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Biodiversity of benthic diatom flora in the coastal zone of Puck Bay (southern Baltic Sea): a case study of the Hel Peninsula

by

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Abstract

The paper presents the results of the analysis of diatoms from surface sediments (stones, sands) and macroflora (seagrass, macroalgae) collected at 16 sampling sites located along the inner coastal zone of Puck Bay (southern Baltic Sea) along the Hel Peninsula. The main diatom species of epilithon, epipsammon and epiphyton were characterized with respect to their autecological preferences (habitat, salinity, trophic status, saprobity). Three groups of diatoms were distinguished with respect to the type of substrate based on the results of benthic flora analysis: diatoms (i) of one type of substrate, (ii) of two types and (iii) those occurring on all types of substrates. Moreover, the distribution of benthic diatom communities indicates ecological differences in the study area. Marine and brackish-water species were observed in large numbers in the coastal zone of the Outer Puck Bay, whereas freshwater flora occurred with a higher frequency in the coastal zone of the Puck Lagoon. The content of polysaprobionts and of α-mesosaprobionts indicates that the region of the Hel Tip is highly eutrophicated and very polluted. The coast in the vicinity of Kuźnica is less polluted, whereas the best environmental conditions are found in the Jurata–Jastarnia region, as evidenced by the frequency of diatoms that are β-mesosaprobionts.

Key words: benthic diatoms, Baltic Sea, Puck Bay, Hel Peninsula, coastal zone, ecology, substrate

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Introduction

Research on the diatom flora preserved in the surface sediments of the Puck Bay region has a long tradition dating back to the interwar period of the 20th century. The pioneer of diatom studies in this region was Schulz (1926), who was the first to publish the list of diatom taxa occurring in the coastal zone. Results of long-term studies focusing on phytoplankton occurring in the euphotic zone and benthos living in the bottom of Puck Bay were published by Pliński (1975; 1982; 1987; 1990). Structural changes in phytoplankton observed in the Puck Lagoon, resulting from increasing eutrophication, were extensively discussed by Pliński (1979). This problem was addressed in many publications on diatom assemblages in Puck Bay (e.g. Pliński et al. 1982; Pliński et al. 1985). The effect of changes in the trophic status of Puck Bay on microphytobenthos was discussed by Fronczak and Pliński (1982) and Pliński and Florczyk (1984). Pliński and Kwiatkowski (1996) studied the relationship between the distribution of epipsammic diatoms and environmental conditions in the shallow littoral zone of the Polish coast, including Puck Bay. Moreover, this area was included in the studies focusing on the calibration of diatom species identified from the Baltic Sea (Snoeijs 1993; Snoeijs & Vilbaste 1994; Snoeijs & Potapova 1995; Snoeijs & Kasperovičienė 1996; Snoeijs & Balashova 1998). Intensive research by Witkowski (1990; 1991; 1994) resulted in significant advances in knowledge of diatom flora currently inhabiting the Puck Bay region. The problem of water pollution based on the benthic diatom community was discussed in detail by Bogaczewicz-Adamczak and Dziengo (2003). Recent research on the diatom flora in the western coastal zone of the Puck Lagoon showed that the abundance of teratological forms may indicate poor water quality (Dziengo-Czaja et al. 2008). The present-day diatom flora of the Puck Lagoon was also characterized by Witak (2001; 2002). Moreover, long-term research carried out in the Outer Puck Bay enabled a detailed description of the structure of planktic and benthic assemblages preserved in its bottom sediments (Witak et al. 2006; Witak & Dunder 2007; Leśniewska & Witak 2008; 2011; Witak 2010; Witak & Pędziński 2018; Pędziński & Witak 2019).

Despite many studies providing information on the relationship between the environmental status and diatom assemblages, our knowledge about effects of the type of substrate on the structure of the benthic diatom flora is still far from complete. The objectives of the present study were (i) to describe diatom communities collected in three types of substrates, i.e. stones, sands and macroflora (seagrass and macroalgae) with respect to floristic spectra and ecological groups, (ii) to compare diatom dominants and subdominants in epilithon, epipsammon, epiphyton and (iii) to determine ecological differences along the coastal zone of the Hel Peninsula in terms of the diversity of diatom floras.

Description of the study area

The Hel Peninsula, a unique form of the Polish coast, is a 36 km long sandy barrier in the western part of the Gulf of Gdańsk in the southern Baltic Sea. In general, the spit is low and relatively flat with visible geological and geomorphological contrasts. Its north-western part is very narrow (mostly up to 300 m wide) with an altitude of up to 5 m a.s.l. The relief is a consequence of strong erosion that started after the completion of the port of Władysławowo and the resulting interruption of the longshore transport of sediments on the Baltic side. This part stretches southward into the shallow Puck Lagoon (western part of Puck Bay), a relatively wide depression of the glacial or fluvioglacial basin filled with Holocene sediments. Genetically, the NW part of the Hel Peninsula is of continental origin, developed along with the adjacent land on the western side. Between Władysławowo and Kuźnica, the Pleistocene sediments are covered with the Lower Holocene organic deposits and a sandy layer deposited due to the Littorina transgression in the Atlantic chronozone. The Holocene deposits form a thin cover of 10 m thickness (Tomczak 1995).

On the other hand, the south-eastern part of the Hel Peninsula is much wider (1–3 km) with more varied relief due to intensive accumulation processes. It is a natural barrier partly separating the waters of the deeper Outer Puck Bay from the open sea. There are many NW–SE forms, including longitudinal embankments and low hills formed during the accretion and migration of the spit in the Middle and Late Holocene (Uścinowicz 2003). In the outer part of the peninsula, there is a well-developed range of dunes, usually more than 15 m high, with a maximum of 22 m. This part of the spit is known to have the maximum thickness of the Holocene sequence in Poland, reaching ca. 100 m. For this reason, numerous biostratigraphic surveys were performed in this area (e.g. Schulz 1926; Sandegren 1935; Bohr & Sokół 1972; Bogaczewicz-Adamczak 1982; Bogaczewicz-Adamczak & Żukowska 1990). The results of these surveys, including diatom analysis, provide a thorough description of the long-term spit development process in the last 11.7 cal. ka. Environmental changes in the successive stages of the Baltic Sea development, from the Yoldia Sea through the well-recorded Ancylus Lake and the Mastogloia Sea to the Littorina Sea, have been demonstrated. The paleoecology of the last stage, i.e. the Post-Littorina Sea near the Hel Tip was studied and discussed by Witak (2000).

