UNIWERSYTET GDAŃSKI
WYDZIAŁ OCEANOGRAFII I GEOGRAFII

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Structural and functional diversity of benthic assemblages on artificial substrates and the adjacent natural bottom in the Gulf of Gdańsk

Strukturalna i funkcjonalna różnorodność zespołów bentosowych na sztucznym podłożu i sąsiadującym z nim dnie naturalnym w Zatoce Gdańskiej.

PhD thesis written under the supervision of
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Abstract

Over centuries of human activity at sea various man-made structures e.g. oil platforms, shipwrecks and wind turbines became an inherent element of the marine environment. As a result of rapid development of the offshore wind industry during the last three decades the number of anthropogenic structures at European Seas grew substantially. With its wind potential estimated at approximately 6000 wind turbines by the year 2050 the Baltic Sea may also face a wide-spread construction of man-made structures in a relatively short time. This may affect various components of the marine environment including macrozoobenthos.

The taxonomic composition of macrobenthic assemblage depends on the type of sediment. Soft bottom made of sand or mud provides a suitable habitat for species that live partially or wholly within sediment. On the other hand hard substrate e. g. bedrock, concrete or metal is impenetrable by infaunal species, but provides a solid foundation for sessile epifaunal species to attach to. Hard substrate macrobenthic assemblages are often characterized by higher species richness and density than their soft bottom counterparts. This is caused by high density of sessile filter-feeding species i.e. mussels, barnacles and various cnidarians. They create a multi-layered, three-dimensional structure over an otherwise featureless flat surface. Such structures can be inhabited by numerous mobile species of crustaceans, polychaetes and gastropods.

Considering the significant difference in properties between artificial hard substrate and natural soft bottom, an introduction of man-made structure into an environment made predominantly of soft sediments may significantly alter taxonomic composition of the local macrobenthic assemblage. The following thesis aimed at providing a comprehensive study of potential impacts of man-made structures on macrobenthic assemblages in the Baltic Sea. Three research problems relevant for biodiversity conservation in this brackish, species-poor environment were chosen.

Because of the relatively low species richness and diversity of the Baltic Sea, any process that could potentially enhance local diversity is worthy of investigation. In the first study included in the thesis benthic communities inhabiting natural and artificial hard substrate in the Gulf of Gdańsk were compared in order to test **hypothesis whether an artificial structure presents a surrogate for natural rocky substrate and supports equal benthic communities in terms of their taxonomic composition, abundance, biomass as well as structural and functional diversity.**

One of the most frequently raised potential negative impacts of man-made structures is that they may facilitate introduction and secondary spread of non-indigenous species. The issue of non-native species is particularly relevant for the Baltic Sea, as it is highly susceptible to biological invasions due to its estuarine character. The study included in the thesis involved a comparison of the abundance and number of non-native species between natural and artificial hard substrates in the Gulf of Gdańsk in order to test the **hypothesis that the artificial substrate offers more favorable habitats for non-indigenous organisms than natural hard bottom.**

Hard bottom benthic communities are often characterized by high abundance and biomass. It has been reported that large density of filter-feeding organisms may result in an increased deposition of organic matter in the vicinity of an artificial structure. To a certain extent it may increase the food source for some macrobenthic species. However an excess of organic matter could lead to diminished oxygen concentration near the bottom and negatively affect benthic organisms. As the Baltic Sea is already strongly affected by hypoxia and anoxia, a potential extension of these phenomena requires investigation. The third study included in the thesis involved a comparison of oxygen concentration and soft bottom benthic assemblages at varying distance from artificial structure in order to test the **hypothesis whether it can lead to a significant decrease in oxygen concentration and in consequence negatively affect benthic invertebrates.**

Sampling was conducted at three sites in the Gulf of Gdańsk from July 2015 to November 2017. Macrobenthic samples were collected at three different types of substrate: artificial hard substrate provided by 70-year old man-made structures, natural hard substrate provided by boulders originating from eroded cliffs and natural sandy bottom near one of the man-made structures. Samples at artificial substrate were collected at several depths (0, 2, 4 and 8 m). Soft bottom assemblages were sampled 1, 7 and 50 m away from a man-made structure. Long-term data on water temperature and oxygen concentration were collected using data loggers at the three distances.

