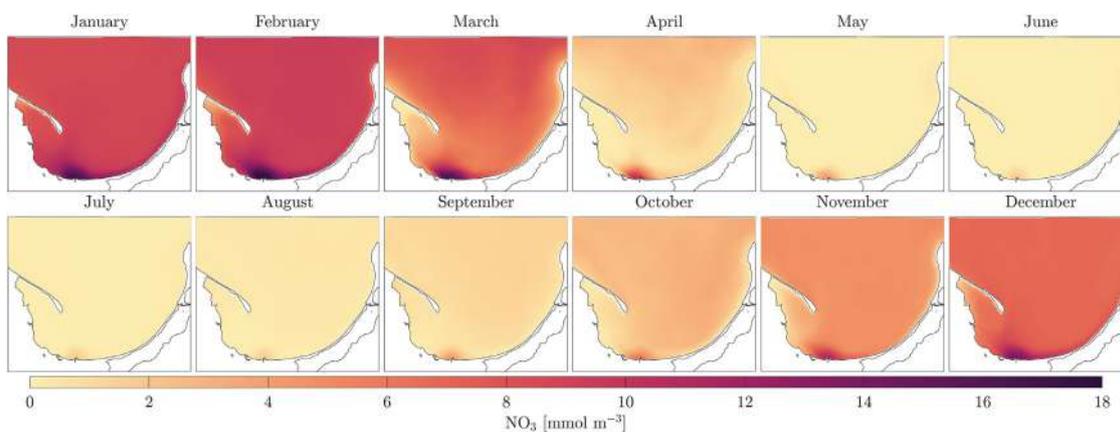


Figure 4 Average monthly concentrations of nitrates (NO_3) in the surface layer for the period 2017–2020.

racy. This is because it is used as an input parameter for the *Fish Module*. In the ICES database for the years 2017–2020, there were 3329 measurements available within the *EcoFish* model domain. After comparing ICES measurements with their corresponding values from the *EcoFish* model, a good reproduction of oxygen concentration variability was obtained for high O_2 concentrations. However, for measurements from great depths with concentrations dropping below 200 mmol m^{-3} the *EcoFish* model tended to slightly overestimate the results. The validation results for oxygen are presented in Table S1. Pearson's correlation coefficients ranged from 0.70 to 0.80 and RMSE from 61.14 to 86.85 mmol m^{-3} . For the entire period 2017–2020, a Pearson correlation coefficient of 0.75 and a root mean square error of 70.86 mmol m^{-3} were obtained.

3.2. Nitrates – NO_3

The highest concentrations of nitrates in the *EcoFish* model were observed in winter and early spring, before the start of the growing season. The lowest concentrations were observed in the summer months (Figure 4). The highest average monthly concentration of nitrates in the surface layer of the *EcoFish* model (calculated for the entire domain area) occurred in February (8.66 mmol m^{-3}), and the lowest in June (0.03 mmol m^{-3}).

By examining the vertical profiles of the nitrate concentrations at station P1 (Figure 5), we can observe that the highest amounts of this compound (concentrations greater than 9 mmol m^{-3}) accumulate at depths from 60 meters to the seabed. Nitrates are also present closer to the surface, but there is a clear seasonal variability associated with the intensity of primary production and phytoplankton blooms. Nitrates in the euphotic zone begin to decline in the spring due to diatom blooms, and subsequently decrease until July, when they are completely depleted in the layer to about 20 meters. In September, slow extraction of nitrates from deeper layers to the surface occurs because of fall storms, causing an increase in their concentrations. In October, due to low primary production, nitrate concentrations in the surface layer can reach values greater than 3 mmol m^{-3} . In the following months, nitrate concentrations on the surface gradually increase, reaching their maximum of around 9 mmol m^{-3} in January and February.

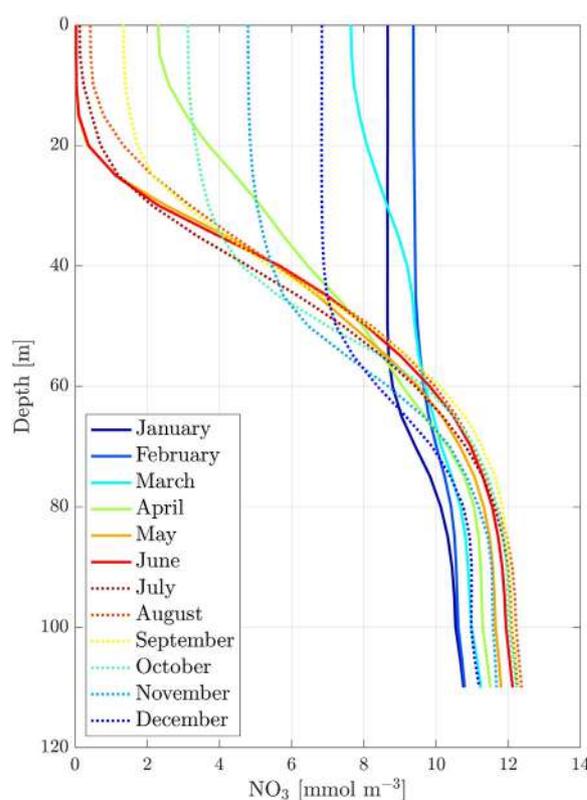


Figure 5 Vertical profiles of mean monthly concentrations of nitrates (NO_3) for the period 2017–2020.

In the ICES database for the years 2017–2020, there were 2370 nitrate concentration measurements available. After comparing the ICES measurements with their corresponding values from the *EcoFish* model, a moderately good representation of the dynamics of nitrate concentrations was obtained. This is because the ICES measurements came mainly from locations that are under strong pressure from the land, in the form of nutrient deposition from rivers flowing into the Puck Bay and Gulf of Gdańsk. The results of the nitrate validation are presented in Table S2. Pearson's correlation coefficients ranged from 0.40 to 0.59 and the root mean square errors ranged from 3.28 to 4.02 mmol m^{-3} . For the entire period 2017–2020, a Pearson correlation coefficient

