Oceanologia 63 (2021) 301—320

Available online at www.sciencedirect.com

ScienceDirect

journal homepage: www.journals.elsevier.com/oceanologia

ORIGINAL RESEARCH ARTICLE

Distribution and extent of benthic habitats in Puck Bay (Gulf of Gdańsk, southern Baltic Sea)

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Received 27 October 2020; accepted 11 March 2021
Available online 28 March 2021

KEYWORDS
Benthic habitats;
Mapping;
Spatial characteristics;
Puck Bay;
Southern Baltic Sea

Abstract The majority of the southern Baltic Sea seabed encompasses homogenous soft-bottom sediments of limited productivity and low biological diversity, but shallow productive areas in the coastal zone such as wetlands, vegetated lagoons and sheltered bays show a high variety of benthic habitat types offering favourable biotopic conditions for benthic fauna. Within Polish marine areas, semi-enclosed Puck Bay (the western part of the Gulf of Gdańsk) features an exceptionally diverse environment covering a range of benthic habitats which underscores its unique biological value and aesthetic quality and providing an impetus for conservation and ecosystem-based development. Full-coverages maps on benthic habitats in this area are therefore a necessary foundation for maritime spatial planning and implementation of strategies for sustainable management and protection of the coastal environment. This study presents the first comprehensive description and distribution of benthic habitats in Puck Bay which were categorised using the revised EUNIS 2019 classification system. Typological analyses were carried out based on inventory datasets from 1995 to 2019 including scientific publications, satellite images, open databases, topographic and geological maps, reports, theses, information available on websites and unpublished data shared willingly by individual researchers and administrative institutions. Collating various spatial data sources, that were first georeferenced and then visualized using techniques available in ArcMap 10.4.1 software (Esri), resulted in the mapping of benthic habitats and sites of important and protected plant species, which can contribute to the high confidence in environmental assessments and monitoring activities.

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Peer review under the responsibility of the Institute of Oceanology of the Polish Academy of Sciences.

Production and hosting by Elsevier

https://doi.org/10.1016/j.oceano.2021.03.001

1. Introduction

Benthic habitats in coastal areas and bays are complex systems with a high degree of geochemical, hydrological and ecological heterogeneity, patchiness and often multiple anthropogenic pressures (Gamito et al., 2012). The habitats are considered key drivers of diversity, functioning and ecosystem services (Torn et al., 2017), and therefore are the subject of regional inventories using hierarchal classification systems and spatial mappings. Comprehensive full-coverage mapping of benthic habitats provides information of critical importance to the identification of the seascape and benthic species distributions and ecosystem functions (Evans et al., 2014) and to the facilitation of habitat-based management such as marine spatial planning and nature conservation (Greene et al., 2007). Additionally, basin-scale benthic habitat maps support the implementation of marine legislation, e.g. the Europe Habitat Directive and the EU Marine Strategy Framework Directive. To this end, different classification schemes have been developed worldwide (Galparsoro et al., 2012). For European seas, the EUNIS (European Union Nature Information System) habitat classification system was implemented in 2004 with the aim of providing a common European reference set of habitat types (Davies et al., 2004). It is only recently (in 2019) that the EUNIS system was revised with all the habitat units at Levels 1 to 3 being re-coded and some of them renamed (https://www.eea.europa.eu). This revision established more consistency, removed ambiguity, eliminated overlaps in definitions of types and extended the typology to the entire European continent and adjacent seas (Chytrý et al., 2020). The EUNIS 2019 system is based on a step-by-step ordering of information on environmental conditions in the area such as water and light transmittance depths, granulometry of surface sediments, hydrological parameters, and macrophyte species composition and biomass (Chytrý et al., 2020). The EUNIS 2004 system, but not yet the EUNIS 2019 scheme, was also successfully employed in the typology of the Baltic Sea bottom (e.g., Sokołowski et al., 2015) although, due to the specific hydrological and ecological features of this area, other classification systems have been proposed in recent years. Systems such as the HELCOM HUB scheme (HELCOM, 2013a) and many local studies, e.g. Olenin (1997), Urbański and Szymelfenig (2003), Riecken et al. (2006), Martin et al. (2013) and Schiele et al. (2015) additionally undertook an accounting of the biotic (biological) properties of the environment. Physical- and biological-based benthic habitat mapping was constructed for several Baltic areas, e.g. the Polish maritime areas (Gic-Grusza et al., 2009), the German Baltic Sea (Schiele et al., 2015), the Estonian marine areas (Torn et al., 2017) and the Gulf of Finland (Martin et al., 2010 2013). The Baltic Sea seabed was inventoried also in the frame of large-scale EU-supported programs that offer free access to classified maps based on selected environmental variables, e.g. EMODnet (https://emodnet.eu/en/what-emodnet) and Al-Hamdani and Reker (2007).

The benthic habitats of Puck Bay have been the subject of several scientific studies and natural inventories in recent years (e.g., Gic-Grusza et al., 2009) but the detailed bottom topology of this water basin is still poorly known. Due to its exceptionally diverse environment covering a range of benthic habitats, Puck Bay forms the most valuable area in the Polish coastal zone in terms of taxonomic diversity and the presence of rare and protected species (Węsławski et al., 2009). The variety of habitats in such a small water-basin underscores its unique biological value and aesthetic quality which provide an impetus for conservation (Sokołowski et al., 2015). An inner part of the bay (the Puck Lagoon) has been designated as a Special Protection Area (PLB 220005) and Special Area of Conservation (PHL 220032) as described in Natura 2000, the EU-wide network of nature protection areas. On the other hand, intensive human activities in this area, e.g. sewage treatment, eluting salt deposits on land and the resultant brine discharge into the coastal waters (Robakiewicz, 2018), dumping materials from the dredging of sediments (Cieślikiewicz et al., 2018), and the testing and evaluation of military equipment raise concerns about their environmental consequences. Previous environmental impact assessments resulted in the accumulation of data but usually the assessments are either local (based on point observations) or are scattered among different sources and/or stored as non-standardised datasets and maps. What is more, maritime spatial planning for the Gulf of Gdańsk, including Puck Bay, assumes the near-future development of additional areas of qualified coastal tourism, mariculture and industrial infrastructure such as installations for the transshipment of gas and pipelines for its transportation) (Study of Conditions of Spatial Development of Polish Sea Areas, 2016; Zaucha, 2010). Implementation of these plans requires a detailed inventory of benthic habitat classes covering the most valuable nearshore marine areas and including protected areas such as the Natura 2000 sites (Martin et al., 2013; Węsławski et al., 2013) as well as the most important vascular plants and macrophytes. Full-coverage maps on the distribution of benthic habitats also form the background for environmental assessments and future monitoring activities, e.g. for Red List work (HELCOM, 2013b) and the fulfilment of the European Union Marine Strategy Framework Directive (MSFD) (2008/56/EC, EU Commission, 2008) (Schiele et al., 2015).

This study has therefore been set up to identify, describe and define the distribution of the main benthic habitats for the whole of Puck Bay using the revised EUNIS 2019 classification system and based on the most up-to-date references and the unpublished sources that were available to the authors. For the first time, detailed and thorough basin-scale mapping of this bay was provided as a necessary foundation for the implementation of maritime spatial planning and development of strategies for sustainable ecosystem-based management and protection of the coastal environment. Merging and harmonising different datasets allowed the construction of maps depicting benthic habitats replete with the location and extent of hydrotechnical infrastructure and underwater objects. Such documentation of marine habitats can serve also as a baseline against which future changes to seafloor conditions in Puck Bay, that may be differentially associated with natural and human-induced processes, can be detected. This aspect is of particular relevance for the assessment of habitat ecological status as recent studies indicate modification of the taxonomic structure of macrobenthic plants and their redistribution on the seafloor in the photic zone of the bay