Due to the genetic differences, the Puck Bay is divided by the sand barrier of the Seagull Reef into two parts, i.e. the shallow Puck Lagoon and the deeper Outer Puck Bay. Their hydrological regime is associated with the depth, climatic conditions and the inflow of saline waters from the Gulf of Gdańsk. Another important factor affecting the hydrology is the freshwater discharge from the surrounding coastal areas. The average salinity of the Puck Lagoon is 7.31 PSU (Nowacki 1993). The maximum salinity occurs in winter (ca. 7.80 PSU), whereas in spring it drops to its lowest value (7.0 PSU) due to the inflow of meltwater. The inflow of saline water from the outer part of Puck Bay through the Głębinka Strait and the Kuźnica Passage causes a slight increase in salinity to 7.4 PSU. The average annual salinity of the surface water in the Outer Puck Bay oscillates between 7.25 PSU in the vicinity of the Hel Peninsula tip and 7.21 near the port of Gdynia. The maximum salinity (7.67–7.94 PSU), resulting from the thermohaline convection and intensive wind mixing in the area, occurs in winter, while it drops to 6.70–6.90 PSU in spring. In summer, the surface water salinity ranged from 6.83 to 7.62 PSU.

The thermal state of both parts of Puck Bay is strongly affected by seasonal changes in air temperature. The mean annual water temperature of the western part is 9.55°C (Nowacki 1993). The waters of Puck Bay are coldest in February (1.52°C), whereas the maximum temperature is recorded in August (19.3°C). The average annual temperature of open waters in Puck Bay is 9.13°C and in the coastal zone – 8.7°C. The minimum average monthly temperature of 1.29°C is recorded in February. Higher temperatures are recorded around the tip of the Hel Peninsula due to the inflow of warmer seawater. In spring, an increase in the surface water temperature from 4.5 to 12.4°C is observed. In the summer period, the temperature rises to between 16.7 and 18.6°C.

Both natural and anthropogenic factors affect the trophic status of Puck Bay (Bolałek et al. 1993). Two natural factors can be attributed to i.a. assimilation and remineralization of nitrogen and phosphorus compounds, as well as saline water inflows from the open sea. Nutrients of anthropogenic origin are supplied by riverine runoff, mostly by the Vistula River in the Outer Puck Bay and by the Reda River in the Puck Lagoon (Kruk-Dowgiałło & Szaniawska 2008). Another important source of biogenic substances is the atmospheric precipitation in the form of rain and aerosols (Trzosińska 1990; Bolałek et al. 1993). Moreover, the supplier of N and P in the Puck Bay is a collector of the sewage treatment plant in Dębogórze (Kruk-Dowgiałło & Szaniawska 2008). Due to the growing season, concentrations of nitrates and phosphates in the euphotic layer decrease from April onwards. In September and October, phosphates have a very low value of 0.97 μmol dm^{-3}, whereas nitrates and nitrites together – 3.87 μmol dm^{-3} (Bolałek et al. 1993). Concentrations of biogenic substances increase again from October to March and reach values of 2.02 μmol dm^{-3} and 8.32 μmol dm^{-3}, respectively.

Hydrodynamic and hydrochemical factors affect the development of submerged macroflora in Puck Bay. Due to relatively poor hydrodynamic conditions in the Puck Lagoon, its bottom is almost completely covered with macrophytes. However, the Outer Puck Bay with stronger hydrodynamic conditions does not favor the growth of macrophytes, which are limited to a depth of 6 m (Pliński & Florczyk 1993). Macroalgae developing on stones along the coastline up to a depth of 2 m play a key role among submerged plants. They are dominated by green algae represented by 17 taxa (Pliński & Florczyk 1993). In addition, several taxa belonging to red algae were also found in this zone. Brown algae are represented only by the unattached species *Pilayella litoralis* (Linnaeus) Kjellman, easily drifting under the influence of currents and waves. Vascular plants with the dominant species *Ruppia rostellata* W.D.J. Koch ex Rchb. are also an important component of the macroflora occurring in the shallows. Of these, only the seagrass *Zostera marina* Linnaeus was observed more frequently at depths below 2 m (Pliński & Florczyk 1993).

The distribution of bottom sediments in Puck Bay is determined by its morphology. The deeper part of the Outer Puck Bay as well as the local depressions of the Puck Lagoon are filled mostly with muddy sediments (Kramarska 1995). However, the seabed of the Rzucewo Deep consists of biogenic deposits, i.e. calcareous gyttja in its north-central part and peat in the southern part. The coastal zone is covered with sandy sediments. The coarse-grained material originating from the erosion of the Pleistocene morainic plateau occurs sporadically and is accumulated under the cliffs. However, the bottom sediments of the central part of the Puck Lagoon as well as the coastal zone of the Outer Puck Bay are composed of fine-grained sands. Moreover, the medium-grained sand occurs along the inner coast of the Hel Peninsula and the northern part of the Puck Lagoon.

Materials and methods

The analyzed material consisted of surface sediments (stones, sands) and macroflora (seagrass, macroalgae) collected in October 2014 from 16 sampling sites located along the inner coastal zone of the Hel Peninsula (Fig. 1). Nine sites were located along the coast of the Outer Puck Bay, including four sites at the Hel Tip (HP1–4/1014) and another five (HP5–9/1014) in the vicinity of Jurata and Jastarnia. Seven sites (HP10–16/1014) were located in the coastal zone of the Puck Lagoon between Kuźnica and Chałupy. Epipsammon and epiphyton were collected from seagrasses at all sites (Table 1). Five samples of macroalgae were collected in different parts of the study area, including Hel, Jastarnia and Chałupy. Moreover, epilithon developed on rocks was collected at 11 sites.

Samples for the diatom analysis (ca. 0.5–1 g of dry sediment) were prepared following the standard procedure for the observation of diatoms under a light microscope (Battarbee 1986). Qualitative diatom analysis was performed on samples collected from all habitats. Diatom samples from sediments were treated with 10% HCl to remove calcium carbonate. The organic matter in all samples was digested using 30% H_2O_2, after which the mineral matter was removed by decantation. In addition, quantitative analysis was carried out on sediment samples. To estimate the concentration of siliceous diatom valves per unit weight of dry sediment (absolute abundance), the random settling technique was used (Bodén 1991). Permanent diatom preparations were mounted in Naphrax® (refractive index n_D = 1.73). The analysis was performed under a NIKON microscope, using the 100 × oil immersion objective. The counting method of Schrader and Gersonde (1978) was used and from 500 to 800 valves were counted in each sample to estimate the percentage abundance of individual taxa. The raw counts were converted into relative abundance

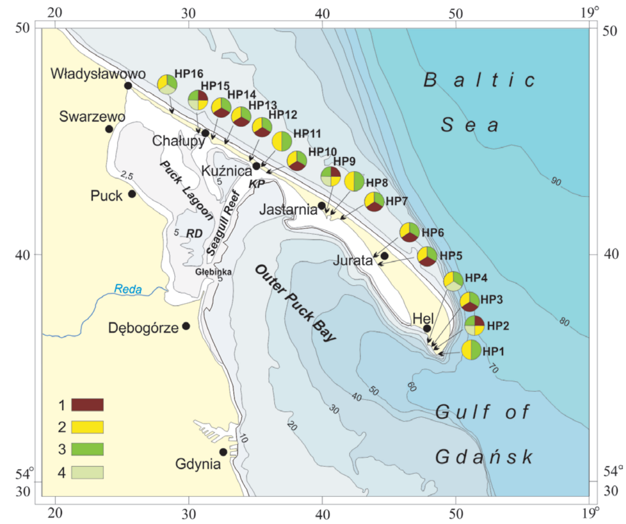

Figure 1

Location of the sampling sites in the Hel Peninsula; 1 – stones, 2 – sands, 3 – seagrass, 4 – macroalgae, RD – Rzucewo Deep, KP – Kuźnica Passage