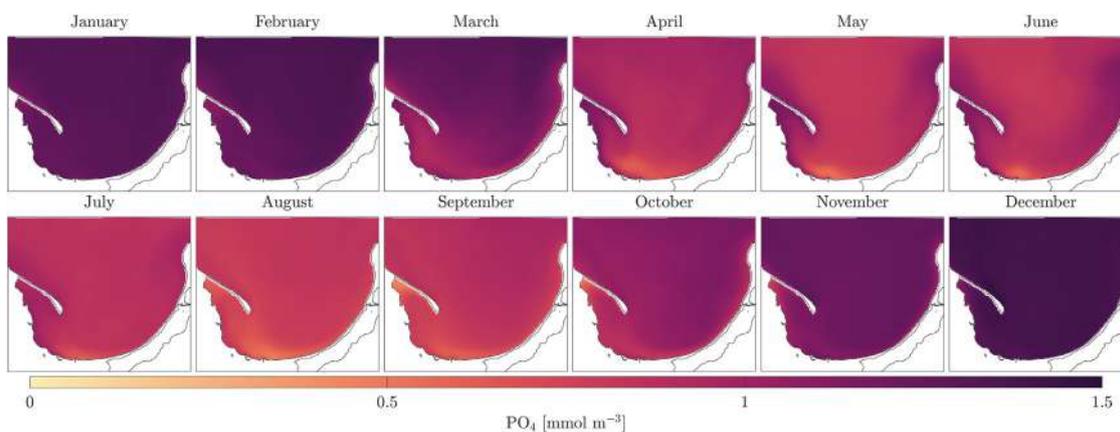


Figure 6 Average monthly concentrations of phosphates (PO_4) in the surface layer for the period 2017–2020.

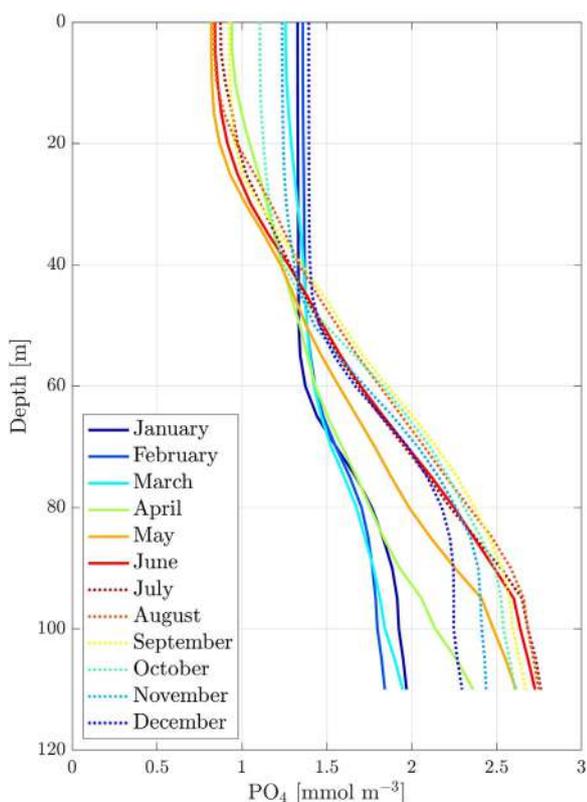


Figure 7 Vertical profiles of mean monthly concentrations of phosphates (PO_4) for the period 2017–2020.

of 0.46 and a mean squared error of 3.77 mmol m^{-3} were obtained.

3.3. Phosphates – PO_4

The highest average monthly concentration of phosphates in the surface layer of the *EcoFish* model (calculated for the entire domain area) occurred in December (1.34 mmol m^{-3}), while the lowest occurred in August (0.89 mmol m^{-3}) (Figure 6).

The vertical profiles of the monthly mean concentrations of phosphates at station P1 (Figure 7) have a similar char-

acter to that of nitrates. The largest amounts of this compound (concentrations of about 2 mmol m^{-3} and higher) also lie at great depths (below 60 meters). Variations in this parameter in the euphotic zone are related to primary production and the vegetative cycle of phytoplankton. Phosphorus is a limiting factor for the growth of all groups of phytoplankton, which means that it is consumed more or less intensively throughout the year.

The decrease in phosphate concentrations in the euphotic zone begins in March with the beginning of diatom blooms and lasts until August, when the highest intensity of primary production associated with cyanobacterial blooms occurs (caused by the highest water temperatures in the surface layer). From September, phosphate concentrations begin to systematically increase (as water temperature drops) until December, when they reach their maximum value for the whole year (approximately 1.4 mmol m^{-3}).

In the bottom layer, the situation is reversed. The highest concentrations occur in summer due to the settling of dead organic matter. There, as a result of the mineralization process, phosphorus is released back into the water column by microorganisms, leading to elevated concentrations. In winter months, because of vertical mixing, phosphate deposits are transported to the surface, replenishing the resources used after the vegetative period of phytoplankton.

In the ICES database for the years 2017–2020, there were 2592 phosphate concentration measurements available. After comparing the ICES measurements with the corresponding values from the *EcoFish* model, we observed that the model systematically overestimates phosphate concentrations. Despite this, high correlations were obtained in individual years, as well as acceptable RMSEs. The results of the phosphate validation are presented in Table S3. Pearson's correlation coefficients were in the range of 0.66 to 0.77, and the root mean squared errors ranged from 0.37 to 0.75 mmol m^{-3} . For the entire comparison period (2017–2020), we obtained a Pearson correlation coefficient of 0.65 and a root mean square error of 0.63 mmol m^{-3} .

3.4. Silicates – SiO_3

Nitrogen and phosphorus are the main factors that limit biological production, however, the primary production of diatoms is also limited by silicates. The *EcoFish* model shows

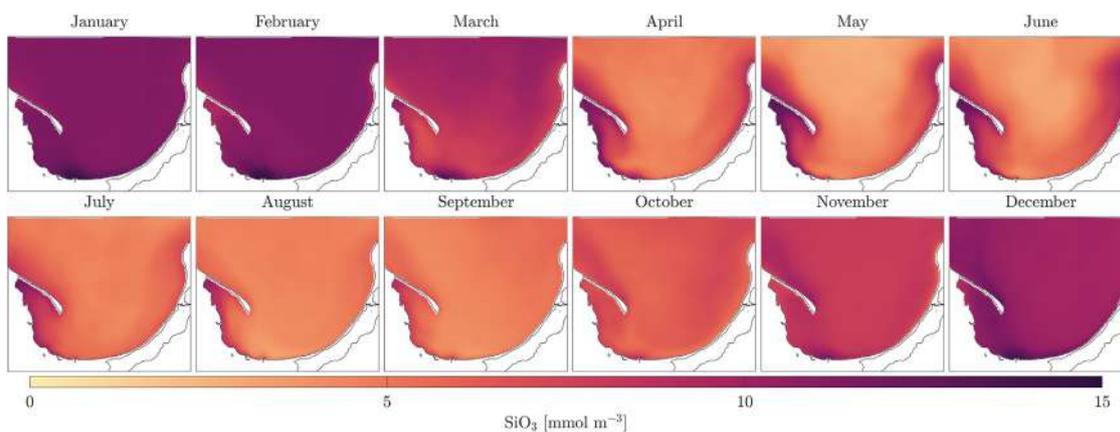


Figure 8 Average monthly concentrations of silicates (SiO_3) in the surface layer for the period 2017–2020.