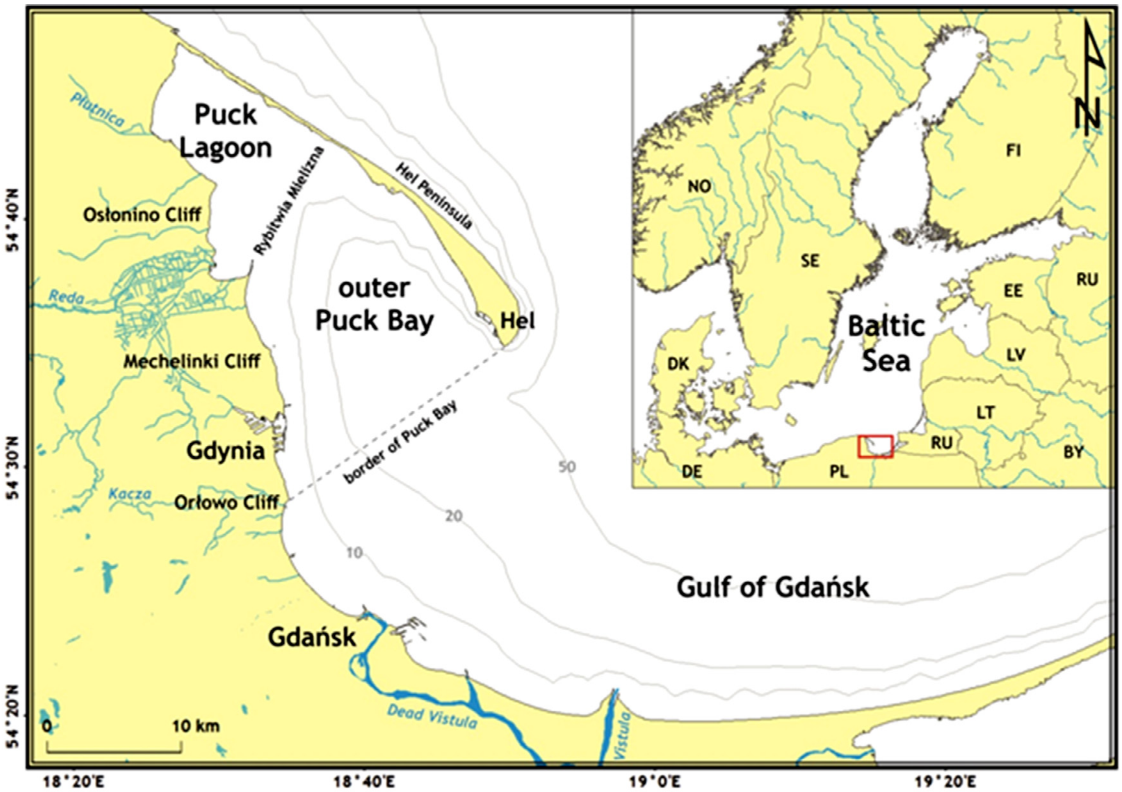

Figure 1 Location of Puck Bay in the Gulf of Gdańsk (southern Baltic Sea).

(e.g., Jankowska et al., 2014, 2018; Jędruch et al., 2019; Węsławski et al., 2013).

2. Material and methods

2.1. Source data

In order to determine the type and spatial distribution of benthic habitats in Puck Bay, a definition, nomenclature, and hierarchical principles from the EUNIS 2019 classification system were adopted. According to the criteria used, three depth zones have been distinguished in the bay: 1) the littoral (hydrolittoral) zone which represents an area of water depth < 0.5 m, 2) the infralittoral (photic zone) and 3) circalittoral (aphotic zone). The boundary layer between infra- and circalittoral zone has been specified as water depth at which 1% Photosynthetically Active Radiation (PAR) reaches the bottom (Al-Hamdani and Reker, 2007; Gic-Grusza et al., 2009). Typological analyses of the bottom habitats were carried out based on inventory datasets from 1995 to 2019 available in the form of scientific publications, satellite images, topographic and geological maps, reports, theses, information available on websites and the data collected by individual authors or research and administrative institutions but not yet published. The data used for classification accounted for hydrological (water and light transmittance depths), geomorphological (a type of sediment), navigation (hydrotechnical infrastructure and anthropogenic objects) and biotic (the presence of benthic vegetation and plant species dominating in the biomass structure) parameters at selected sites located in the area of Puck Bay. Due to scattered and discontinuous data, which in most cases are based on point observations and thus of low spatial resolution, information on macrofaunal species was not included in the analyses. In addition, according to Węsławski et al. (2013) the occurrence of uniform seabed forms in the bay is weakly related with the distributions of individual benthic species or multi-species assemblages due presumably to specific characteristics of the local macrofauna which is dominated by highly tolerant, eurytopic species of opportunistic strategies. A straight line from the tip of the Hel Peninsula in the north to the Orłowo Headland of the Orłowo Cliff in the south was conventionally treated as the eastern border of the bay (Figure 1) (Majewski, 1990).

A total of 19 data sources were used in the analysis which included 17 published and two unpublished references. Specifically, geomorphological and biotic data were extracted from 15 published references and three unpublished references shared by the Maritime Office in Gdynia and individual researchers. Distribution of surface sediments by type and location of anthropogenic deposits were defined based on four analogue maps (Table 1). Fourteen data sources (eight analogue maps and six tabular field survey datasets with geographical coordinates) provided information on the presence of benthic vegetation and plant species dominating in the biomass structure. When necessary, sample data were averaged per stations/area and standardised to the area of 1.0 m^2. If the confidence in dataset maps or tabular data on distribution of macrobenthic plants was low,

Table 1 Sources of the spatial data layers presented in the study.

Geospatial data model	Layer	Type and processing of input data	Reference
Vector (points)	Wrecks and other underwater objects (metal and concrete constructions, other artificial objects, boulders and pebbles)	Hydrographic survey data with geographical coordinates, dimensions and description of the objects [1] on the basis of which the data layer was created by authors.	1) Hydrographic Office of the Polish Navy (unpubl. data)
Vector (lines, polygons)	Hard coastal protection structures (seawalls, breakwaters), ports and other hydrotechnical objects	Technical documentation of maritime administration with geographical coordinates and description of the objects [2), 3)] supplemented by the analysis of recent satellite images carried out by the authors with geographical coordinates and description [4), 5)] on the basis of which the data layer was created by authors; the dimensions of objects were calculated in the GIS software by the authors.	2) Maritime Institute in Gdańsk (2013) 3) Michałek and Kruk-Dowgiałło (2013) 4) Google Maps (2018) 5) Sentinel Hub (2018)
Vector (polygons)	Types of surface sediments (mixed sand and gravel, coarse-grained sand, medium-grained sand, fine-grained sand, vari-grained sand, silty sand, sand-silt-clay, clayey silt, silty clay)	Digitized and georeferenced analogue maps of the distribution of sediment types [6), 7)] on the basis of which the data layer was created by authors; the geographical coordinates and the area of particular sediment types were calculated in the GIS software by the authors.	6) Kramarska (1995) 7) Smoła et al. (2014)
Vector (polygons)	Anthropogenic sediments (post-dredging pits, dumping site)	Digitized and georeferenced analogue maps of the distribution of anthropogenic sediments [8), 9)] on the basis of which the data layer was created by authors; the geographical coordinates and the area of sites were calculated in the GIS software by the authors.	8) Maritime Office in Gdynia (2011) 9) Szefler et al. (2012)
Vector (polygons)	*Zostera marina* beds	Field survey data (including underwater observation by a SCUBA diver) with geographical coordinates and description of the sites [10), 11), 12), 13), 14)] supplemented by digitized and georeferenced analogue maps [15), 16), 17), 18), 19), 20), 21)] and geospatial data layer of the distribution of macrophytes [22)] on the basis of which the data layer was created by authors; the missing geographical coordinates and the area of sites were calculated in the GIS software by the authors.	10) Włodarska-Kowalczuk et al. (2014) 11) Sokołowski et al. (2015) 12) Jankowska et al. (2016) 13) Bałazy (unpubl. data) 14) Zgrundo (unpubl. data). 15) Gic-Grusza et al. (2009) 16) Kruk-Dowgiałło et al. (2009) 17) Smoła (2012) 18) Smoła et al. (2014) 19) Bełdowska et al. (2015) 20) Dąbrowska et al. (2016) 21) Jędruch et al. (2019) 22) https://www.iopan.pl/projects/Zostera 23) Michałek and Kruk-Dowgiałło (2015)

(*continued on next page*)

Table 1 (*continued*)

Geospatial data model	Layer	Type and processing of input data	Reference
Vector (polygons)	*Stuckenia pectinata* and other angiosperms (i.e. *Zannichellia* sp., *Ruppia* sp., *Myriophyllum* sp.)	Field survey data (including underwater observation by a SCUBA diver) with geographical coordinates and description of the sites [10), 12), 13), 14)] supplemented by digitized and georeferenced analogue maps of the distribution of macrophytes [15), 18), 20)] on the basis of which the data layer was created by authors; the missing geographical coordinates and the area of sites were calculated in the GIS software by the authors.	
Vector (polygons)	*Chara* spp.	Field survey data (including underwater observation by a SCUBA diver) with geographical coordinates and description of the sites [10), 12), 13), 14)] supplemented by digitized and georeferenced analogue maps of the distribution of macrophytes [15), 18), 20)] on the basis of which the data layer was created by authors; the missing geographical coordinates and the area of sites were calculated in the GIS software by the authors.	
Vector (lines)	Reeds	Digitized and georeferenced analogue map of the distribution of macrophytes [23)] on the basis of which the data layer was created by authors; the geographical coordinates and the area of sites were calculated in the GIS software by the authors.	
Vector (points)	Macroalgae (i.e. *Furcellaria lumbricalis* (filamentous algae))	Field survey data (including underwater observation by a SCUBA diver) with geographical coordinates and description of the sites [10), 11), 12), 13), 14)] supplemented by digitized and georeferenced analogue maps [15), 16), 17), 18), 19), 20), 21)] and geospatial data layer of distribution of macrophytes [22)] on the basis of which the data layer was created by authors; the missing geographical coordinates and the area of sites were calculated in the GIS software by the authors.	

an expert judgment was used. Navigation data on harbour infrastructure, industrial and military hydrotechnical structures and coastal protection engineering structures such as bands, stone embankments and breakwaters were obtained from one publication, one unpublished source and three open-access databases including Google maps supported by CNES/Airbus and Maxiar Technologies satellite images. Information on underwater anthropogenic (e.g., shipwrecks, sunken anchors, pipelines, sewage treatment plant collectors) and natural objects (e.g., larger boulders and stones) were compiled from tabular datasets which were provided willingly by the Hydrographic Office of the Polish Navy and the Maritime Office in Gdynia. Each object was assigned accurate GPS coordinates, depth of submergence, length, width, height and water depth above it. Dimensions were measured to the nearest 0.1 m and 3.0 m for submerged and immersed objects, respectively. Since the exact dimensions of some objects were difficult to determine due to unknown construction and a degree of destruction or burial, the non-public databases, available literature datasets (Dubrawski and Zawadzka-Kahlau, 2006; Hydrographic Office of the Polish Navy, Maritime Institute in Gdańsk, 2013; https://www.google.pl/maps) and own measurements were used to estimate their surface area. The percentage contribution of surface area of a given habitat was estimated as a ratio of the surface area covered by the habitat to the total area of Puck Bay. Similarly, the percentage share of a given habitat along the shore was calculated as a ratio of a coastline length occupied by the habitat to the total length of the bay coastline. The contour map and the bathymetry of the study area were provided by the GIS Centre of the University of Gdańsk (www.cgis.oig.ug.edu.pl).