The obtained results revealed that the macrobenthic assemblage inhabiting artificial substrate is not a surrogate for the natural hard substrate community. The assemblage at artificial structure was characterized by lower species richness but higher biomass. Overall functional diversity of macrozoobenthos was relatively low at both types of substrate due to a high dominance of traits expressed by sessile filter-feeding species.

The direct comparison of assemblages between natural and artificial substrate at the same depth did not indicate that non-native species preferred artificial structure over natural substrate. The average richness and relative abundance of non-native species was higher at natural substrate than at artificial structure. However individual non-indigenous species were found in greater numbers at lower depths where only artificial substrate was present.

An oxygen depletion near the structure was observed. The five-month average at 1 m was 0.6 mg · L^{-1} lower compared to 7 and 50 m away from the structure. The monthly average was lower at 1 m compared to the two other sites by up to 1.0 mg · L^{-1} in September, October and November of 2017. The highest observed difference in single measurements between 1 m and the other sites was 3.7 mg · L^{-1}. However the negative impact on oxygen concentration close to the structure was not reflected in soft bottom macrobenthic assemblage. Taxonomic richness, abundance and biomass of benthic macrofauna were generally similar or higher at the two sites close to the structure compared to 50 m away.

In conclusion the impact of man-made structure on macrobenthic assemblages was reflected mainly by their enhanced density and biomass on the structure itself and at nearby soft bottom. A positive impact on biodiversity is debatable as the community was heavily dominated by few species and did not provide a surrogate for natural hard substrate assemblage. Moreover the provision of suitable habitats for non-native species particularly at lower depths is a potential threat for biodiversity. High density of macrofauna on the structure resulted in an oxygen depletion in its vicinity, but not to such an extent, that would negatively affect the macrofaunal assemblage.

Streszczenie

Na przestrzeni wieków działalność człowieka na morzach sprawiła, że obiekty pochodzenia antropogenicznego takie jak platformy wiertnicze, wraki statków i turbiny wiatrowe stały się nieodłącznym elementem środowiska morskiego. Na skutek gwałtownego rozwoju morskiej energetyki wiatrowej w ciągu ostatnich trzech dekad liczba budowli morskich na morzach europejskich znacząco wzrosła. Do roku 2050 na Morzu Bałtyckim może powstać nawet 6000 turbin wiatrowych, co wiązałoby się z wprowadzeniem do środowiska znaczącej liczby sztucznych obiektów w stosunkowo krótkim czasie. Może to wpłynąć na różne elementy środowiska morskiego, w tym na makrozoobentos.

Skład taksonomiczny zespołów makrobentosowych zależy w dużej mierze od rodzaju osadu, na którym występują. Dno piaszczyste lub muliste, w literaturze anglojęzycznej określane mianem „dna miękkiego" (ang. *soft bottom*), stanowi odpowiednie siedlisko dla gatunków żyjących częściowo lub całkowicie pod powierzchnią osadu. Natomiast twarde podłoże, np. głazy, kamienie lub betonowe i metalowe elementy budowli stanowią stabilne podłoże dla osiadłych gatunków przytwierdzających się na stałe do dna. Zespoły makrobentosowe zasiedlające podłoże twarde często charakteryzują się większym bogactwem gatunkowym i zagęszczeniem niż te występujące na dnie miękkim. Wynika to z dużej liczebności osiadłych organizmów filtrujących takich, jak omułki i pąkle. Tworzą one wielowarstwową, trójwymiarową strukturę na płaskiej powierzchni. Taka struktura stanowi sprzyjające siedlisko dla licznych gatunków mobilnych skorupiaków, wieloszczetów i ślimaków.