Table 1

Parameters of the analyzed samples

Samples	φ	λ	Location	Type of substrate			
				sediments		macroflora	
				stones	sand	seagrass	macroalgae
HP1/1014	54°35′34.2″N	18°48′38.8″E	Hel		✓	✓	
HP2/1014	54°35′39.3″N	18°48′35.7″E	Hel	✓	✓	✓	✓
HP3/1014	54°35′41.2″N	18°48′30.6″E	Hel	✓	✓	✓	
HP4/1014	54°36′22.7″N	18°47′59.6″E	Hel		✓	✓	✓
HP5/1014	54°40′51.98″N	18°42′29.48″E	Jurata	✓	✓	✓	
HP6/1014	54°40′56.3″N	18°42′36.4″E	Jurata	✓	✓	✓	
HP7/1014	54°41′38.6″N	18°40′21.1″E	Jastarnia	✓	✓	✓	
HP8/1014	54°41′45.5″N	18°40′13.8″E	Jastarnia		✓	✓	
HP9/1014	54°47′10.4″N	18°25′18.3″E	Jastarnia	✓	✓	✓	✓
HP10/1014	54°41′05.4″N	18°40′13.3″E	Kuźnica	✓	✓	✓	
HP11/1014	54°44′01.2″N	18°35′13.2″E	Kuźnica		✓	✓	
HP12/1014	54°44′13.3″N	18°34′42.7″E	Kuźnica	✓	✓	✓	
HP13/1014	54°44′52.1″N	18°32′47.1″E	Chałupy	✓	✓	✓	
HP14/1014	54°45′30.3″N	18°30′59.1″E	Chałupy	✓	✓	✓	
HP15/1014	54°45′40.6″N	18°30′24.1″E	Chałupy	✓	✓	✓	✓
HP16/1014	54°46′29.9″N	18°27′56.5″E	Chałupy		✓	✓	✓

of all frustules counted. Diatoms were grouped according to their ecological (habitat, salinity, trophic and saprobic status) requirements. The classification of autecological preferences is shown in Table 2. The percentage content of all ecological groups was estimated in each sample.

Taxonomy and ecological information was primarily based on Hustedt (1927–1966), Krammer and Lange-Bertalot (1986; 1988; 1991a; 1991b), Pankow (1990), Denys (1991), Vos and de Wolf (1993), van Dam et al. (1994), Witkowski et. al. (2000) and Lange-Bertalot (2001). In addition, autecological preferences of all identified taxa were complemented based on the OMNIDIA 6.08 software. In the case of some marine and brackish-water species, i.e. *Denticula creticola* (Østrup) Lange-Bertalot & Krammer, *Fallacia clepsidroides* Witkowski, *Gomphonemopsis obscura* (Krasske) Lange-Bertalot, *Mastogloia pumila* (Grunow) Cleve, *M. smithii* Thwaites ex W. Smith and *Navicula paul-schulzii* Witkowski & Lange-Bertalot, trophic and saprobic preferences are irrelevant. To avoid accidental presence, only species with a frequency of more than 3% in at least one sample were selected for diatom diagrams using Tilia version 2.0.37 (Grimm 2011).

Results

The diatom analysis indicates that the diatom flora observed on all types of substrates was generally well preserved, particularly on plants. Benthic diatoms observed in sandy sediments were slightly less preserved and contained some broken valves. A total of 133 species, subspecies, varieties and forms belonging to 43 genera were identified in the material studied (Table 3). However, the results show some differences in the number of identified taxa, depending on the type of substrate. The highest

Table 2

Classification of the diatom flora according to autecological preferences

Habitat:	Salinity:
planktic – living in the water column	**euhalobous** – marine species with the optimum at salinity of 30–40 PSU
benthic – developing on any type of substrate:	**mesohalobous** – brackish-water species living at salinity of 5–20 PSU
epilithon – growing on stones	**oligohalobous** – species living in fresh water:
epiphyton – growing on plants	**halophilous** – reaching the optimum at salinity < 5 PSU
epipsammon – growing on sands	**indifferent** – euryhaline forms tolerating a low content of salts
	halophobous – stenohaline forms that do not tolerate even the lowest salinity
Trophic status:	**Saprobity:**
eutraphentic – living in very fertile water	**polysaprobous** – living in heavily polluted water
eu-mesotraphentic – living in fertile water	**α-mesosaprobous** – living in moderately polluted water
mesotraphentic – living in water of moderate fertility	**α-β-mesosaprobous** – living in intermediate conditions between α- and β-mesosaprobity
meso-oligotraphentic – living in relatively nutrient-poor water	**β-mesosaprobous** – living in less polluted water
oligotraphentic – living in nutrient-poor water	**oligosaprobous** – living in low polluted water
eu-dystraphentic – diatoms with high nutrient tolerance	**xenosaprobous** – living in clean water

Table 3

The number of diatom taxa (species, subspecies, varieties, forms) vs ecological preferences

	Salinity*				Trophic status**						Saprobity***							Total
	eh	mh	oh	oi	et	emt	mt	ot	edt	ir	ps	ams	abms	bms	os	x	ir	
Epilithon	8	27	16	21	35	10	2	5	1	19	2	17	3	24	4	-	22	72
Epipsammon	12	36	17	25	39	13	4	8	1	25	2	13	4	26	8	1	36	90
Epiphyton	13	33	17	22	33	8	4	7	2	31	2	16	3	22	2	1	39	85
Total	19	50	24	40	51	17	7	12	2	44	2	21	5	36	13	1	55	133

* eh – euhalobous, mh – mesohalobous, oh – oligohalobous halophilous, oi – oligohalobous indifferent
**et – eutraphentic, emt – eu-mesotraphentic, mt – mesotraphentic, ot – oligotraphentic, edt – eu-dystraphentic, ir – irrelevant
***ps – polysaprobous, ams – α-mesosaprobous, abms – α-β-mesosaprobous, bms – β-mesosaprobous, os – oligosaprobous, x – xenosaprobous, ir – irrelevant

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diversity was observed in the diatom flora occurring in sandy sediments (90 species and 38 genera). In the epiphyton, 38 genera represented by 85 species were identified. The lowest number of taxa was observed in the epilithon. In this group, 72 species, subspecies and variates belonging to 37 genera were identified. Groups of mesohalobous eutraphentic diatoms were most varied (27–36 and 33–39 taxa, respectively) on all types of substrates. In terms of saprobic preferences, the group of β-mesosaprobic forms was most diverse, represented by 22–26 species.