2.2. Data processing and visualisation methods

The analysis and visualisation of the geographic data were carried out using ArcMap 10.4.1 software (Esri) with the WGS 1984 coordination system and the UTM zone 34N projection for data presentation. Methods of data transformation and the mapping of benthic habitats using the Geographical Information Systems (GIS) were described in detail in Urbański and Szymelfenig (2003) and are presented here only in brief. Analogue maps were first aligned to the correct location using the georeferencing tool and the existing spatial data. This process involved the identification of a series of control points that linked locations on the map with locations in the spatially referenced data. To determine the correct coordinate location of the source data, the first-order polynomial transformation was used. This type of transformation is commonly employed to georeference an image. However, it does not guarantee local accuracy and tends to give a small random type error. The georeferenced data were then digitalised manually by tracing the lines or points from the scanned or downloaded source datasets. The manual digitisation and vectorisation is the preferred method when dealing with historical maps and the data with low resolution (Kaim et al., 2016). The vectorisation of the source map was performed by tracing the individual pixels of the image and placing the vertex of a newly created shape at each outside corner pixel. The point data with known spatial location obtained from the provided databases, documents or unpublished fieldwork reports were converted into features following format unification of geographical coordinates. The data layers, containing information on a single attribute (e.g., water and light transmittance depth, sediment type, the presence of vegetation, the presence of submerged objects) were generated after applying on the created features the commonly used geoprocessing tools, including extract and overlay analysis. The final ensemble map of benthic habitats was generated by intersecting individual spatial data layers of different seabed properties based on a predetermined classification scheme as shown in Table 2. To ensure data integrity all created maps were closely examined for errors such as multipart, overlapping and sliver polygons (small polygons resulting from layer intersection) or gaps between polygons which were identified and corrected using a geodatabase topology. The resulting seabed classification map and its individual layers generated in this study are available on request from the authors. The taxonomic nomenclature of plants, macroalgae and animals followed AlgaeBase (www.algaebase.org) and the World Register of Marine Species (WoRMS, www.marinespecies.org).

3. Results

In the littoral (coastal), infralittoral and circalittoral zones of Puck Bay, a total of eight benthic habitats were distinguished, taking a level 2 as the most detailed categorisation criterion according to the adopted EUNIS 2019 classification system (https://www.eea.europa.eu). All habitats in the bay were classified to the superior marine habitat category (level 1; EUNIS 2019 code M) and, depending on the water and light transmittance depths, and a substrate type (level 2), were divided into eight subcategories (Figure 2, Table 2).

3.1. Habitat *Littoral sand*

The habitat *Littoral sand* (MA5) occupies a narrow strip of the bottom (excluding sections with hydrotechnical structures) along the coastline which periodically emerges as a result of water level changes (Kramarska, 1995; Smoła et al., 2014). This habitat reaches a water depth of about 0.5 m and is characterised by a relatively small area and high diversity of the resident benthic macroplants (level 3; *Baltic hydrolittoral sand* — MA53, including two habitats at level 4 *Baltic hydrolittoral sandy substrata characterized by emergent vegetation* — MA531 and *Baltic hydrolittoral sand characterised by submerged rooted plants* — MA532, and three habitats at level 5, i.e. *Baltic hydrolittoral sand dominated by common reed* — MA5311, *Baltic hydrolittoral sand dominated by Potamogeton perfoliatus and/or Stuckenia pectinata* — MA5321 and *Baltic hydrolittoral sand dominated by Charales* — MA5324 (https://www.eea.europa.eu). The percentage contribution of this habitat to the total area of the Puck Bay seabed was estimated at 1.3% (5.1 km^2). The length of the Puck Bay coastline with the typical marshy common reed *Phragmites australis* was estimated at 16.5 km, i.e. 13.8% of the total shoreline length of the bay.

3.2. Habitats *Infralittoral rock* and *Circalittoral rock*

All types of the hard bottom can be classified into two subcategories (level 2) according to the EUNIS 2019 hierarchy: *Infralittoral rock* (MB1) and *Circalittoral rock* (MC1) (https://www.eea.europa.eu) (Table 2). The total surface area of hard substrate in Puck Bay is estimated at 0.6 km^2, which is nearly 0.02% of the bay seabed surface area, including anthropogenic and natural hard objects (Table 3).

3.2.1. Anthropogenic objects

Objects of anthropogenic origin (level 4: *Baltic infralittoral hard anthropogenically created substrates* — MB13M

Table 2 Types and codes of the benthic habitats distinguished in Puck Bay at different levels of the EUNIS classification system (https://www.eea.europa.eu).

Level 1	Level 2	Level 3	Level 4	Level 5
(M) Marine benthic habitats	(MA5) Littoral sand	(MA53) Baltic hydrolittoral sand	(MA531) Baltic hydrolittoral sandy substrata characterized by emergent vegetation	(MA5311) Baltic hydrolittoral sand dominated by common reed
			(MA532) Baltic hydrolittoral sand characterised by submerged rooted plants	(MA5321) Baltic hydrolittoral sand dominated by *Potamogeton perfoliatus* and/or *Stuckenia pectinata*
				(MA5324) Baltic hydrolittoral sand dominated by Charales
	(MB1) Infralittoral rock	(MB13) Baltic infralittoral rock	(MB131) Perennial algae on Baltic infralittoral rock and boulders	
			(MB13M) Baltic infralittoral hard anthropogenically created substrates	
	(MB3) Infralittoral coarse sediment	(MB33) Baltic infralittoral coarse sediment	(MB332) Baltic infralittoral coarse sediment characterised by submerged rooted plants	(MB3325) Baltic infralittoral coarse sediment dominated by *Zostera marina*
	(MB5) Infralittoral sand	(MB53) Baltic infralittoral sand	(MB532) Baltic infralittoral sand characterised by submerged rooted plants	(MB5321) Baltic infralittoral sand dominated by *Potamogeton perfoliatus* and/or *Stuckenia pectinata*
				(MB5324) Baltic infralittoral sand dominated by Charales
				(MB5327) Baltic infralittoral sand dominated by *Zostera marina*
	(MB6) Infralittoral mud	(MB63) Baltic infralittoral mud	(MB632) Baltic infralittoral mud sediment characterised by submerged rooted plants	(MB6321) Baltic infralittoral mud sediment dominated by *Potamogeton perfoliatus* and/or *Stuckenia pectinata*
				(MB6327) Baltic infralittoral mud sediment dominated by *Zostera marina*
			(MB63E) Baltic infralittoral soft anthropogenically created substrates	
	(MC1) Circalittoral rock	(MC13) Baltic ciralittoral rock	(MC13G) Baltic circalittoral hard anthropogenically created substrates	
	(MC5) Circalittoral sand	(MC53) Baltic circalittoral sand		
	(MC6) Circalittoral mud	(MC63) Baltic circalittoral mud	(MC63D) Baltic circalittoral soft anthropogenically created substrates	

Table 3 Total surface area (km^2) of benthic habitats (classified according to the revised EUNIS 2019 classification system) and their contribution to the total area of in Puck Bay and its inner and outer part (%). 0.00 indicates values < 0.01.