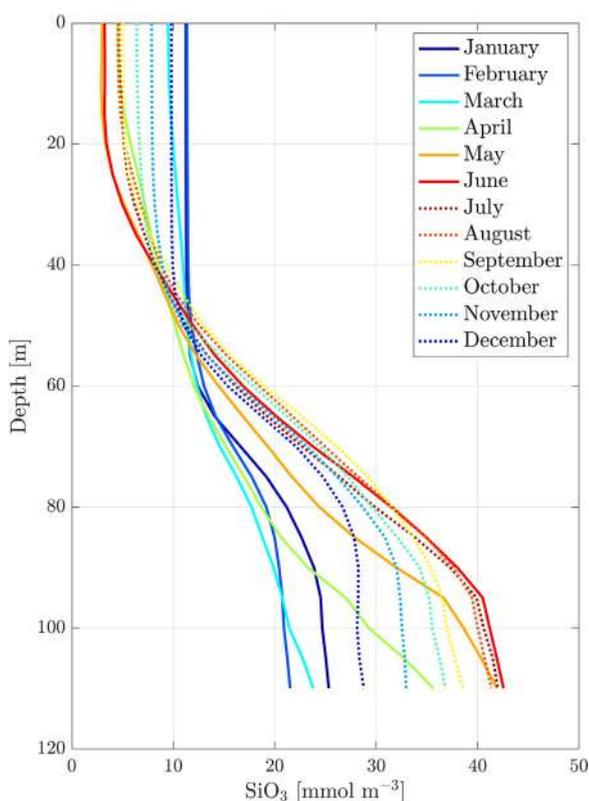


Figure 9 Vertical profiles of mean monthly concentrations of silicates (SiO_3) for the period 2017–2020.

the highest concentrations of silicates in winter and early spring, before the start of the growing season (Figure 8). In March, when intense spring diatom blooms begin, silicate concentrations begin to decrease and remain at lower levels until autumn. The highest average monthly concentrations of silicates in the surface layer occurred in February ($10.69 \text{ mmol m}^{-3}$) and January ($10.67 \text{ mmol m}^{-3}$), while the lowest occurred in May (6.49 mmol m^{-3}).

Analysis of vertical profiles of mean monthly silicate concentrations at station P1 reveals large differences between values at depths below 80 meters (Figure 9). Silicate concentrations from May to August are up to twice as high as concentrations in winter months (from December to March).

In the layer between 40 and 60 meters, silicates remain at similar levels (usually between 10 and 15 mmol m^{-3}) regardless of the month analyzed. In the euphotic layer, there is an inverse relationship compared to the bottom. Silicate concentrations are higher in the winter months, outside of the phytoplankton growing season. Lower values are observed from spring to fall and are closely related to their consumption in the primary production process to increase the biomass of diatoms.

In the ICES database for the years 2017–2020, there were 2610 silicate concentration measurements available. A comparison of *in situ* data from the ICES database with the corresponding values from the *EcoFish* model confirmed that the model performs well in reproducing the dynamics of silicate concentrations, although there is a noticeable tendency to underestimate the results, mainly for high SiO_3 concentrations above 40 mmol m^{-3} . The results of the silicate validation are presented in Table S4. Pearson correlation coefficients ranged from 0.51 to 0.74, and root mean square errors ranged from 7.45 to $12.58 \text{ mmol m}^{-3}$. For the entire comparison period (2017–2020), we obtained a Pearson correlation coefficient of 0.62 and a root mean square error of $10.32 \text{ mmol m}^{-3}$.

3.5. Chlorophyll *a*

In the *EcoFish* model, phytoplankton is divided into three groups. The first group represents nano- and pico-sized phytoplankton, whose growth is limited by nitrogen, phosphorus, temperature, and light. The second group represents large phytoplankton, mainly diatoms, whose production is limited by the same factors plus silica. The third group is cyanobacteria, which have the ability to fix nitrogen directly from the atmosphere and whose production is limited only by phosphorus, light, and temperature.

The highest concentrations of chlorophyll *a* are observed relatively close to the shore, where the access to nutrients is greatest due to the deposition of biogenic substances carried by rivers. The highest modeled monthly mean chlorophyll *a* concentration for the period 2017–2020 in the surface layer occurred in April and was 3.91 mg m^{-3} (Figure 10). The lowest concentrations were observed in the winter months, with a minimum of 0.29 mg m^{-3} (in December).

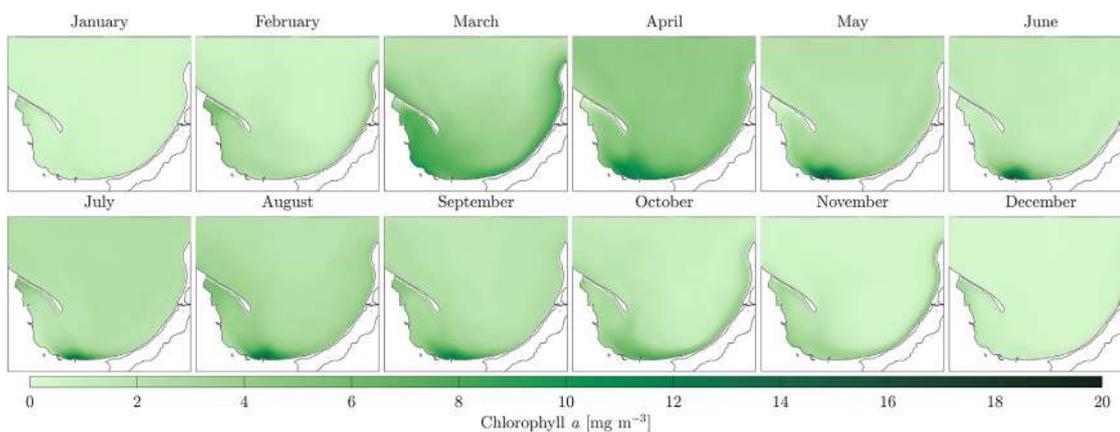


Figure 10 Average monthly concentrations of chlorophyll *a* in the surface layer for the period 2017–2020.