Epilithon

The epilithic assemblage of the Hel Peninsula was dominated by diatoms preferring higher concentrations of nutrients and organic matter (Fig. 2). The frequency of the eutraphentic group usually exceeded 60%, with *Nitzschia frustulum* (Kützing) Grunow being the most important component (Fig. 3). This β-mesosaprobiont occurred abundantly at one of the sites in Chałupy (HP13/1014, ca. 80%), while was very rare in the town of Hel (HP3/1014, ca. 2%). At the latter site, *Diatoma moniliformis* (Kützing) D.M. Williams was regularly observed. Both species are known as oligohalobous halophilous, with the former being a β-mesosaprobiont and the latter being a β-meso-oligosaprobiont. They were accompanied by the marine species *Opephora krumbeinii* Witkowski, Witak & Stachura and the brackish-water species *Gedaniella mutabilis* (Grunow) Li & Witkowski. Less frequent were α-mesosaprobionts: *Gedaniella flavovirens* (Takano) Li, Witkowski & Ashworth, *Halamphora coffeaeformis* (C. Agardh) Levkov, *Rhoicosphaenia abbreviata* (C. Agardh) Lange-Bertalot, and *Planothidium delicatulum* (Kützing) Round & Bukhtiyarova representing β-mesosaprobionts. The eu-mesotraphentic group occurred very rarely and was usually represented by *Cocconeis placentula* var. *placentula* Ehrenberg occurring at only one site in Jastarnia (HP9/1014). In the eastern part of the Hel Peninsula, at the Hel sites (HP2–3/1014) and in Jurata (HP5/1014), mesotraphentic diatoms were observed frequently. At these sites, *Navicula perminuta* Grunow in Van Heurck, considered to be mesohalobous, tolerant of higher concentrations of organic matter and pollution, occurred regularly. *Denticula creticola* – a species preferring higher salinity – was observed with high frequency in the town of Hel (HP2/1014).

Epipsammon

The results of the quantitative analysis indicate considerable differences in the concentration of diatom valves in sandy sediments (Fig. 2). The lowest concentration was observed at the Hel Tip. At sites HP1–4/1014, the values ranged from 1.2 to 4.2 × 10^6 valves g^{-1}. In the vicinity of Jurata (HP6/1014), the concentration of valves increased to 28 × 10^6 valves g^{-1}. The value decreased from 18 to 10 × 10^6 valves g^{-1} at the Jastarnia sites (HP7–8/1014). Along the coast of the Puck Lagoon, diatoms occurred mostly with higher abundance in sediments. The highest concentrations were observed at two sites in Kuźnica, i.e. HP10/1014 (42 × 10^6 valves g^{-1}) and HP13/1014 (60 x 10^6 valves/g).