Level	Habitat type (code in the EUNIS 2019 system)	Area, km^2 (percentage contribution, %)					
		Puck Lagoon		outer Puck Bay		Puck Bay	
		105.5	(26.7)	289.4	(73.3)	395.0	(100.0)
2	**Littoral sand (MA5)**	**1.9**	**(1.8)**	**3.2**	**(1.1)**	**5.1**	**(1.3)**
3	Baltic hydrolittoral sand (MA53)	1.9	(1.8)	3.2	(1.1)	5.1	(1.3)
4	Baltic hydrolittoral sandy substrata characterized by emergent vegetation (MA531)	0.4	(0.4)	0.8	(0.3)	5.1	(1.3)
5	Baltic hydrolittoral sand dominated by common reed (MA5311)	0.4	(0.4)	0.8	(0.3)	5.1	(1.3)
4	Baltic hydrolittoral sand characterised by submerged rooted plants (MA532)	0.3	(0.3)	1.3	(0.4)	1.6	(0.4)
5	Baltic hydrolittoral sand dominated by *Potamogeton perfoliatus* and/or *Stuckenia pectinata* (MA5321)	0.3	(0.2)	1.3	(0.4)	1.6	(0.4)
5	Baltic hydrolittoral sand dominated by Charales (MA5324)	0.02	(0.02)	0.01	(0.0)	0.03	(0.01)
2	**Infralittoral rock (MB1)**	**0.1**	**(0.1)**	**0.0**	**(0.0)**	**0.1**	**(0.0)**
3	Baltic infralittoral rock (MB13)	0.1	(0.1)	0.0	(0.0)	0.1	(0.0)
4	Perennial algae on Baltic infralittoral rock and boulders (MB131)	0.0	(0.0)	0.01	(0.0)	0.01	(0.0)
4	Baltic infralittoral hard anthropogenically created substrates (MB13M)	0.1	(0.1)	0.01	(0.00)	0.1	(0.0)
2	**Infralittoral coarse sediment (MB3)**	**0.0**	**(0.0)**	**1.9**	**(0.6)**	**1.9**	**(0.5)**
3	Baltic infralittoral coarse sediment (MB33)	0.0	(0.0)	1.9	(0.6)	1.9	(0.5)
4	Baltic infralittoral coarse sediment characterised by submerged rooted plants (MB332)	0.0	(0.0)	0.4	(0.1)	0.4	(0.1)
5	Baltic infralittoral coarse sediment dominated by *Zostera marina* (MB3325)	0.0	(0.0)	0.4	(0.1)	0.4	(0.1)
2	**Infralittoral sand (MB5)**	**101.6**	**(96.3)**	**143.1**	**(49.4)**	**244.7**	**(62.0)**
3	Baltic infralittoral sand (MB53)	101.6	(96.3)	143.1	(49.4)	244.7	(62.0)
4	Baltic infralittoral sand characterised by submerged rooted plants (MB532)	66.3	(62.8)	14.3	(5.0)	80.6	(20.4)
5	Baltic infralittoral sand dominated by *Potamogeton perfoliatus* and/or *Stuckenia pectinata* (MB5321)	50.4	(47.8)	6.7	(2.3)	57.1	(14.5)
5	Baltic infralittoral sand dominated by Charales (MB5324)	4.6	(4.3)	0.0	(0.0)	4.6	(1.2)
5	Baltic infralittoral sand dominated by *Zostera marina* (MB5327)	11.2	(10.6)	7.7	(2.6)	18.9	(4.8)
2	**Infralittoral mud (MB6)**	**2.7**	**(2.5)**	**16.2**	**(5.6)**	**18.9**	**(4.8)**
3	Baltic infralittoral mud (MB63)	2.7	(2.5)	16.2	(5.6)	18.9	(4.8)
4	Baltic infralittoral mud sediment characterised by submerged rooted plants (MB632)	0.8	(0.7)	0.0	(0.0)	0.8	(0.2)
5	Baltic infralittoral mud sediment dominated by *Potamogeton perfoliatus* and/or *Stuckenia pectinata* (MB6321)	0.2	(0.2)	0.0	(0.0)	0.2	(0.1)

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Table 3 (*continued*)

Level	Habitat type (code in the EUNIS 2019 system)	Area, km^2 (percentage contribution, %)					
		Puck Lagoon		outer Puck Bay		Puck Bay	
		105.5	(26.7)	289.4	(73.3)	395.0	(100.0)
5	Baltic infralittoral mud sediment dominated by *Zostera marina* (MB6327)	0.6	(0.5)	0.0	(0.0)	0.6	(0.1)
4	Baltic infralittoral soft anthropogenically created substrates (MB63E)	0.8	(0.7)	1.9	(0.7)	2.7	(0.7)
2	**Circalittoral rock (MC1)**	**0.0**	**(0.0)**	**0.0**	**(0.0)**	**0.0**	**(0.0)**
3	Baltic circalittoral rock (MC13)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)
4	Baltic circalittoral hard anthropogenically created substrates (MC13G)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)
2	**Circalittoral sand (MC5)**	**0.0**	**(0.0)**	**1.3**	**(0.5)**	**1.3**	**(0.3)**
3	Baltic circalittoral sand (MC53)	0.0	(0.0)	1.3	(0.5)	1.3	(0.3)
2	**Circalittoral mud (MC6)**	**0.0**	**(0.0)**	**123.0**	**42.5)**	**123.0**	**(31.2)**
3	Baltic circalittoral mud (MC63)	0.0	(0.0)	123.0	(42.5)	123.0	(31.2)
4	Baltic circalittoral soft anthropogenically created substrates (MC63D)	0.0	(0.0)	6.4	(2.2)	6.4	(1.6)

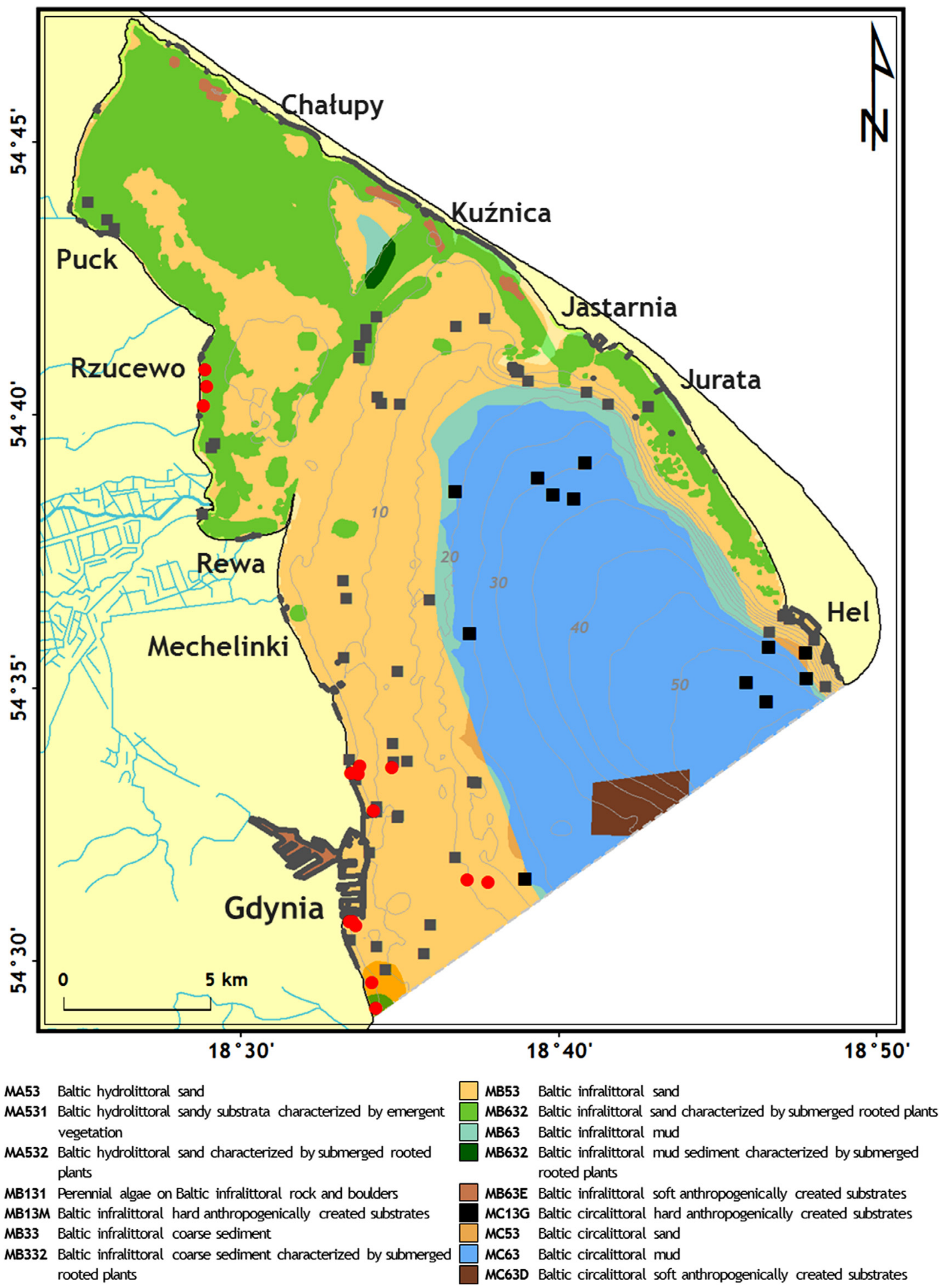

Figure 2 Spatial map of benthic habitats in Puck Bay at EUNIS 2019 level 2, 3 and 4 (where applicable). EUNIS 2019 codes are explained in Table 2.