Biorąc pod uwagę istotne różnice w właściwościach między sztucznym twardym podłożem a naturalnym dnem miękkim, pojawienie się konstrukcji antropogenicznej w środowisku zdominowanym przez osady piaszczyste i muliste może doprowadzić do istotnych zmian w składzie taksonomicznym lokalnych zespołów makrobentosowych. Celem niniejszej pracy było poznanie potencjalnego wpływu budowli morskich na zespoły makrobentosowe w Morzu Bałtyckim. Wybrano trzy problemy badawcze istotne z punktu widzenia ochrony bioróżnorodności w tym ubogim gatunkowo środowisku.

Ze względu na stosunkowo niskie bogactwo gatunkowe i różnorodność biologiczną makrobentosu Morza Bałtyckiego, każdy proces mogący potencjalnie zwiększyć ww. cechy wymaga bliższego zbadania. W ramach pierwszego problemu badawczego porównano zespoły bentosowe zasiedlające naturalne i sztuczne twarde podłoże w Zatoce Gdańskiej, aby sprawdzić hipotezę mówiącą, że budowla morska może

stanowić substytut dla naturalnego podłoża kamienistego oraz siedlisko dla zespołów bentosowych o podobnym składzie taksonomicznym, liczebności, biomasie oraz różnorodności strukturalnej i funkcjonalnej.

Jednym z najczęściej wymienianych w literaturze negatywnych skutków powstawania budowli morskich jest to, że mogą ułatwiać introdukcję i wtórne rozprzestrzenianie gatunków obcych. Problem gatunków obcych jest szczególnie istotny dla Morza Bałtyckiego, które ze względu na swój słonawowodny charakter jest wyjątkowo podatne na inwazje biologiczne.

W ramach drugiego problemu badawczego porównane zostały liczba i zagęszczenie gatunków obcych występujących na naturalnym i sztucznym twardym podłożu w Zatoce Gdańskiej, aby sprawdzić hipotezę, czy sztuczne podłoże stanowi bardziej sprzyjające siedlisko dla gatunków obcych niż naturalne dno kamieniste.

Zespoły bentosowe na twardym dnie często charakteryzują się wysokim zagęszczeniem i biomasą. Może to prowadzić do zwiększonego transportu materii organicznej do dna w pobliżu morskich budowli. Do pewnego stopnia może to stanowić dodatkowe źródło pokarmu dla organizmów makrobentosowych. Jednak nadmiar materii organicznej może prowadzić do obniżenia stężenia tlenu w pobliżu dna i negatywnie wpływać na organizmy bentosowe. Problem hipoksji i anoksji jest bardzo istotny dla Morza Bałtyckiego. Dlatego potencjalne zwiększenie zasięgu tych zjawisk wymaga zbadania. W ramach trzeciego problemu badawczego porównano stężenie tlenu oraz zespoły makrobentosowe na dnie miękkim w różnych odległościach od budowli morskiej, aby sprawdzić hipotezę, że obecność budowli morskiej może prowadzić do istotnego spadku stężenia tlenu rozpuszczonego w wodzie, a w konsekwencji negatywnie wpływać na bezkręgowce bentosowe.

Zbiór prób przeprowadzono na trzech stacjach badawczych w Zatoce Gdańskiej w okresie od lipca 2015 do listopada 2017. Próby makrozoobentosu zebrano z trzech typów podłoża: sztucznego twardego podłoża (budowle morskie z okresu II Wojny Światowej), naturalnego twardego podłoża (głazy pochodzące z erozji klifów) oraz naturalnego piaszczystego dna w pobliżu jednej z budowli. Próbki z budowli zostały zebrane na kilku głębokościach (0, 2, 4 i 8 m). Próby makrozoobentosu z dna piaszczystego pobierano w odległości 1, 7 i 50 m od budowli. Oprócz tego w podanych odległościach prowadzono długoterminowe pomiary temperatury i stężenia tlenu.