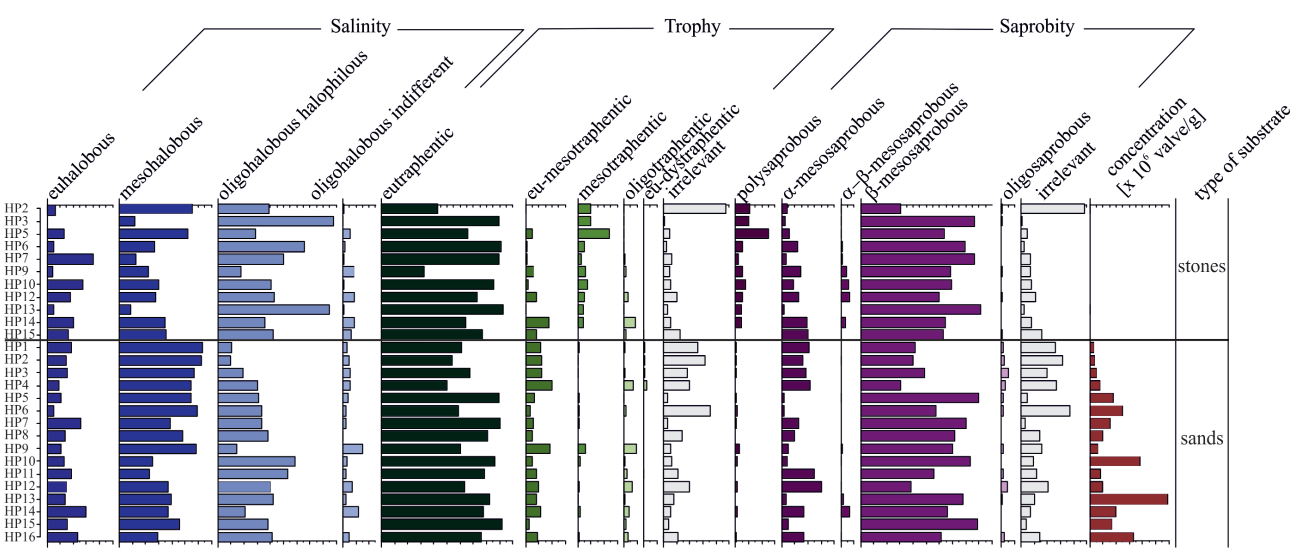

Figure 2

Percentage content of the diatom ecological groups in epilithon and epipsammon

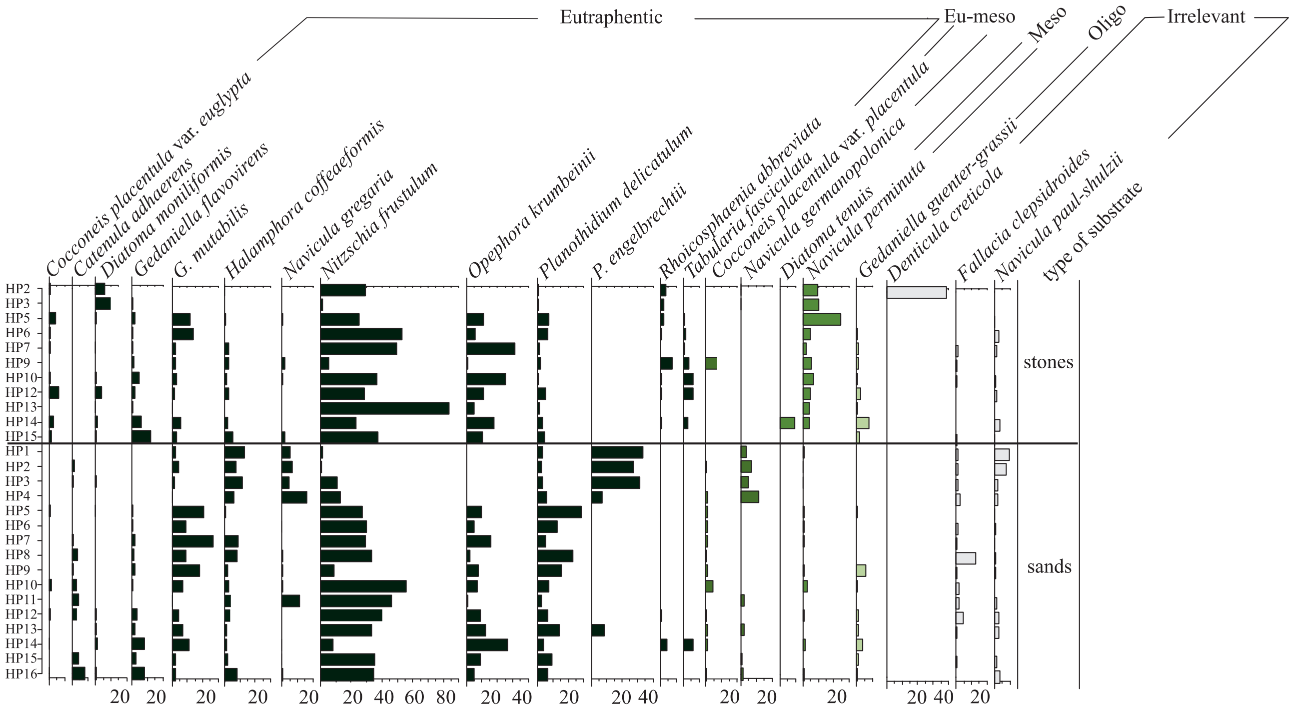

Figure 3

Frequency of the main diatom taxa in epilithon and epipsammon; eu-meso – eu-mesotraphentic, meso – mesotraphentic, oligo – oligotraphentic

In the western part of the study area, the concentrations were lower and reached 36 × 10^6 valves g^{-1} at HP16/1014 and 19 × 10^6 valves g^{-1} at HP15/1014.

The results of the taxonomic analysis show that the epipsammon of the Hel Peninsula was characterized by abundant occurrence of eutraphentic taxa and β-mesosaprobionts (Fig. 2). In sandy sediments, between Chałupy and Jurata (HP5–16/1014), *Nitzschia frustulum, Opephora krumbeinii, Gedaniella mutabilis* and *Planothidium delicatulum* dominated (Fig. 3). Other diatoms, i.e. *Catenula adhaerens* Mereschkovsky, *Gedaniella flavovirens, Rhoicosphaenia abbreviata, Tabularia fasciculata* (C. Agardh) D.M. Williams & Round were observed sporadically. However, the assemblage at the Hel Tip (HP1–4/1014) was represented by α-mesosaprobionts – *Halamphora coffeaeformis* and *Navicula gregaria* Donkin, and the β-mesosaprobiont *Planothidium engelbrechtii* (Cholnoky) Round & Bukhtiyarova. The latter species was also found at one site near Chałupy (HP13/1014). In the region of the Hel Tip (HP1–4/1014), the mesohalobous species *Navicula germanopolonica* Witkowski & Lange-Bertalot, tolerant of higher concentrations of biogenic salts, was observed regularly. In the inner coast of the Hel Peninsula, two species with indifferent trophic and saprobic preferences, i.e. *Fallacia clepsidroides* and *Navicula paul-schulzii* were found. The former species was recorded with a higher frequency in Jastarnia (HP8/1014), whereas the latter – near the town of Hel (HP1-2/1014).

Epiphyton

In general, epiphytic diatoms recorded in the study area belong mainly to eutraphentic forms and β-mesosaprobionts (Fig. 4). The main components of the diatom flora occurring on seagrasses of the eastern part of the Hel Peninsula (HP1–4/1014) were *Rhoicosphaenia abbreviata, Cocconeis pediculus* Ehrenberg, *C. placentula* var. *euglypta* (Ehrenberg) Grunow, *C. scutellum* var. *scutellum* Ehrenberg and *Diatoma moniliformis* (Fig. 5). These species show different salinity preferences, however, they developed well in moderately/slightly polluted waters with decaying organic matter. At site HP1/1014, the α-β-mesosaprobiont *Tabularia fasciculata* occurred with abundance of ca. 40%. All these taxa occur on macroalgae, but mostly with a relatively low frequency, except for *Rhoicosphaenia abbreviata*, the content of which exceeded ca. 30%. Along the coast between Jurata and Kuźnica (HP5–9/1014) as well as in the vicinity of Chałupy (HP15–16/1014), *Nitzschia frustulum*, *Opephora krumbeinii*, *Gedaniella mutabilis* and *Planothidium delicatulum* were observed

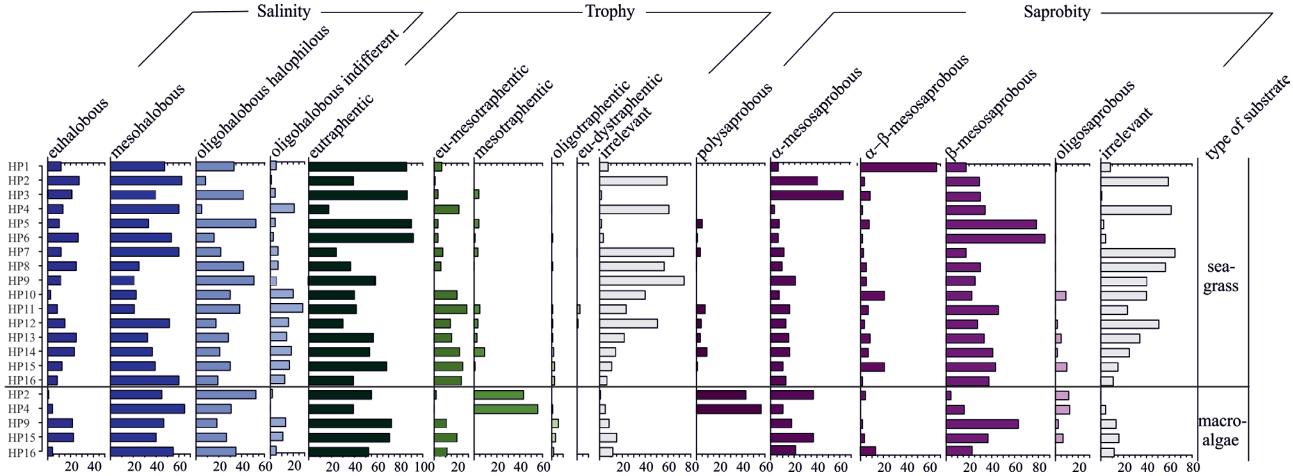

Figure 4

Percentage content of diatom ecological groups in epiphyton (seagrass and macroalgae)