and *Baltic circalittoral hard anthropogenically created substrates* — MC13G) are located both in the spraying zone along the coastline (e.g. harbour infrastructure, industrial and military hydrotechnical structures, coastal protection engineering structures such as bands, stone embankments, breakwaters) as well as in the shallow euphotic and deeper dysphotic zones (linear and free-standing underwater objects such as pipelines, sewage treatment plant collectors, shipwrecks, sunken anchors and other individual ship components). Artificial manmade objects are located mainly in the outer part of Puck Bay and in the sandbank Rybitwia Mielizna that was used as a military training ground in the past (Hydrographic Office of the Polish Navy, unpubl. data; Maritime Institute in Gdańsk, 2013; Michałek and Kruk-Dowgiałło, 2013). The total length of the coastline with protection engineering and hydrotechnical structures was estimated at 61.0 km including the 18.0 km-long concrete sea walls and the 43.0 km-long harbour infrastructure which together make up 50.9% of the total coastline length of the bay. Additionally, there were identified structures extending into the sea such as piers or footbridges of a total length of 2.1 km. Given that the mean water depth along linear structures is 0.5 m and mean water depth at the harbour structures and piers is 13.0 m, the hydrotechnical infrastructure on the shore provides 0.6 km^2 of artificial hard substrate. On the seafloor of Puck Bay, there were defined 34 free-standing anthropogenic objects including non-linear hydrotechnical constructions such as torpedo houses and piles (total surface area 0.02 km^2) and individual structures such as anchor blocks, pipes, navigational barriers, measurement platforms and their remains (a total surface area 0.001 km^2) (Maritime Institute in Gdańsk, 2013). What is more, 45 submerged metal and wooden shipwrecks were recognised at different depths in the bay (Hydrographic Office of the Polish Navy, unpubl. data). The sunken vessels differ in size ranging from small fishing boats (e.g., 6.1 m long) to large commercial vessels such as hospital ship s/s Stuttgart (168 m long) in the vicinity of Gdynia harbour. The estimated surface area of all shipwrecks is 0.01 km^2.

3.2.2. Natural hard substrate

The natural hard substrates are unique in Puck Bay, including primarily boulders, pebbles and gravels on an abrasive platform of the eroded cliffs in the areas adjacent to Mechelinki (the Mechelinki Cliff), Osłonino-Rzucewo (the Osłonino Cliff) and Gdynia Orłowo (the Orłowo Cliff) (Smoła et al., 2014) (Figures 3 and 4). Their estimated total surface area is 0.01 km^2.

3.3. Habitat *Infralittoral sand* and *Infralittoral coarse sediment*

The largest bottom area of Puck Bay is occupied by the habitat *Infralittoral sand* (MB5) at level 2 which encompasses the habitats *Baltic infralittoral sand* (MB53) and *Baltic infralittoral sand characterised by submerged rooted plants* (MB532) at levels 3 and 4 of the EUNIS 2019 classification system, respectively. This habitat occupies as much as 244.7 km^2 of the seafloor and represents 62.0% of the total surface area of the bay. Submerged rooted plants form multi- and monospecies assemblages in the Puck Lagoon, on the selected sites along the Hel Peninsula and near the Orłowo Cliff (Figure 2 and 5). In terms of biomass, vascular plants are dominated by the pondweed *Stuckenia* spp. and the seagrass *Zostera marina* whose communities are classified as separate habitats (level 5): *Baltic infralittoral sand dominated by Potamogeton perfoliatus and/or Stuckenia pectinata* (MB5321) and *Baltic infralittoral sand dominated by Zostera marina* (MB5327) (https://www.eea.europa.eu) (Figure 2 and 5; Table 2). The surface area of the bottom covered by meadows of *Stuckenia* spp. and seagrass has been estimated at 57.1 km^2 and 18.9 km^2, respectively, i.e. 14.5% and 4.8% of the total surface area of the bay. When only a narrow strand of water depth between 0.5—5.0 m (excluding hard substrate, muddy and gravelly sediments, post-dredging pits and natural hollows) is considered, i.e. the area most commonly reported to host *Zostera marina* in the southern Baltic Sea (e.g., Kautsky et al., 2017; Kruk-Dowgiałło and Szaniwaska, 2008), the contribution of surface area occupied by the seagrass to the total surface area of the zone (119.1 km^2) amounts to 17.5% of the total surface area of the bay. Small sheltered areas in the photic zone of the Puck Lagoon (4.6 km^2) host several species of the family Charophyceae which form the separate habitat *Baltic infralittoral sand dominated by Charales* (MB5324).

Along the cliff coast in the southern part of the bay surface sediments contain large fraction coarse sand that are classified as the separate habitat *Infralittoral coarse sediment* (MB3) of a total surface area of 1.9 km^2 (Figure 2).

3.4. Habitats *Infralittoral mud* and *Circalittoral mud*

In the outer part of Puck Bay two benthic habitats prevail: *Infralittoral mud* (MB6) and *Circalittoral mud* (MC6) which together make up 36% (141.9 km^2) of the total area of the bay. Muddy substrate can be also found at the Gdynia dumping site (surface area 6.4 km^2) where materials from the dredging of sediments in harbour basins and approach channels were deposited (level 3: *Baltic circalittoral mud* — MC63 and level 4: *Baltic circalittoral soft anthropogenically created substrates* — MC63D). In addition, anthropogenic muddy sediments dominate at post-dredging pits (surface area 6.4 km^2) located in the shallow part of the Puck Lagoon along the Hel Peninsula: Władysławowo, Chałupy, Kuźnica II, Kuźnica I and Jastarnia (level 3: *Baltic infralittoral mud* — MB63, level 4: *Baltic infralittoral soft anthropogenically created substrates* — MB63E) (Figure 2).

4. Discussion

4.1. Types and distribution of benthic habitats

The first full-coverage seabed classification map of Puck Bay (southern Baltic Sea) provides essential information about benthic habitats that can be important for ecosystem-based management (Cooper et al., 2019). Detailed habitat typology with information on the extent and areal cover of different habitat types also contributes to the basis for the high confidence in environmental assessments and the subsequent designing of programs that monitor the status of the seabed.

The composition and distribution of surface sediments in Puck Bay reflect the postglacial history of this area and the genetic and morphometric variation of its two parts. The seabed of the shallower inner part (the Puck Lagoon) is comprised of lacustrine and riparian accumulation relicts, shoals, hollows and lamellar flats ranging in depth from 0.1 m to 5.0 m as well as dredging depressions of up to 14.0 m deep. The bottom sediments are primarily sandy and muddy but there are also gravelly and rocky areas (Kruk-Dowgiałło and Szaniawska, 2008). The seafloor of the outer part consists of glacial and glaciofluvial relicts, and delta and marine accumulation-erosion relicts;