Uzyskane wyniki wykazały, że zespół makrobentosowy zasiedlający sztuczne podłoże różni się od zespołu na naturalnym podłożu kamienistym. Zespół zasiedlający

budowlę charakteryzował się niższym bogactwem gatunkowym, ale większą biomasą organizmów. Różnorodność funkcjonalna makrozoobentosu była stosunkowo niska na obu typach podłoża, ze względu na dominację cech biologicznych reprezentowanych przez osiadłe gatunki filtratorów.

Bezpośrednie porównanie zespołów z naturalnego i sztucznego podłoża na tej samej głębokości nie wykazało, aby podłoże sztuczne stanowiło siedlisko bardziej sprzyjające gatunkom obcym. Liczba gatunków obcych i ich udział w całkowitym zagęszczeniu makrozoobentosu były wyższe na podłożu naturalnym. Jednakże niektóre gatunki obce występowały licznie na mniejszych głębokościach, na których występowało wyłącznie sztuczne podłoże.

Zaobserwowano spadek stężenia tlenu w pobliżu budowli. Średnie stężenie tlenu z pięciu miesięcy było o 0.6 mg · L^{-1} niższe w odległości 1 m od budowli niż w odległości 7 i 50 m. We wrześniu, październiku i listopadzie 2017 r różnica w średniej miesięcznej wynosiła 1.0 mg · L^{-1}. Największa zaobserwowana różnica w pojedynczym pomiarze wyniosła 3.7 mg · L^{-1}. Jednakże ten spadek stężenia tlenu nie miał znaczącego negatywnego wpływu na zespoły makrobentosowe zasiedlające dno piaszczyste. Bogactwo gatunkowe, zagęszczenie i biomasa makrozoobentosu w bliskim sąsiedztwie budowli były na ogół zbliżone lub wyższe niż w odległości 50 m.

Podsumowując, wpływ budowli morskich na zespoły makrobentosowe przejawia się głównie wysokim zagęszczeniem i biomasą na samych strukturach oraz na dnie miękkim w ich bezpośrednim sąsiedztwie . Potencjalny pozytywny wpływ na różnorodność biologiczną jest niepewny, ponieważ zespoły te są silnie zdominowane przez pojedyncze gatunki i nie stanowią substytutu dla zespołów naturalnego twardego podłoża. Ponadto tworzenie dogodnych siedlisk dla gatunków obcych, szczególnie na mniejszych głębokościach, stanowi potencjalne zagrożenie dla bioróżnorodności. Wysokie zagęszczenie i biomasa makrofauny na budowli powoduje spadek stężenia tlenu w ich pobliżu, jednak nie w stopniu, który negatywnie wpływałby na zespoły makrobentosowe.

List of publications included in the doctoral thesis

1. **Brzana, R**., Peschke, M. B., & Janas, U. (2024). Biodiversity and functioning of benthic macrofauna associated with natural and artificial hard substrate in the Gulf of Gdańsk (Baltic sea). *Marine Environmental Research*, *199*, 106592. https://doi.org/10.1016/j.marenvres.2024.106592

   IF: 3.2, points of the Ministry of Education and Science: 100

2. **Brzana, R**., & Janas, U. (2025). Natural hard substrate and 70-year-old artificial offshore structures as habitats for non-indigenous species in the brackish environment of the Baltic Sea. *Marine Environmental Research*, 107222. https://doi.org/10.1016/j.marenvres.2025.107222

   IF: 3.2, points of the Ministry of Education and Science: 100

3. **Brzana, R**., Janas, U., & Tykarska, M. B. (2019). Effects of a 70-year old artificial offshore structure on oxygen concentration and macrobenthos in the Gulf of Gdańsk (Baltic Sea). *Estuarine Coastal and Shelf Science*, *235*, 106563. https://doi.org/10.1016/j.ecss.2019.1065632