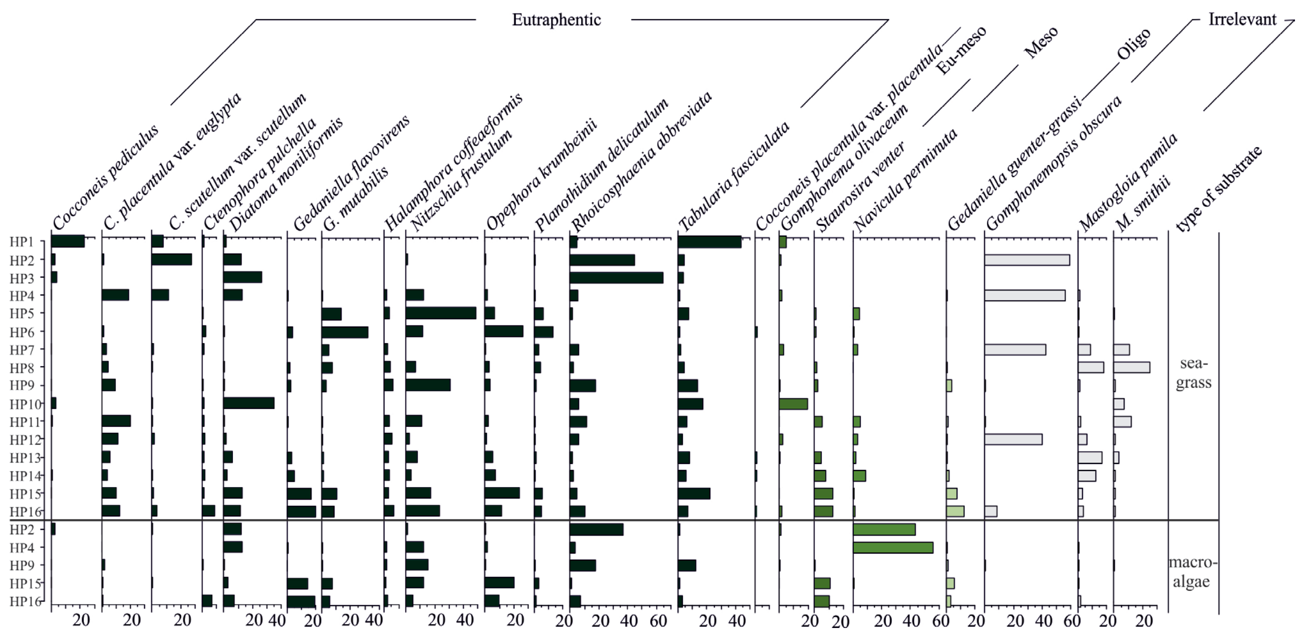

Figure 5

Frequency of the main diatom taxa in epiphyton (seagrass and macroalgae); eu-meso – eu-mesotraphentic, meso – mesotraphentic, oligo – oligotraphentic

on seagrasses with a relatively high frequency. In addition, in the Chałupy area, the diatom flora of seagrasses was represented by *Diatoma moniliformis*, *Gedaniella flavovirens* and *Tabularia fasciculata*. They were also observed on macroalgae in this part of the Hel Peninsula. In the diatom community recorded on seagrasses in the regions of Kuźnica and Chałupy (HP10–16/1014), *C. placentula* var. *euglypta* and *Rhoicosphaenia abbreviata* were abundant. The content of *Diatoma moniliformis* was high only at HP10/1014, where it exceeded ca. 35%. The eu-mesotraphentic species *Gomphonema olivaceum* (Hornemann) Ehrenberg and *Staurosira venter* (Ehrenberg) Cleve & Möller were recorded at almost all sites. The polysaprobiont *Navicula perminuta* was abundant on macroalgae collected at the town of Hel (HP2,4/1014). Moreover, the brackish-water species *Gomphonemopsis obscura* was observed on seagrasses, particularly abundantly at Hel (HP2,4/1014), Jastarnia (HP7/1014) and Kuźnica (HP12/1014), with a frequency exceeding 40%. Between Jurata and Chałupy (HP7–16/1014), the marine form of *Mastogloia* *pumila* and the halophilous form of *M. smithii* were also observed. *C. placentula* var. *placentula* and *Ctenophora pulchella* (Ralfs ex Kützing) D.M. Williams & Round were rare in the epiphyton of the Chałupy region.

Discussion

Diatoms versus habitats

The comparative analysis of diatom dominants and subdominants observed in the epilithon, epipsammon, and epiphyton enabled us to distinguish three major groups. Despite significant differences in environmental parameters between the Puck Lagoon and the Outer Puck Bay, such as hydrodynamic conditions, bathymetry and salinity, there is a group of diatom taxa observed on all types of substrates, i.e. stones, sands, seagrasses and macroalgae (Table 4). However, there are also several species observed on only one type of substrate and those found on two types of substrates.

One substrate. The first group includes diatom taxa recorded on only one type of substrate. This group included two species in the epilithon, *Denticula creticola* at site HP2/1014 at the town of Hel and *Diatoma tenuis* at HP14/1014 in Chałupy. The former species is known as an epilithic form (Snoeijs & Vilbaste 1994) and the latter one is described as an epiphytic form (Snoeijs 1993). Diatoms typical for the epipsammon were represented by *Catenula adhaerens*, *Navicula germanopolonica* and *Planothidium engelbrechtii*. Their habitat preferences correspond to the observations in other parts of the Baltic Sea (Snoeijs 1993; Snoeijs & Potapova 1995). The former species was more frequently observed in Kuźnica and Chałupy, while the remaining species mentioned

Table 4

Distribution and autecology of the main diatom taxa in the study area

Diatom taxa	Salinity*	Trophic status*	Saprobity*	Habitat		
				Epilithon	Epipsammon	Epiphyton
Cocconeis pediculus Ehrenberg	oh	et	bms			✓
C. placentula var. *euglypta* (Ehrenberg) Grunow	oi	et	bms	✓	✓	✓
C. placentula var. placentula Ehrenberg	oi	et	bms		✓	
C. scutellum var. *scutellum* Ehrenberg	eh	et	bms			✓
Catenula adhaerens Mereschkovsky	eh	et	bms		✓	
Ctenophora pulchella (Ralfs ex Kützing) D.M. Williams & Round	oh	et	ams			✓
Denticula creticola (Østrup) Lange-Bertalot & Krammer	mh	ir	ir	✓		
Diatoma moniliformis (Kützing) D.M. Williams	oh	et	bms	✓	✓	
Diatoma tenuis C. Agardh	oi	mt	ams	✓		
Fallacia clepsidroides Witkowski	mh	ir	ir	✓	✓	
Gedaniella flavovirens (Takano) Li, Witkowski & Ashworth	mh	et	ams	✓	✓	
G. guenter-grassii (Witkowski & Lange-Bertalot) Li, Sato & Witkowski	mh	ot	os	✓	✓	✓
G. mutabilis (Grunow) Li & Witkowski	mh	et	bms	✓	✓	✓
Gomphonema olivaceum (Hornemann) Ehrenberg	oi	emt	bms			✓
Gomphonemopsis obscura (Krasske) Lange-Bertalot	mh	ir	ir			✓
Halamphora coffeaeformis (C. Agardh) Mereschkowsky	eh	et	ams	✓	✓	
Mastogloia pumila (Grunow) Cleve	eh	ir	ir			✓
M. smithii Thwaites ex W. Smith	oh	ir	ir			✓
N. germanopolonica Witkowski & Lange-Bertalot	mh	emt	bms		✓	
N. gregaria Donkin	mh	et	ams	✓	✓	
N. paul-schulzii Witkowski & Lange-Bertalot	mh	ir	ir	✓	✓	
N. perminuta Grunow in Van Heurck	mh	mt	ps	✓	✓	
Nitzschia frustulum (Kützing) Grunow	oh	et	bms	✓	✓	✓
Opephora krumbeinii Witkowski, Witak & Stachura	eh	et	bms		✓	✓
Planothidium delicatulum (Kützing) Round & Bukhtiyarova	mh	et	bms	✓	✓	
P. engelbrechtii (Cholnoky) Round & Bukhtiyarova	mh	et	bms		✓	
Rhoicosphaenia abbreviata (C. Agardh) Lange-Bertalot	oh	et	ams	✓	✓	
Staurosira venter (Ehrenberg) Cleve & Möller	oi	met	bms			✓
Tabularia fasciculata (C.Agardh) D.M.Williams & Round	mh	et	abms		✓	✓