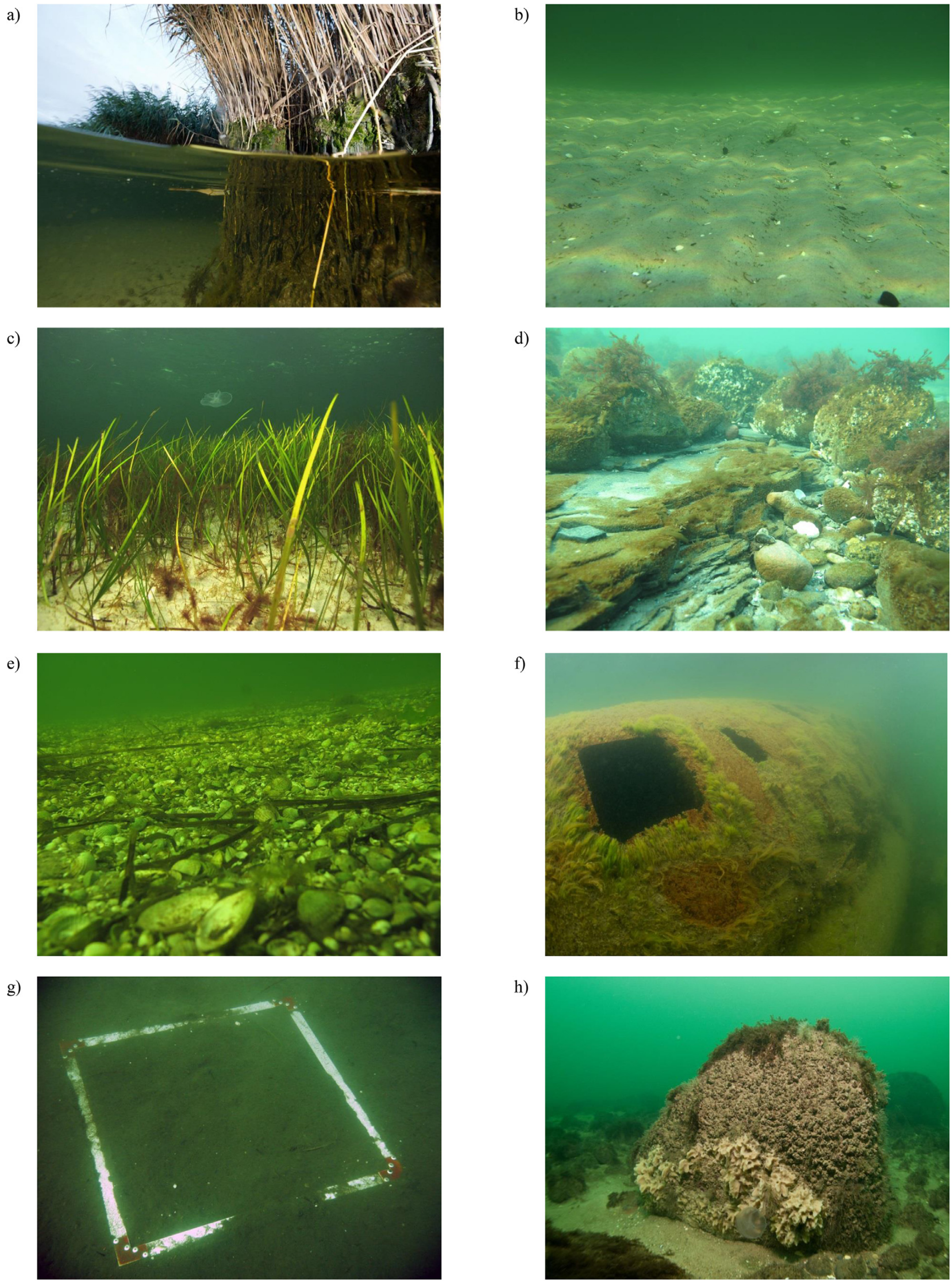

Figure 3 Different benthic habitat types in Puck Bay: a) Płutnica river plume (photo: P. Bałazy); b) sandy sediments in the sublittoral zone close to Kuźnica (photo: A. Sokołowski); c) meadows of the seagrass *Zostera marina* adjacent to Jastarnia (photo: P. Bałazy); d) pebbles and stone outcrops overgrew with macrophytes at the foot of the Orłowo Cliff (photo: A. Sokołowski); e) sandy bottom covered with bivalve shells in the vicinity of Kuźnica (photo: A. Sokołowski); f) hull of the wreck of ORP *Kujawiak* submarine resting on the sandbank Rybitwia Mielizna overgrown by macroalgae (photo: P. Bałazy); g) muddy bottom rich in organic matter in the central outer part of Puck Bay (photo: P. Bałazy); h) boulder at the foot of the Orłowo cliff (photo: P. Bałazy).

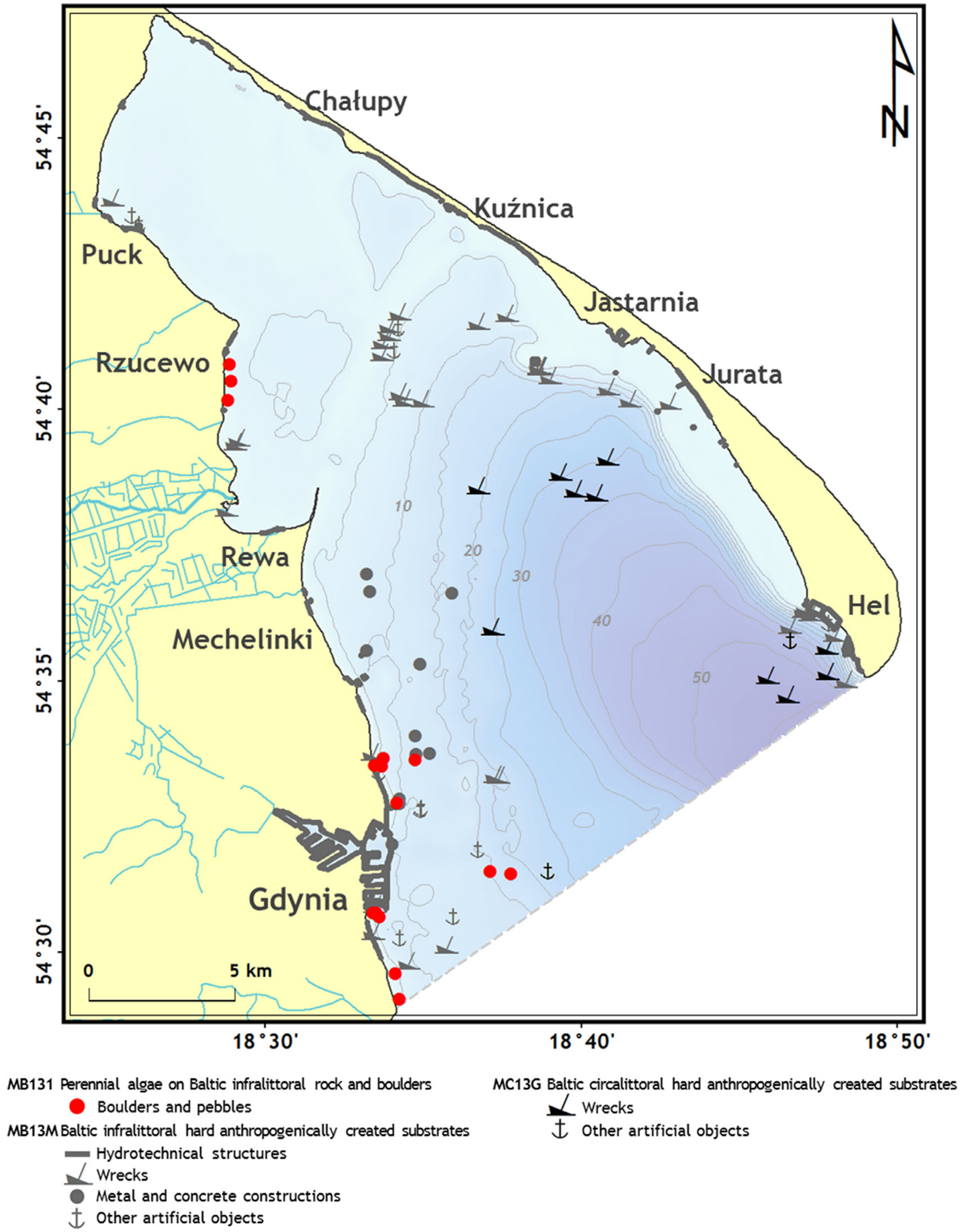

Figure 4 Hard substrates in Puck Bay (Hydrographic Office of the Polish Navy; Maritime Office in Gdynia; www.google.pl/maps; Michałek and Kruk-Dowgiałło, 2013 modified). EUNIS 2019 codes are explained in Table 2.

the sediments are dominated by sand and mud. Bare soft sediments prevail in most coastal areas of the eastern and western Baltic Sea where sandy and muddy habitats cover from 84.9% in the Estonian marine area up to 99.9% in the western Gulf of Finland (Martin et al., 2013). Due to high water dynamics (waves, currents), the surface sediments in Puck Bay are usually well sorted, homogeneous and of small organic matter content (0.1—5.0%) (Jankowska et al., 2014; Sokołowski, 2009; Sokołowski et al., 2015) especially in exsposed shallows such as the sandbank Rybitwia Mielizna (Kruk-Dowgiałło and Szaniwaska, 2008) which is the natural boundary between the inner and outer part of the bay. In the outer part of the bay, the cone shape of the seafloor (the so-called decantation basin) and large water depth enhance the deposition of suspended particles resulting in augmented organic matter content in the surface sediments that can reach 6.0% (Sokołowski, 2009). The accumulation of fine-grained organic-rich particles on the seafloor, low