   IF: 2.6, points of the Ministry of Education and Science: 100

General introduction

Macrobenthos is a group of aquatic organisms larger than 1 mm, that dwell at the bottoms of water bodies. Benthic macrofauna consists mainly of invertebrates. The most commonly represented taxonomic groups are crustaceans, bivalves, gastropods, echinoderms and polychaetes (Tagliapietra & Sigovini, 2010). Macrobenthic assemblages are an important component of aquatic ecosystems for many reasons. They are crucial for vital processes such as nutrient cycling, sediment bioturbation and energy flow within food webs (Boudreau, 1994; Graf and Rosenberg, 1997; Tagliapietra & Sigovini, 2010; Janas et al., 2019; De Borger et al., 2025). Many macrobenthic species are an important food source for commercially important fish species e.g. cod, while others like mussels and shrimps are directly harvested and consumed by humans (Haase et al., 2020; Soliño & Figueras, 2025; Urzúa & Gebert, 2025). Additionally macrobenthos is a reliable bioindicator of the environmental health due to its sensitivity to habitat changes (Han & Han, 2024). Finally macrobenthos is a highly diverse group of organisms which makes it relevant for biological diversity conservation (Snelgrove, 1999; Gislason et al., 2017).

Benthic organisms' ecology is strongly related to the type of substrate they dwell on. Substrate type is often the most influential factor in determining structure and diversity of a benthic assemblage (Newell et al., 2001; Anderson, 2008, Cooper & Barry, 2017). Many benthic species live wholly or partly within the bottom sediments for food availability and shelter. Such organisms require soft substrate i.e. sand or silt that allows them to bury in and/or create burrows. On the other hand many sessile species attach permanently to the bottom substrate and may require a stable, hard surface i.e. bedrock, boulders.

Macrobenthic assemblages that develop on hard substrate are often characterized with higher species richness and abundance than those found at soft bottom. This is mainly caused by high density of sessile filter-feeding species i.e. mussels, barnacles and various cnidarians. They create a multi-layered, three-dimensional structure over an otherwise featureless flat surface. Such structures can be inhabited by numerous mobile species of crustaceans, polychaetes, gastropods (Suchanek, 1985; Borthagaray and Carranza, 2007; Silliman et al., 2011; Bagur et al., 2016). Such habitats are believed to benefit commercially important species of demersal fish and megafaunal invertebrates, as they can act as shelter and food source (Sheehan et al., 2013; Krone et al., 2017; Støttrup et al., 2019; Schwartzbach et al., 2020; Flávio et al., 2023).

Not only natural hard substrate like bedrock and boulders provide surfaces suitable for benthic epifauna to settle on. Over centuries human activity has led to an introduction of countless man-made structures at sea. Buoys, oil platforms, breakwaters, jetties, artificial reefs, shipwrecks and offshore windfarms have become an inherent element of the marine environment (Bugnot et al., 2020; Elrick-Barr et al., 2021). Such structures provide hard surfaces that are colonized by epifaunal macrobenthic organisms in a short time after introduction (Dziubińska & Janas, 2007, Joschko et al., 2008; De Mesel et al., 2015; Zupan et al., 2023). If left undisturbed they can develop into a dense assemblage (Zintzen et al., 2005; Coolen et al., 2018; Schutter et al., 2019). When an artificial hard substrate is introduced to a habitat made predominantly of soft sediment, it can be a significant change for local benthic assemblage (Macreadie et al., 2011; Dannheim et al., 2025; De Borger et al., 2025). Moreover man-made structures exhibit unique features that they do not share with natural hard substrates (Coolen et al., 2018). Most importantly they can span through the entire water column providing a linkage between the surface zone and the seabed (Lindeboom et al., 2011).

Although an introduction of artificial hard substrate may significantly alter benthic habitat it has been generally perceived as having potentially positive effects, as marine hard substrates are associated with relatively high abundance and richness of epifaunal invertebrates that can potentially positively affect fish (Dannheim et al., 2019; Buyse et al., 2022; Witte et al., 2024).