* for explanations see Table 3

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above were observed in the vicinity of Hel. In the epiphyton developing on seagrasses, the most typical were *Cocconeis pediculus*, *C. scutellum* var. *scutellum*, *Gomphonema olivaceum*, *Gomphonemopsis obscura*, *Mastogloia pumila* and *M. smithii*. All the above-mentioned taxa are known as epiphytic diatoms (Snoeijs 1993; Snoeijs & Potapova 1995). However, *G. olivaceum*, *M. pumila* and *M. smithii* were also recorded in the epilithon of the Baltic Sea (Snoeijs 1993). *Cocconeis* spp. were recorded in large numbers at the town of Hel. *G. olivaceum* occurred frequently in Kuźnica, while *Mastogloia* spp. on the coast between Jastarnia and Chałupy. Noteworthy is the occurrence of the brackish-water species *G. obscura* on seagrasses at the same sites i.e. in vicinity of Hel, Jastarnia, Kuźnica and Chałupy. The clear decrease in its frequency from SE to NW can be related to the distance from the open sea waters.

Two substrates. The second group consisted of diatoms observed on two types of substrates, i.e. sands and stones. It is represented by *Fallacia clepsidroides* and *Navicula paul-schulzii*. They were more frequently recorded on sands than on stones. However, the former species was observed only in the epipelon of the Baltic Sea (Witkowski 1994; Snoeijs & Potapova 1995). *Ctenophora pulchella* known from the Baltic epiphyton (Snoeijs 1993) and *Staurosira venter* considered an epipsammic species (Snoeijs & Balashova 1998) were observed on seagrasses and macroalgae at many sites of the Hel Peninsula, with a higher frequency near Chałupy.

All types of substrates. The third group includes species occurring on both types of sediments (stones and sands) and macroflora (seagrasses and macroalgae). It is represented by *Gedaniella flavovirens*, *Halamphora coffeaeformis* and *Nitzschia frustulum*. The former species was observed in the epilithon and epiphyton of the Baltic Sea (Snoeijs & Potapova 1995), whereas the latter only in the epilithon (Snoeijs 1993). They were observed along the whole coastline of the Hel Peninsula. *Nitzschia frustulum* played the key role on all types of habitats, especially in the epilithon and epipsammon. This group also includes *Rhoicosphaenia abbreviata* and *Tabularia fasciculata*, but in general their frequency in the epiphyton is much higher than in the epilithon and epipsammon. Noteworthy is their mass occurrence on seagrasses collected at the Hel Tip. The epiphytic diatoms *Cocconeis placentula* var. *euglypta* and *Diatoma moniliformis* (Snoeijs 1993), found on macroflora at almost all sites, were also collected on both types of sediments. The latter species is one of the main species on the macroflora in the Hel region. It is interesting that *Cocconeis placentula* var. *placentula*, referred to as an epiphytic species, was regularly observed in the epipsammon, but was very rarely found on seagrasses and macroalgae. However, this species occurred abundantly in the epilithon at site HP9/1014 located in Jastarnia. Between Jurata and Chałupy, this group comprised *Opephora krumbeinii*, *Gedaniella mutabilis* and *Planothidium delicatulum*. Although these species are considered to be epipsammic and epilithic forms (Snoeijs 1993; Witkowski 1994; Witak 2002; 2013), they are also known from other habitats along the whole coastline of the Hel Peninsula, except for the area in the vicinity of Hel. They were particularly common in the regions of Jurata and Chałupy. Another species associated with the sandy bottom, *Gedaniella guenter-grassii*, was also observed in the epilithon and epiphyton. *Navicula perminuta* was observed on all habitats at almost all sites. It was regularly observed in the epilithon, but it reached the maximum frequency on macroalgae in the region of Hel.

Diatoms versus location

Hel Tip region. The direct impact of saline waters leads to the abundant occurrence of diatoms preferring higher salinity with occasional occurrence of freshwater forms in the vicinity of the town of Hel. Despite the major impact of open sea waters, the benthic diatom flora found on all types of substrates clearly indicates that this is the most polluted region in the study area. This is evidenced by the high frequency of the polysaprobiont species *Navicula perminuta* (Witak 2010; Majewska et al. 2012) in diatom communities developed on macroalgae and stones. Moreover, α-mesosaprobionts were observed in large numbers. Even if *Gomphonemopsis obscura* and *Rhoicosphaenia abbreviata* belonging to this group observed in epiphyton were transported with seagrasses by hydrodynamic factors, other species, i.e. *Halamphora coffeaeformis* and *Navicula gregaria* known as epipsammon, are an autochthonous component of the diatom flora. The higher content of pollutants in this part of Puck Bay is also evidenced by the maximum frequency of species that are α-β-mesosaprobionts – *Cocconeis pediculus* and *Tabularia fasciculata*. In addition, the eutraphentic species *Planothidium engelbrechtii* was observed in the sand of this region. These taxa were recorded in the superficial sediments of the Outer Puck Bay (Witak 2000; 2010; Witak et al. 2006; Witak & Dunder 2007). The dominance of diatoms that tolerate high concentrations of nutrients and pollutants indicates intensive eutrophication and saprobication of water in the vicinity of Hel. This phenomenon is caused by a number of anthropogenic factors, including the development of shipping, the functioning of a fishing port as well as a yacht and military port and advanced infrastructure. Due to increased tourist traffic in the 21st century, the inflow of municipal sewage to Puck Bay has also significantly increased (Andrulewicz & Witek 2002; Kruk-Dowgiałło & Szaniawska 2008; Warzocha et al. 2018). These factors caused the accumulation of biogenic methane in subsurface sediments and, consequently, chemical changes in the water column (Reindl & Bolałek 2012), dissolution of siliceous diatom valves and their resuspension. These phenomena could cause a very low concentration of diatoms in sandy sediments. Another reason could be the high hydrodynamic conditions, which cause mechanical damage to diatom frustules (Nowacki et al. 2009; Dybowski et al. 2019).