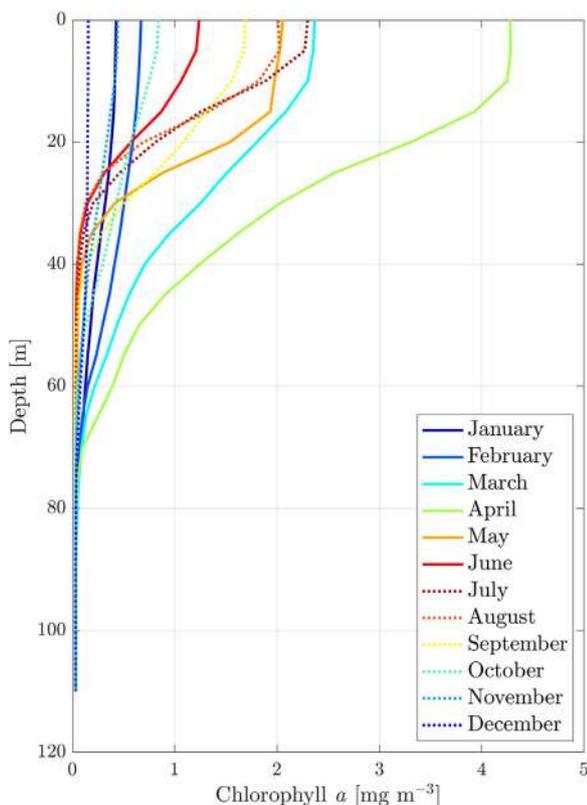


Figure 11 Vertical profiles of mean monthly concentrations of chlorophyll *a* for the period 2017–2020.

In vertical distribution, chlorophyll *a* concentrations reach their highest values in the upper layer of the water column. Then the concentration values decrease with depth. Below 60 meters deep, chlorophyll *a* occurs in negligible amounts or is not detected at all (Figure 11).

The highest chlorophyll *a* concentration values occur in spring (in April and March) when there is a maximum in phytoplankton biomass due to the spring diatom bloom and in July due to the growth of cyanobacteria. In months with primary production, concentrations rapidly decrease with depth. This is particularly visible in summer. There are no longer nitrates in the euphotic zone, and cyanobacteria grow only in the surface layer, where they are in direct contact with nitrogen fixed from the atmosphere.

In the ICES database for the years 2017–2020, only 972 chlorophyll *a* concentration measurements were available. Most of the measurements were taken in the area of Puck Bay and the southern part of the Gulf of Gdansk, close to the coast (Figure 1). After comparing the ICES measurements with the corresponding values from the *EcoFish* model, we obtained a moderately good representation of the chlorophyll *a* variability. The results of the chlorophyll *a* validation are presented in Table S5. Pearson's correlation coefficients ranged from 0.50 to 0.63, and root mean square errors ranged from 1.77 to 3.63 mg m^{-3} . For the entire comparison period (2017–2020), we obtained a Pearson correlation coefficient of 0.50 and a root mean square error of 2.77 mg m^{-3} .

3.6. Primary production

An important aspect studied in this article is primary production, which is a key function of marine ecosystems. Primary production is a process in which photosynthetic organisms, such as phytoplankton, use solar energy to produce organic compounds. In this way, primary production forms the basis for the entire marine food chain, providing energy and organic compounds for zooplankton and other marine organisms. Studying the seasonal variability of primary production in the Gulf of Gdansk is important to understand the impact of climate change and other factors on marine ecosystems and their ability to adapt to changing conditions.

Primary production in the water column was calculated for each of the modeled phytoplankton groups at three selected locations (Figure 1).

- PB1 – (54°43'N, 18°29'E) – the inner part of the Puck Bay, depth of about 10 m,
- ZN2 – (54°22'N, 18°57'E) – the mouth of the Vistula River, depth of about 20 m,
- P116 – (54°39'N, 19°17'E) – the central part of the Gulf of Gdansk, depth of about 90 m.

The location PB1 comes from a very shallow area (inner part of Puck Bay), which is geographically limited from the northeast by the Hel Peninsula and from the east by the Rybitwia Mielizna, effectively preventing the mixing of water from Puck Bay with both the open Baltic Sea and the

Outer Puck Bay. Six rivers flow into the inner part of Puck Bay (Zagórska Stream, Reda, Mrzezino Canal, Gizdepka, Żelistrzewo Canal and Płutnica), causing the PB1 station to be regularly supplied with moderate amounts of nutrients.

The ZN2 station is located in the shallow coastal part of the Gulf of Gdańsk, close to the mouth of the Vistula River. The Vistula is the largest river in the region and carries more than $1000 \text{ m}^3 \text{ s}^{-1}$ of freshwater on average, along with huge amounts of nutrients, strongly affecting the primary production of phytoplankton at this location.

The P116 station, with a depth of approximately 90 meters, is located in the open waters of the central part of the Gulf of Gdańsk. It is located far from the river mouths and is not geographically constrained by any factors.

The rate of primary production in the chosen locations was determined from the *EcoFish* model for a one-year period, from January 1 to December 31, 2021. Production values were calculated for the entire water column and compared with the limiting functions. The temperature of the water, the availability of light and the phosphates are limiting factors for the growth of all phytoplankton groups implemented in the *EcoFish* model. The growth of the group representing nano- and pico-sized phytoplankton is additionally limited by the availability of nitrates, while the growth of diatoms is additionally limited by the availability of nitrates and silicates.

The beginning of phytoplankton bloom in the first weeks of the year is primarily dependent on the amount of light available. At station PB1, the annual cycle of primary production begins in mid-February with a low intensity (up to $1000 \text{ mg C m}^{-2} \text{ d}^{-1}$) and a short-lived diatom bloom, which ends in the first days of March (Figure 12a). This is due to the shallow depth at this location. All available nitrogen in the water column is rapidly depleted and reaches zero values at the end of February (Figure 12d). As a result of such a short diatom bloom period, a very small amount of phosphate is consumed. It remains in the water column in large amounts until mid-June, when a bloom of cyanobacteria begins due to the appropriately high water temperature (Figure 12b). Due to favorable conditions (available light, high water temperature, and a large amount of phosphates), this process is very intense (more than $2000 \text{ mg C m}^{-2} \text{ d}^{-1}$) and lasts until mid-September, when it is stopped due to decreasing water temperature and replaced by a bloom of small phytoplankton (Figure 12c). The cycle of primary production at this station in 2021 slows down in the first days of November, which is due to a low amount of available light and a drop in the water temperature. The period of unfavorable conditions for phytoplankton bloom, which lasts until next spring, allows the replenishment of the nutrient fields (Figure 12d).