Although man-made structures have been present in marine environments for many centuries, a particularly rapid rise in their number has been observed in the last 3 decades especially at the European seas (Dannheim et al., 2019; Birchenough & Degraer, 2020). In 2023, the European Union adopted a set of proposals to make its policies fit for reducing net greenhouse gas emissions by at least 55% by 2030, compared to 1990 levels. The ultimate goal of the European Union is to become climate-neutral by the year 2050 (www.europa.eu). In order to achieve these commitments many European countries began development of numerous renewable energy projects. With a limited space on land for the required infrastructure in the already heavily urbanized continent, marine offshore areas have been recognized as suitable sites for construction of renewable energy equipment, mainly wind turbines. The first offshore wind farm consisting of 11 wind turbines was constructed in 1991 off the coast of Denmark (www.balticwind.eu). Since then over 120 new windfarms consisting in total of over 6000 turbines have been constructed at European Seas, mainly on the North Sea. Currently the development of

offshore renewables on the Baltic Sea is speeding up as well. The European Commission estimates the total offshore wind potential of the Baltic Sea region at 93 GW by 2050 which translates to approximately 6000 new wind turbines (www.balticwind.eu).

The Baltic Sea, particularly in its southern part, is dominated by sandy and muddy bottoms (Gogina & Zettler, 2010; Kyryliuk & Kratzer, 2016). The natural rocky bottom in the southern Baltic Sea is present in several areas e.g. in Słupsk Bank, off the coast of Rowy and in few spots in the Gulf of Gdańsk (Andrulewicz et al., 2004; Grzelak & Kuklinski, 2010; Sokołowski et al., 2021). With that in mind the expected wide-scale construction of offshore wind farms and simultaneous introduction of a substantial amount of artificial hard substrate may significantly alter benthic habitats over large areas.

The majority of research concerning the potential effects of offshore man-made structures on macrobenthic assemblages has been conducted in the North Sea, where the development of offshore wind farm industry is far more advanced. Some of these observations can be applied universally to other regions. On the other hand the Baltic Sea is characterized by several important distinguishing features that result in specific structure of benthic macrofauna (Zettler et al., 2008; Leppäkoski et al., 2009). Most importantly high freshwater input combined with limited seawater exchange with the North Sea result in a salinity gradient ranging from 20 in the south-western part to 2 in the north-eastern part of the Baltic Sea (Gogina & Zettler, 2010; Kniebusch et al., 2019; Lehmann et al., 2022). In the Baltic Proper salinity ranges from 5 to 8 (Gogina & Zettler, 2010; Ojaveer et al., 2010). Such salinity range has been described as particularly challenging for both marine and freshwater organisms (Gogina & Zettler, 2010; Zettler et al., 2013). As a result biota in the south-eastern Baltic Sea is characterized with relatively low richness and diversity and consists mainly of opportunistic organisms with high adaptive potential (Bonsdorff, 2006; Ojaveer et al., 2010; Włodarska-Kowalczuk et al., 2010). In case of Baltic macrozoobenthos it leads to an absence of some influential groups such as echinoderms, megafaunal decapods and sessile cnidarians.

On a wide scale the most commonly found macrobenthic species in the southern Baltic Sea are associated with sandy or muddy sediment (Gogina et al., 2016; Sokołowski et al., 2021). These include amphipods *Monoporeia affinis, Pontoporeia femorata, Corophium volutator,* isopod *Saduria entomon*, bivalves *Mya arenaria, Macoma balthica, Cerastoderma glaucum* (fig. 1), gastropods from Hydrobidae family and polychaetes *Hediste diversicolor, Pygospio elegans* and *Marenzellaria* spp. (Janas & Kendzierska, 2014; Gogina et al., 2016).

Fig. 1. *Cerastoderma glaucum* buried in sandy sediment (photograph by R. Brzana) .

The key sessile epifaunal species associated with hard substrates are blue mussel *Mytilus trossulus* (fig. 2), barnacle *Amphibalanus improvisus* (fig. 3) and bryozoan *Einchornia crustulenta*. They are accompanied by various species of mobile invertebrates, mainly crustaceans (predominantly amphipods and isopods), polychaetes and gastropods (fig. 4) (Andrulewicz et al. 2004; Grzelak & Kukliński, 2010; Brzana & Janas, 2016; Balazy et al., 2019).