Jurata–Jastarnia region. In the coastal section between Jurata and Jastarnia, the abundance of diatoms with very high edaphic requirements indicates the presence of eutrophic waters. In Jurata, the frequency of eutraphentic forms reached 90% in the epilithon and epipsammon, which can be related to tourism and developed hotel infrastructure. However, the distribution of saprobic groups clearly indicates that the environment status in the Jurata area is more favorable than in Jastarnia. A good indicator of lower pollution in the coastal zone in Jurata is the higher content of β-mesosaprobionts associated with increased frequency of euhalobous (*Opephora krumbeinii*), mesohalobous (*Gedaniella mutabilis*, *Planothidium delicatulum*) and oligohalobous halophilous (*Nitzschia frustulum*) taxa. All mentioned taxa were observed in the Outer Puck Bay (Witak 2000; 2010; Witak et al. 2006; Witak & Dunder 2007; Li et al. 2018, Pędziński & Witak 2019). The lower content of contaminants is likely due to the closure of a large part of the coastline between Hel and Jurata. It is also worth noting that the concentration of epipsammic diatoms is higher compared to the Hel community, which is associated with weaker hydrodynamic conditions. Slightly worse water status in Jastarnia, evidenced by the decrease in the content of β-mesosaprobionts combined with the increase of α-mesosaprobionts in the epilithon and epipsammon, may be connected with the presence of the fishing port.

Kuźnica region. Compared to the coastal zone of the Outer Puck Bay, a decrease in the content of marine and brackish-water species in epilithon and epipsammon was observed in the Kuźnica area. They were replaced by oligohalobous halophilous (*Nitzschia frustulum*) and indifferent (*Cocconeis placentula* + varr.) taxa. This is related to a distance from the open sea waters and the presence of the sandy barrier of the Seagull Reef, which hinders the inflow of more saline waters to the Puck Lagoon (Krzymiński et al. 2004; Kruk-Dowgiałło & Szaniawska 2008; Robakiewicz 2014). The higher content of diatoms that are α-mesosaprobionts (*Gedaniella flavovirens, Halamphora coffeaeformis*, *Navicula gregaria*) accompanied by polysaprobionts (*Navicula perminuta*) may be caused by the functioning of the fishing port. In addition, the waterway on the Kuźnica Passage was modernized and a new harbor infrastructure was built in 2012 (Stelmaszyk-Świerczyńska & Małkiewicz 2014).

Chałupy region. In the NW part of the Puck Lagoon, the freshwater species *Staurosira venter* known from the seagrass and macroalgae may be an autochthonous element in the diatom community. However, despite the location of this area at a fairly large distance from the open sea waters, a relatively high content of marine diatoms (*Catenula adhaerens*, *Halamphora coffeaeformis*, *Opephora krumbeinii*) and brackish-water forms (*Gedaniella guenter-grassii*, *G. mutabilis*, *Planothidium delicatulum*) was recorded. These diatom taxa were observed in different parts of the Puck Lagoon (Witak 2002). Some of these taxa [i.e. *H. coffeaeformis* named as *Amphora coffeaeformis* (C.Agardh) Kützing, *G. mutabilis* named as *Opephora olsenii* M.Møller, *P. delicatulum* named as *Achnanthes delicatula* (Kützing) Grunow] were observed in superficial sediments in the coastal zone of the Puck Lagoon (Witkowski 1990). It is very likely that these species constitute an allochthonous component of the diatom flora. Their occurrence can be explained by successive artificial expansion of the beach by the camping owners due to intensive development of tourism and water sports (windsurfing, kitesurfing) in the Chałupy region. For this reason, also the higher content of eutraphentic α-mesosaprobionts is observed. Apart from local municipal sewage, the sewage treatment plant in Swarzewo may be another source of pollution in this area (Rönnbreg & Bonsdorff 2004; Dziengo-Czaja et al. 2008; Obarska-Pempkowiak et al. 2015). At some sites with reduced anthropopressure, i.e. HP13/1014 and HP16/1014, the concentration of diatom valves in epipsammon is much higher than in the camping area.

Conclusions

Based on the results of the diatom study carried out in the inner coastal zone of the Hel Peninsula, three groups of assemblages are distinguished, depending on the type of substrate:

- *Denticula creticola* and *Diatoma tenuis* were observed only in the epilithon, whereas diatoms recorded only in the epipsammon were represented by *Catenula adhaerens*, *Navicula germanopolonica* and *Planothidium engelbrechtii*. *Cocconeis pediculus*, *C. scutellum* var. *scutellum*, *Gomphonema olivaceum*, *Gomphonemopsis obscura*, *Mastogloia pumila* and *M. smithii* were recorded only in the epiphyton.

- The group of diatoms developed on two types of substrates includes *Fallacia clepsidroides* and *Navicula paul-schulzii*, known mostly from the epilithon and epipsammon. Moreover, *Ctenophora pulchella* and *Staurosira venter* were found on seagrasses and macroalgae.

- The group of diatoms inhabiting all types of substrates is represented by *Cocconeis placentula* var. *euglypta*, *C. placentula* var. *placentula*, *Diatoma moniliformis*, *Gedaniella flavovirens*, *Halamphora coffeaeformis*, *Navicula perminuta*, *Nitzschia frustulum*, *Opephora krumbeinii*, *Gedaniella mutabilis*, *Planothidium delicatulum*, *Rhoicosphaenia abbreviata* and *Tabularia fasciculata*.

In addition, the distribution of benthic diatom communities indicates ecological differences in the study area:

- The high frequency of the polysaprobiont *Navicula perminuta* associated with α-mesosaprobionts *Halamphora coffeaeformis* and *Navicula gregaria* indicates the highest concentrations of nutrients and pollutants in the vicinity of the Hel Tip. The abundance of α-mesosaprobionts, accompanied by species that are polysaprobionts, indicates a lower level of saprobication in the Kuźnica region. In addition, the higher content of diatoms that are β-mesosaprobionts, i.e. *Opephora krumbeinii*, *Gedaniella mutabilis*, *Planothidium delicatulum*, *Nitzschia frustulum*, is a good indicator of generally cleaner coastal waters in the Jurata–Jastarnia region.

- The differences in the frequency of marine and brackish-water forms in the epilithon and epipsammon between the sampling sites located on the coast of the Outer Puck Bay and the Puck Lagoon are related to the distance from the open sea. This picture is additionally complicated by the distribution of epiphyton, which can be transported by hydrodynamic factors.

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