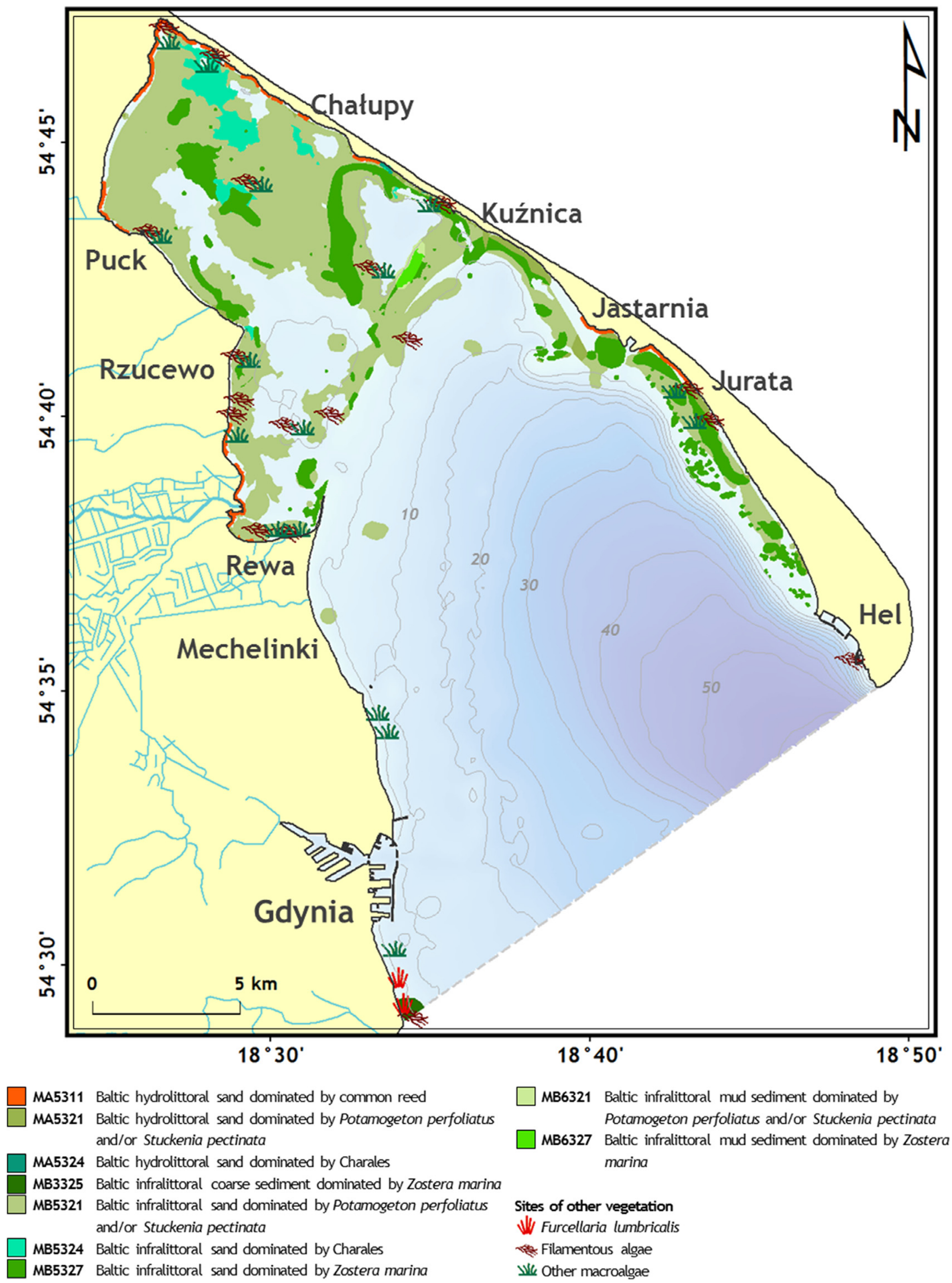

Figure 5 Areas and individual sites of the presence of benthic vegetation in Puck Bay (Bałazy (unpubl. data); Bełdowska et al., 2015; Gic-Grusza et al., 2009 (modified); Jankowska et al., 2016; Jędruch et al., 2019; Kruk-Dowgiałło et al., 2009; Smoła, 2012; Smoła et al., 2014; Sokołowski et al., 2015; Włodarska-Kowalczuk et al., 2014; Zgrundo (unpubl. data); https://www.iopan.pl/projects/Zostera (modified)).

hydrodynamics and relatively stable thermal conditions in the bottom zone all create favourable habitat conditions for the cold-water benthic macrofauna in this area. However, at limited dissolved oxygen concentration microbially and/or chemically mediated mineralisation of organic matter often leads to a periodic oxygen deficiency (hypoxia) that adversely affects many taxa. The harmful effects can be more severe if anoxia in the interstitial and/or overlying bottom water is accompanied by the production of toxic hydrogen sulphide and pH reduction. In consequence, the taxonomic diversity and density of the resident macrofaunal communities decline and opportunistic and oxygen deficiency-resistant species become dominant (Janas et al., 2004). Similar habitat conditions are also observed on the bottom of the post-dredging pits located in the shallow part of the Puck Lagoon along the Hel Peninsula (five post-dredging pits: Władysławowo, Chałupy, Kuźnica II, Kuźnica I and Jastarnia). These depressions are relatively small in size (total surface area of all post-dredging pits is 1.5 km^2) with water depth much greater (up to 12.8 m) than the natural depressions of the lagoon (Graca and Burska, 2009; Graca et al., 2004). They have been formed artificially due to sand extraction by stationary suction dredging for nourishing the open sea beach of the Hel Peninsula at its connection with the mainland (Piekarek-Jankowska et al., 2009; Uścinowicz et al., 2014).

More sheltered areas of variable bottom profiles with numerous furrows, shoals, and depressions generate diverse geo-physical environments in the bottom zone. The greatest diversity of benthic habitats occurs in the littoral and infralittoral zones where macroalgae and rooted vascular plants (halophilous vegetation, reed, rush, and submerged vegetation) grow abundantly (Schiewer, 2008). The shoreline vegetation assemblages are dominated by the typical marshy common reed *P. australis* which can form dense rushes adjacent to river plumes and in shallow inlets in the Puck Lagoon (Obolewski and Konkel, 2007). The reeds enhance the accumulation of organic matter and create thus favourable conditions for invertebrate species. Reed beds provide also breeding and feeding areas as well as refuges/shelter from predation for juvenile and adult fish (Díaz et al., 2015; Kraufvelin et al., 2018) and nesting and wintering grounds for sea birds (Obolewski and Konkel, 2007) and contribute to natural shore stabilisation (Michałek and Kruk-Dowgiałło, 2015). Sandy sediments to a maximum depth of about 6—8 m (depth of photosynthetic activity) also host abundant underwater macrophyte assemblages which are dominated by the pondweed *Stuckenia* spp. and seagrass *Z. marina* (Sokołowski et al., 2015). These habitats are classified as separate habitats (level 5): Baltic infralittoral sand dominated by *Potamogeton perfoliatus* and/or *Stuckenia pectinata* (MB5321) and Baltic infralittoral sand dominated by *Zostera marina* (MB5327). The seagrass meadows are among the most valuable of the habitats in the Polish coastal zone and the trajectory of the eelgrass presence in the inner Puck Bay has therefore been the subject of several floristic investigations. Extensive meadows were present in the bay in the 1950s when more than half of the seafloor (57.4%) was overgrown by *Z. marina* (Figure 6). From the late 1950s to the 1980s, the eelgrass area gradually decreased until it reached 4 km^2 in 1979 (Ciszewski et al., 1992). The decline was attributable largely to eutrophication and the resultant massive growth of filamentous algae that reduced the light transmittance and oxygen level in the bottom zone (Kruk-Dowigałło, 1991). Another reason for the degradation of this habitat includes intensive dredging the bottom for collection of the black carrageen *Furcellaria lumbricalis* for the production of agar (Węsławski et al., 2013). The low areal cover of eelgrass was observed until the early 2000s when it was estimated to amount to 3.2 km^2 (Węsławski et al., 2013). However, in 1984, Pliński (1986) reported an elevated total surface area covered by the meadows (21.1 km^2) in the Puck Lagoon. Within the last ten years a natural recovery of the eelgrass meadows has been observed, and today their area is estimated to reach 11.8 km^2 (Figure 6). The recovery is following a general trend observed for European seagrasses that have experienced an increase in areal distribution since the 2000s, related to national and regional actions to conserve and restore seagrass meadows by reducing nutrient loading and improving water quality (e.g. the measured induced by Europe Habitat Directive and the EU Water Framework Directive; de los Santos et al., 2019). In a manner similar to the reed beds, pondweed and seagrass meadows serve as shelter and as spawning, feeding and nursery grounds for many species of fish and benthic infauna and epifauna such as the mussel *Mytilus trossulus* (Figure 7) (Salo et al., 2009). Through increased accumulation of organic matter in surface sediments, increased microbiological activity (Jankowska et al., 2016) and the presence of other plants (macroalgae and epiphytes), they form a diversified and rich food base for animals of different trophic modes (herbivores, detritivores, omnivores and predators) (Sokołowski et al., 2015). This promotes the development of faunal assemblages of high taxonomic and functional diversity, and complex food links (Jankowska et al., 2018; Ziółkowska et al., 2018). The vicinities of the river mouths in the Puck Lagoon are also numerously covered by the filamentous green algae *Chaetomorpha linum* (Michałek and Kruk-Dowgiałło., 2013), whereas in the northern part of the lagoon the protected species of the Baltic stonewort *Chara baltica* can be found (Sokołowski et al., 2015). They together cover an area of 4.6 km^2 (1.2% of the total surface area of the bay).

Puck Bay is a semi-enclosed coastal area under pressure from various human activities such as shipping, bottom-contact fishing, tourism, industry and naval exercises that all cause serious environmental disturbances and directly impact benthic habitats. Artificial objects introduced in this area include linear hydrotechnical constructions (e.g., harbour infrastructure, industrial and military hydrotechnical structures, coastal protection engineering constructions) and free-standing underwater objects (e.g. pipelines, sewage treatment plant collectors, shipwrecks, sunken anchors). Though their total surface area is relatively low (0.2%), the large extent (nearly 50.9% of the total coastline length of the bay) and a high number of anthropogenic objects make them an important substratum for sessile and mobile benthic fauna. The distribution area and ecological functions provided by hard substrates in coastal systems vary markedly in different Baltic regions. In the western part of Baltic Sea, natural hard-substrate habitats, classified as photic/aphotic mixed substrate dominated by Mytilidae and by the epibenthic community, constitute 4.2% of the total area of the German Baltic (Schiele et al., 2015). In the Estonian marine areas (northern Baltic Sea), which include parts of the Gulf of Finland, the Gulf of Riga, the whole West Estonian Archipelago Sea and part of the Baltic Proper, habitats defined as reefs occupied as much as 52.8% of the seafloor (Torn et al., 2017). A high percentage contribution of sheltered and moderately exposed hard bottoms of up to 15.1% was also reported along the west coast of the Gulf of Riga by Martin et al. (2013). In contrast, hard bottom makes up as little as 0.3% and 0.1% of the surface area in the