In the P116 station, the annual cycle of primary production (similar to the PB1 station) begins in mid-February. It is initiated by the appearance of appropriately strong light and favorable water temperature (Figure 13a). However, unlike station PB1, this bloom does not end in the first half of March due to the depletion of available nitrate. Station P116 is located at a great depth in the central part of the Gulf of Gdańsk. Because of the vertical mixing, nitrates are carried from greater depths toward the surface, sustaining the bloom of diatoms until mid-April. Then, the nitrate resources are depleted (Figure 13d), leading to a slowdown in production (around 200 to $300 \text{ mg C m}^{-2} \text{ d}^{-1}$), but not

enough to completely stop it (Figure 13a). Diatoms remain in the water column at a level of around 10 – 20 mmol C m^{-3} until the first days of July. In mid-July, a cyanobacterial bloom begins (Figure 13b). This is a month later than at the PB1 station (Figure 12b), which is a consequence of the lower water temperature in the open water. The shallow, enclosed coastal zone where station PB1 is located heats up much faster than the deep waters of the central part of the Gulf of Gdańsk. However, cyanobacterial production is not as intense as at station PB1. In addition to the lower water temperature, the decisive factor here may be a smaller amount of available phosphate (Figure 13d), which was partially consumed during the diatom bloom that began in mid-February. In 2021, small phytoplankton practically does not occur at this station (Figure 13c), which is also related to lower levels of phosphate in summer compared to the PB1 station and competition for access to nitrogen and phosphorus with diatoms.

At the ZN2 station located at the mouth of the Vistula River, the diatom bloom begins in a period similar to that of the other stations, i.e., in mid-February (Figure 14a). The highest intensity of diatom primary production occurs here in May and June, reaching rates of up to $4000 \text{ mg C m}^{-2} \text{ d}^{-1}$. In July 2021, diatom production is slowed and a very intense bloom of small phytoplankton begins, which lasts until the end of October, with peak production in August.

However, the cyanobacteria bloom has a completely different pattern than at the other stations. The station is located in a shallow coastal area, which means that the water temperature is high enough for the cyanobacterial blooms to start in mid-May (Figure 14b). However, cyanobacteria do not appear until the end of July, competing for phosphate with small phytoplankton (Figure 14c) that grow at the same time. This leads to a very low primary production rate associated with this species (below $1000 \text{ mg C m}^{-2} \text{ d}^{-1}$) causing suppression of cyanobacterial blooms. The production of cyanobacteria ends in October because the water temperature is too low.

It should be noted that station ZN2 is located at the mouth of the Vistula River. Nitrates and silicates do not deplete here after spring diatom bloom and are available throughout the year (Figure 14d). This is related to the massive deposition of nutrients from the Vistula.

4. Discussion

4.1. The *EcoFish* model evaluation

The article presents the biochemical component of the three-dimensional numerical model *EcoFish*, which was used to analyze the basic biochemical parameters that characterize the dynamics of the Gulf of Gdańsk ecosystem. To increase the accuracy of the results obtained in the *EcoFish* model, a module was implemented to assimilate satellite data for SST and chlorophyll *a*. The source of these data is the *SatBałtyk*³ system (Woźniak et al. 2011a,b).

Statistical validation of the *EcoFish* model, allowed us to verify the accuracy of the results in terms of the spatiotemporal variability of nitrate, phosphate, silicate, dis-

³ www.satbaltyk.pl.

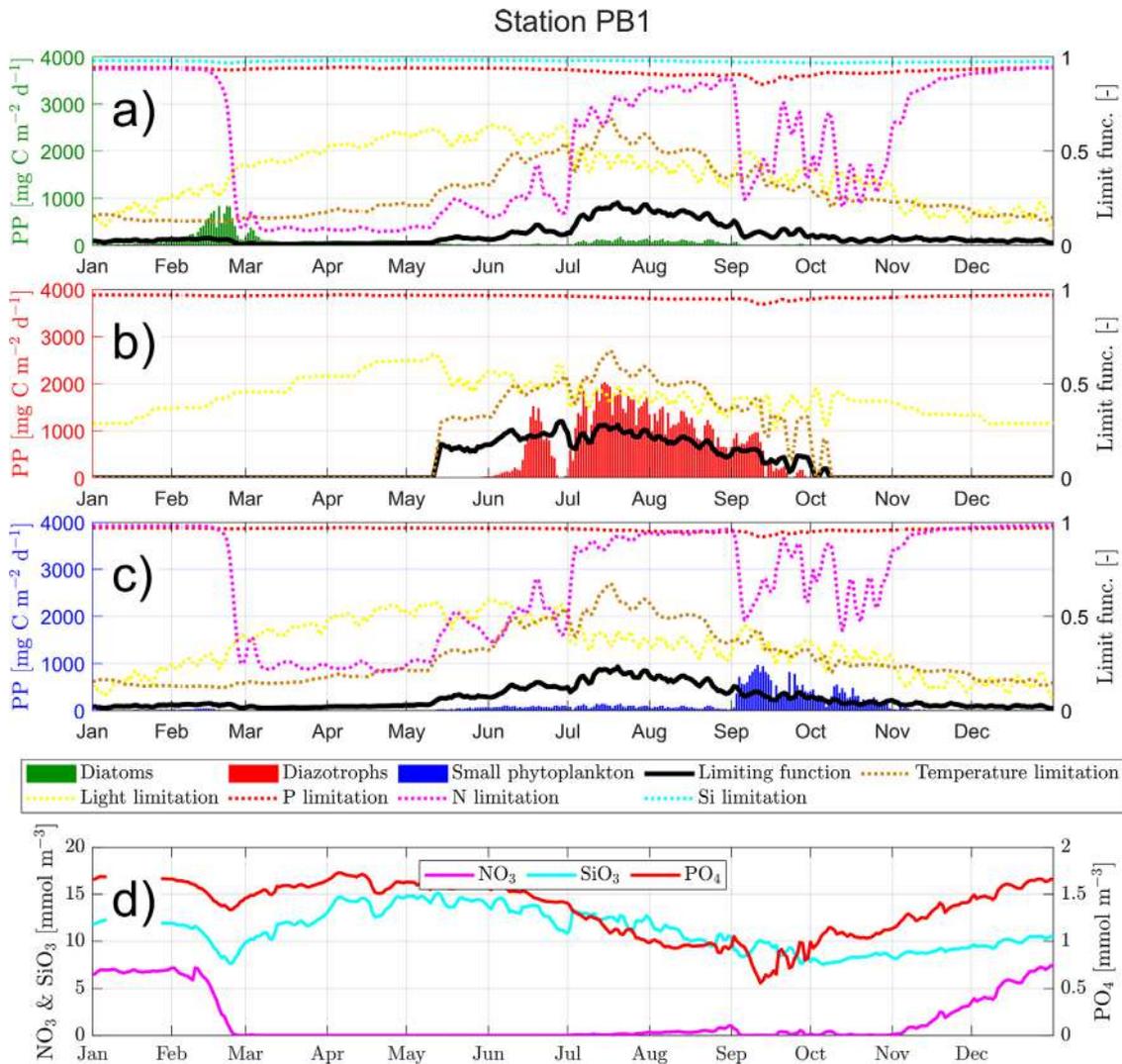


Figure 12 Primary production rate in 2021 for the entire water column at PB1 station for a) diatoms, b) cyanobacteria, and c) small phytoplankton, compiled with limiting factors, and d) concentrations of nutrients.

solved oxygen, and chlorophyll *a* concentrations. Validation was carried out using available *in situ* data from the ICES database for the period from January 1, 2017 to December 31, 2020, and basic statistical quantities were determined.