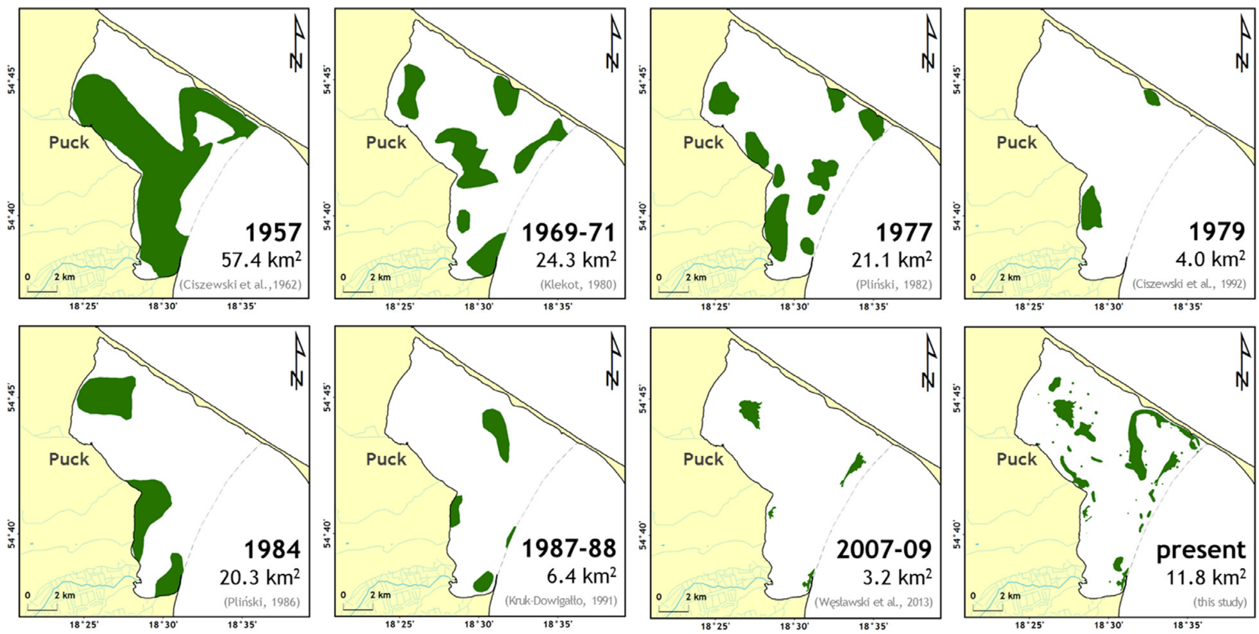

Figure 6 Long term changes in the distribution of the *Zostera marina* meadows in the Puck Lagoon. Inserts present a total surface area occupied by the seagrass. Klekot (1980), Pliński (1982), Ciszewski et al. (1962).

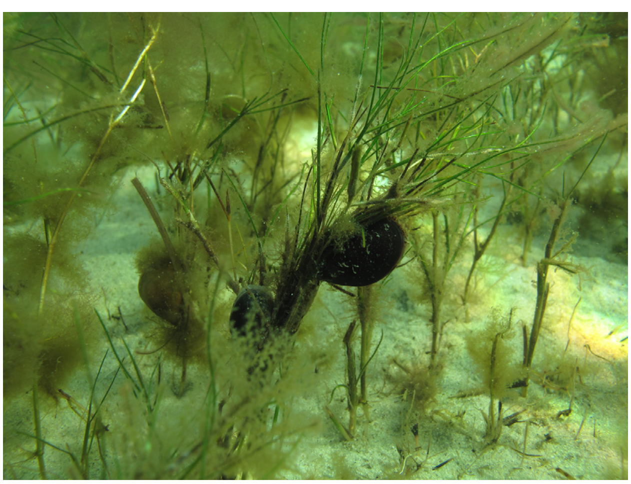

Figure 7 Mussel *Mytilus trossulus* attached to the pondweed *Stuckenia* spp. in the sublittoral zone near Kuźnica (photo: A. Sokołowski).

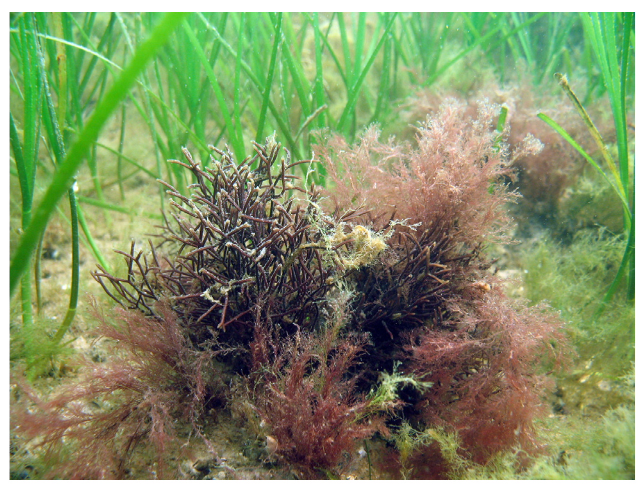

Figure 8 The black carrageen *Furcellaria lumbricalis* growing on stones in the vicinity of the seagrass *Zostera marina* meadows in the coastal zone close to the Orłowo Cliff (photo: P. Bałazy).

eastern and western parts of the Gulf of Finland, respectively (Martin et al., 2010 2013). In Puck Bay, the hard substrate promotes development not only of benthic epifaunal (fouling) species but also of phytophilous animals and even infauna (Balazy et al., 2019). Under favourable light and thermal conditions in the shallow-water areas of restricted hydrodynamics the hard substratum is massively overgrown with macroalgae (mainly green algae of the genera *Ulva* and *Cladophora*; Figure 3) and red algae such as *Polysiphonia fucoides* and *Ceramium diaphanum* (Kruk-Dowgiałło and Szaniwaska, 2008; Kruk-Dowgiałło et al., 2009) and microphytobenthos which creates a thin organic-rich layer inhabited by small infauna (Sokołowski et al., 2017a, 2017b). On hard substratum, a valuable natural biotic structure is also formed by the protected red algae *F. lumbricalis* that is observed on the stony bottom at the foot of the Orłowo Cliff (Figure 8). Communities of these plants do not have the status of separate habitats in the EUNIS 2019 classification system, but the areas of occurrence of the most important vascular plants and macrophytes were listed in Figure 5. The macrofaunal communities inhabiting the hard substrate show a usually greater taxonomic diversity and density than those occurring on adjacent sandy and muddy sediments (Balazy et al., 2019). Underwater anthropogenic objects, boulders and stones located in species-poor soft sediments are even referred to as "biodiversity hot spots" with increased biodiversity (Meyer et al., 2016) and stepping-stones for the dispersal and potential biogeographical range shifts of organisms (Firth et al., 2016).

4.2. Evaluation of the classification map — completeness of the data and limitations

Typological analyses of the bottom habitats were based on inventory datasets from 1995 to 2019 which accounted for hydrological (water and light transmittance depths), geomorphological (a type of sediment), navigation (hydrotechnical infrastructure and anthropogenic objects) and biotic (the presence of benthic vegetation and dominant plant species) parameters at selected sites located in the area of Puck Bay. Information on taxonomic composition and distribution of macrobenthic faunal species was not included in the analysis due to scattered and discontinuous faunistic data. Biological-based classification can be therefore a subject of future study using spatial modelling techniques that link environmental data with biological features (e.g. the HELCOM HUB system). However, the implementation of an environmental-based classification approach to define seabed habitats has been considered to show several appealing advantages over a more biological-based classification (Brown et al., 2011; Cooper et al., 2019). The physical terrain is less likely to vary seasonally or over years, thus reducing temporal variability within and among habitats. Though the datasets used in this study covered a long time period, and extrapolation was made for some seabed point data, the resulting classification map of benthic habitats is satisfying, discriminates well between different seabed types, and provides valuable information.

The final map of benthic habitats was generated by merging individual maps (layers) of different seabed properties, and such an ensemble map has been used as a way of improving classification performance (Diesing et al., 2020). The overall accuracy of the map was considered satisfactory.

5. Summary

Recognising the necessity of mapping benthic habitats in Puck Bay (southern Baltic Sea), induced by its high unique biological value and aesthetic quality on one side and by the increasing use of this area by a human on the other, a consistent benthic habitat map was constructed combining substrate characteristics and benthic plant communities. Detailed maps of the distribution of the main benthic habitats (according to the revised EUNIS 2019 classification system) were presented along with their surface area and location of the most important vascular plants, macrophytes (often of protective status) and man-made hydrotechnical structures and underwater objects. Such comprehensive documentation of the bay seafloor provided a fundamental spatial organizing framework to implement and integrate research (including monitoring) programs and to provide the capability to effectively communicate information and results to coastal ecosystem managers.

Declaration of Competing Interest

The authors Adam Sokołowski, Emilia Jankowska, Piotr Balazy and Agnieszka Jędruch of the manuscript "A comprehensive description of benthic habitats in Puck Bay (Gulf of Gdańsk, southern Baltic Sea)" declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors wish to thank Lang Lab s.c. for proofreading the text.

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