The *EcoFish* model tends to systematically overestimate (for oxygen, nitrates, and phosphates) and underestimate (for chlorophyll *a* and silicates) the results. However, these values are not significantly different from the measurement data and are acceptable after careful examination of the causes. The main reason for the lower correlations, especially in the validation of chlorophyll *a* and nitrates, is the specificity of the ICES experimental database itself. The map with the distribution of measurements for individual variables (Figure 1) shows that the vast majority of measurements come from shallow coastal areas with depths that generally do not exceed 30 meters. Approximately half of all measurements were taken within 2 km from the shore. Only a small number of points are located in the open sea or at greater depths. More open-water measurements can only be found in the ICES database for oxygen concentra-

tion, resulting in the highest correlation (0.75) between all biochemical variables we analyzed.

Another cause is the construction of the numerical model itself. The *EcoFish* model is a z-type model. It means that the model maintains the thickness of layers in a cell rather than the number of layers, in contrast to sigma-type models, where the same number of layers exists at each point, but they differ in their thickness. Z-type models are less capable of dealing with shallow water areas, where the water column often consists of only two or three layers. This configuration of the model, combined with the measurement database, where most measurements come from shallow coastal locations, negatively affects the validation results.

Worse results in the validation of nutrients may be related to inaccurate data for rivers (especially the Vistula) and the constant concentrations adopted for some rivers (according to Pastuszak et al., 2018). The volume of fresh water carried into the Gulf of Gdańsk by rivers was determined on the basis of long-term averages, which can result in insufficiently accurate deposition modeling, es-

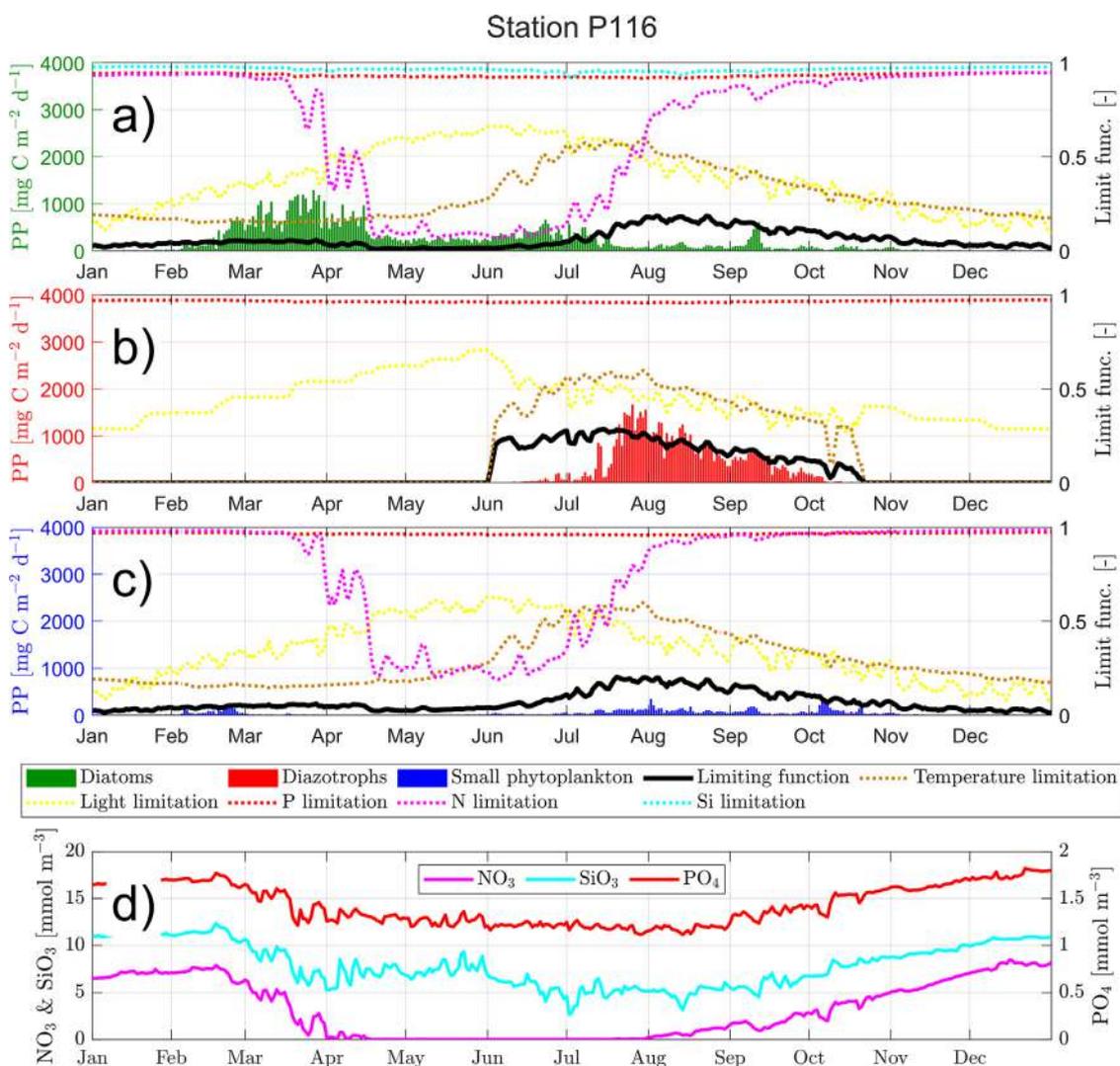


Figure 13 Primary production rate in 2021 for the entire water column at P116 station for a) diatoms, b) cyanobacteria, and c) small phytoplankton, compiled with limiting factors, and d) concentrations of nutrients.

pecially during periods of high daily variability. To ensure the numerical stability of the *EcoFish* model, large rivers were subjected to distribution, that is, the volume of fresh water along with the nutrients carried by them was divided into several model cells (several dozen for the Vistula).

4.2. Nutrients

The oxygen present in seawater primarily comes from photosynthesis and gas exchange with the atmosphere. However, when organic matter decomposes, oxygen is consumed, leading to potential deficits. In the central Baltic Sea, there are regular periods of stagnation in deep waters due to limited water exchange with the North Sea and consistent haline stratification (Conley et al., 2009, 2002; Meier et al., 2017). During these periods, nitrates are depleted, phosphates and ammonia concentrations increase, and dissolved oxygen levels decrease significantly at greater depths. Consequently, toxic hydrogen sulfide can emerge (Kuliński et al., 2022). The situation can improve temporar-

ily when salty and oxygen-rich waters from the North Sea enter the Baltic Sea. However, such strong inflows have become increasingly infrequent in recent times, with only a few events occurring every decade (Mohrholz, 2018). In the deep basins of the Baltic Sea (including the area of the Gdańsk Deep), hypoxia and anoxia have increased significantly over the past century (Carstensen et al., 2014), and in 2019, the area of hypoxia covered approximately 32% of the surface of the Baltic Proper (Hansson et al., 2019). Despite efforts made to substantially decrease nutrient deposition in the waters of the Baltic Sea over the past few decades, areas suffering from oxygen deficiency (mainly caused by eutrophication) have not experienced reoxygenation. This is because a considerable amount of nutrients has accumulated in the sediments and is gradually released into the water column, leading to prolonged oxygen depletion (McCrackin et al., 2018).

Nitrogen is one of the main limiting factors for primary production and an element causing eutrophication of the marine environment (Andersen et al., 2017; Malone and Newton, 2020). It is present in the water column in the form

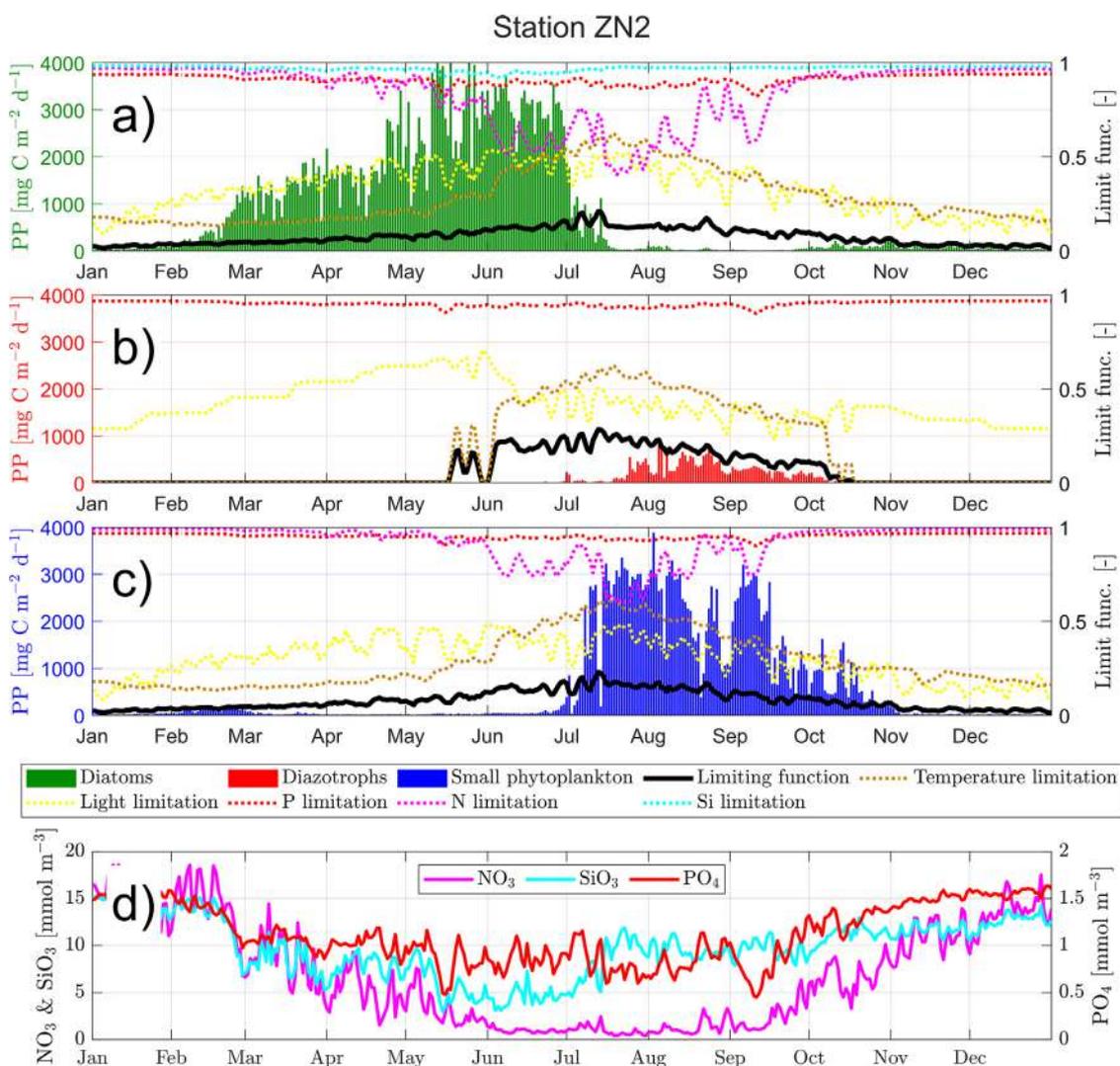


Figure 14 Primary production rate in 2021 for the entire water column at ZN2 station for a) diatoms, b) cyanobacteria, and c) small phytoplankton, compiled with limiting factors, and d) concentrations of nutrients.

of nitrates (NO_3), nitrites (NO_2) and ammonia (NH_4). Nitrogen concentrations in surface waters of the Gulf of Gdańsk vary spatially – higher concentrations occur at the mouth of the Vistula River, and lower in the central part of the Gulf. These compounds show a strongly marked seasonal cycle. The highest concentrations are recorded in early spring (March), when the melting waters of the Vistula River flow into the Gulf. Then, as a result of nitrogen consumption by phytoplankton and underwater plants, nitrogen compound concentrations decrease, eventually falling below the measurement capabilities of the methods used.

The basic difference between nitrogen and phosphorus is that the most plant-available forms (nitrates and nitrites) are not as easily regenerated as phosphates (Paytan and McLaughlin, 2007; Vitousek and Howarth, 1991). Therefore, practically every year from May to the end of September, seawater is devoid of nitrates and nitrites, which should limit the development of phytoplankton in summer. However, existing phosphate resources promote the development of Cyanobacteria, which can directly fixate nitrogen (N_2) from the atmosphere. Among them are species that

produce toxins, such as *Nodularia spumigena* and *Aphanizomenon flos-aquae*, which pose a potential threat to other organisms that live in the Gulf of Gdańsk and to the health and lives of people resting by the sea.

Phosphorus, along with nitrogen, is the main element that causes eutrophication of the marine environment (Tamminen and Andersen, 2007). Phosphates in the Gulf of Gdańsk exhibit a strong seasonal cycle, similar to that of nitrates. The highest concentrations of phosphates are recorded in winter and early spring, before the start of the growing season. Then, as a result of the consumption of phosphorus by phytoplankton and underwater vegetation, phosphate concentrations decrease to low levels but are not completely depleted, as is the case with nitrates. Phosphates are compounds with a short regeneration period, which means that they are easily and quickly released by microorganisms (bacteria) from dead organic matter (Paytan and McLaughlin, 2007). Therefore, shortly after the spring bloom, they appear in marine waters in amounts sufficient to provide a food base for species developing in the summer (e.g., cyanobacteria).

Although chlorophyll *a* concentration is not a direct measure of phytoplankton biomass, it is one of the parameters often used in oceanographic and limnological studies as an indicator of the quantitative presence of phytoplankton in water (Boyer et al., 2009; Gons et al., 2002; Randolph et al., 2008). The increase in phytoplankton biomass in the waters of the Gulf of Gdańsk has a seasonal cycle. The stages of phytoplankton development are similar throughout the area. The cycle begins in early spring (usually around February and March) with high nitrate concentrations and seawater temperatures of a few degrees Celsius. The rate of primary production is usually very high during this period. Due to the short life span of these microscopic plants and the high productivity of the euphotic layer, phytoplankton is the main source of energy for other components of the ecosystem (Mosharov et al., 2022). Some phytoplankton is directly consumed by herbivorous zooplankton, but a large amount of phytoplankton sinks to the bottom.

4.3. Primary production cycle

The analysis of primary production (for the year 2021) is presented in Results (see 3.6. Primary production). The results were compared with the limiting functions and concentrations of nitrates, phosphates, and silicates, which are the most important nutrients that limit the growth of phytoplankton.

As a result of this analysis, we confirm that in the first weeks of the year, the factors determining the beginning of the vegetation period are the availability of light and water temperature. At each of the three locations analyzed (PB1, P116, and ZN2), the first group that began the annual production cycle in mid-February 2021 was diatoms. However, the length and intensity of this bloom varied depending on the location. The diatoms bloomed for the shortest time (only until mid-March) at the PB1 station, where the available nitrate was rapidly depleted due to the shallow depth. The availability of nitrates also determined the end of the diatom bloom at station P116, but it lasted a bit longer, until mid-April. After the spring diatom bloom, there was a period without production (or with very low production) at these stations until the water temperature reached the optimal level for the start of cyanobacterial blooms (June/July). These species can directly fix atmospheric nitrogen, so their growth is not dependent on the availability of nitrates in the water column.

A completely different situation prevailed at the ZN2 station, where due to the continuous supply of nutrients (mostly nitrates and silicates) deposited with the Vistula waters, the diatoms grew very intensively until July. Due to this long growth period, diatoms consumed a very large amount of phosphorus and, despite its continuous supply by the Vistula, their level was lower than at the other stations, effectively suppressing the intensity and duration of toxic cyanobacterial blooms.

In the available scientific literature, many articles can be found that analyze primary production in the Gulf of Gdańsk (Mosharov et al., 2022; Ostrowska et al., 2022; Wasmund et al., 2001; Wittek et al., 1997; Zdun et al., 2021). In the study by Ostrowska et al. (2022), the total yearly primary production in the Gulf of Gdańsk (for the period 2010–2019) ranged from 124 to 145 g C m⁻² year⁻¹. The values we

obtained for the year 2021 were higher, reaching 160.1 g C m⁻² year⁻¹ at station P116, 168.2 g C m⁻² year⁻¹ at station PB1, and 553.1 g C m⁻² year⁻¹ at station ZN2.

The lowest monthly means of daily primary production occur in December, reaching 19.7 mg C m⁻² day⁻¹ at station P116, 25.9 mg C m⁻² day⁻¹ at station PB1 and 64.9 mg C m⁻² day⁻¹ at station ZN2. This result is consistent with previous studies for this region (e.g., Ostrowska et al., 2022; Zdun et al., 2021).

The highest monthly means of daily primary production occur during the summer months. At station P116, it was observed in August, with a value of 1021.6 mg C m⁻² day⁻¹. The highest average of 1690.1 mg C m⁻² day⁻¹ was recorded in July at station PB1. Station ZN2, on the other hand, exhibited the highest primary production in June, with a value of 3111.5 mg C m⁻² day⁻¹.

The maximum primary production in the Gulf of Gdańsk, as reported by Ostrowska et al. (2022), is most often observed in July and does not extend to August. The values obtained in that study range from 603 mg C m⁻² day⁻¹ in 2017 to 1066 mg C m⁻² day⁻¹ in 2010. Zdun et al. (2021), obtained the highest values in April and May, with primary production exceeding 2000 mg C m⁻² day⁻¹.

The beginning of the vegetation period, as reported by other studies (Ostrowska et al., 2022; Zdun et al., 2021), is also in good agreement with our results. Furthermore, our results agree with the experiment conducted by Sommer et al. (2012), where it was confirmed that light availability and temperature are the most important factors for the timing of the spring bloom.

5. Conclusions

The *EcoFish* numerical model is part of the *Knowledge transfer platform FindFISH* service, providing information on hydrodynamic and biochemical variables for the Gulf of Gdańsk area. Thanks to the numerical simulations from the *EcoFish* model and the results for temperature, salinity (presented in Janecki et al. 2021), and oxygen concentration, it is possible to operate the key element of the platform, the *Fish Module*. Using these variables and the applied fuzzy logic method, the *Fish Module* allows the creation of maps of the most favorable environmental conditions (Habitat Suitability Index) for the industrial fishing of herring, sprat, and flounder in the Gulf of Gdańsk area.

By presenting the most important biochemical variables of the *EcoFish* model and conducting the validation, we have confirmed that the results of numerical simulations are consistent with *in situ* data and will provide a reliable set of input data for the *Fish Module*.

In the analysis of primary production, we show that geomorphological conditions and the deposition of nutrients from rivers have a significant impact on its pattern and intensity. The availability of nutrients can significantly alter the biomass distribution of all phytoplankton groups.

An overly strong focus on limiting nitrate deposition in river waters to inhibit marine eutrophication may ultimately lead to the opposite situation, where short and weak diatom blooms in spring will be followed by long and intense cyanobacterial blooms in summer. This is consistent with the

results obtained from a numerical experiment conducted for Puck Bay by Dybowski et al. (2022). A reasonable approach to any legislative decisions in this regard is particularly important in the era of climate change and increasing water temperatures in seas and oceans, which will further prolong the period of optimal temperature for the bloom of this toxic and unwanted species from the perspective of the region's specificity.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.oceano.2023.05.001>.

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