The following thesis aims at providing a comprehensive study of potential impacts of man-made structures on macrobenthic assemblages in the southern Baltic Sea. Benthic assemblages associated with artificial structures and natural bottoms located in the Gulf of Gdańsk were investigated. The structures chosen for sampling were constructed over 70 years prior to the research, which allowed the study of mature benthic assemblages.

Fig. 2. Blue mussels *Mytilus trossulus* (photograph by R. Brzana).

Fig. 3. Barnacle *Amphibalanus improvisus* attached to *Mytilus trossulus* shell (photograph by R. Brzana).

Fig. 4. An amphipod *Gammarus* sp. on epifaunal assemblage of mussels *Mytilus trossulus* and barnacles *Amphibalanus improvisus.*

Research problems and hypotheses

1. **Structural and functional diversity of macrobenthic assembalges on artificial and natural hard substrate.**

As the brackish environment of the Baltic Proper supports a relatively low species richness and diversity, any process that could potentially enhance local diversity is worthy of investigation. In the first study included in the following thesis benthic communities inhabiting natural and artificial hard substrate in the Gulf if Gdańsk were compared in order to test hypotheses whether an artificial structure presents a surrogate for natural rocky substrate and supports equal benthic communities in terms of their taxonomic composition, abundance, biomass as well as structural and functional diversity.

2. **Artificial and natural hard substrate as habitats for non-native species.**

Although an introduction of artificial hard substrate has been reported to have mostly positive effects for macrobenthic assemblages it is not without potential negative impacts. One of the most frequently raised issues is that man-made structures may facilitate introduction and secondary spread of non-indigenous species (NIS) that can outcompete native species at uninhabited surfaces provided by newly built structures

(Glasby et al., 2006; Kerckhof et al. 2011; De Mesel et al., 2015). The issue of non-native species is particularly relevant for the Baltic Sea, as it is highly susceptible to biological invasions due to its estuarine character (Leppäkoski et al., 2002; Streftaris et al., 2005). The study included in the following thesis involved a comparison of the number and abundance of non-native species between natural and artificial hard substrates in the Gulf of Gdańsk in order to test the hypothesis that the artificial substrate offers more favourable habitats for non-indigenous organisms over natural hard bottom.

3. Effects of an artificial offshore structure on oxygen concentration and soft bottom macrobenthos

The richness of hard bottom benthic communities is often paralleled by high abundance and biomass. It has been reported that large density of filter-feeding organisms may result in an increased deposition of organic matter in the vicinity of an artificial structure and in consequence influence diversity and abundance of soft bottom benthic communities (Dannheim et al., 2019; Dannheim et al., 2025; De Borger et al., 2025)**.** To a certain extent it could have positive outcomes for soft bottom organisms living close to the structure, as it may increase the food source for some species (Ysebaert et al., 2008; Maar et al., 2009). In extreme cases however an excess of organic matter not consumed by macrofauna could lead to diminished oxygen concentration near the bottom and negatively affect benthic organisms leading to lower abundance and diversity (Chamberlain et al., 2001; Wilding, 2012, 2014). As the Baltic Sea is already strongly affected by hypoxia and anoxia, a potential extension of these phenomena requires investigation (Diaz & Rosenberg, 1995; Rosenberg et al., 2002; Kendzierska & Janas, 2024). The third study included in the thesis compared oxygen concentration and soft bottom benthic assemblages at varying distance from artificial structure in order to test the hypothesis whether it can lead to a significant decrease in oxygen concentration and in consequence negatively affect benthic invertebrates.

Material and methods

The research described in the three publications included in the thesis was conducted entirely in the Gulf of Gdansk, the southern Baltic Sea, at three sites (fig. 5). Two sites (B and O) were located off the western coast of the gulf and one site (J) was located off the northeastern coast of the gulf. The majority of the research was conducted at site B (Babie Doły), which was located 900 m offshore at 8 m depth. Site O (Orłowo)

was located 320 m offshore at 5 m depth. Site J (Jastarnia) was located over 2.17 km offshore at 4 m depth. Sampling was carried out from July 2015 to November 2017.

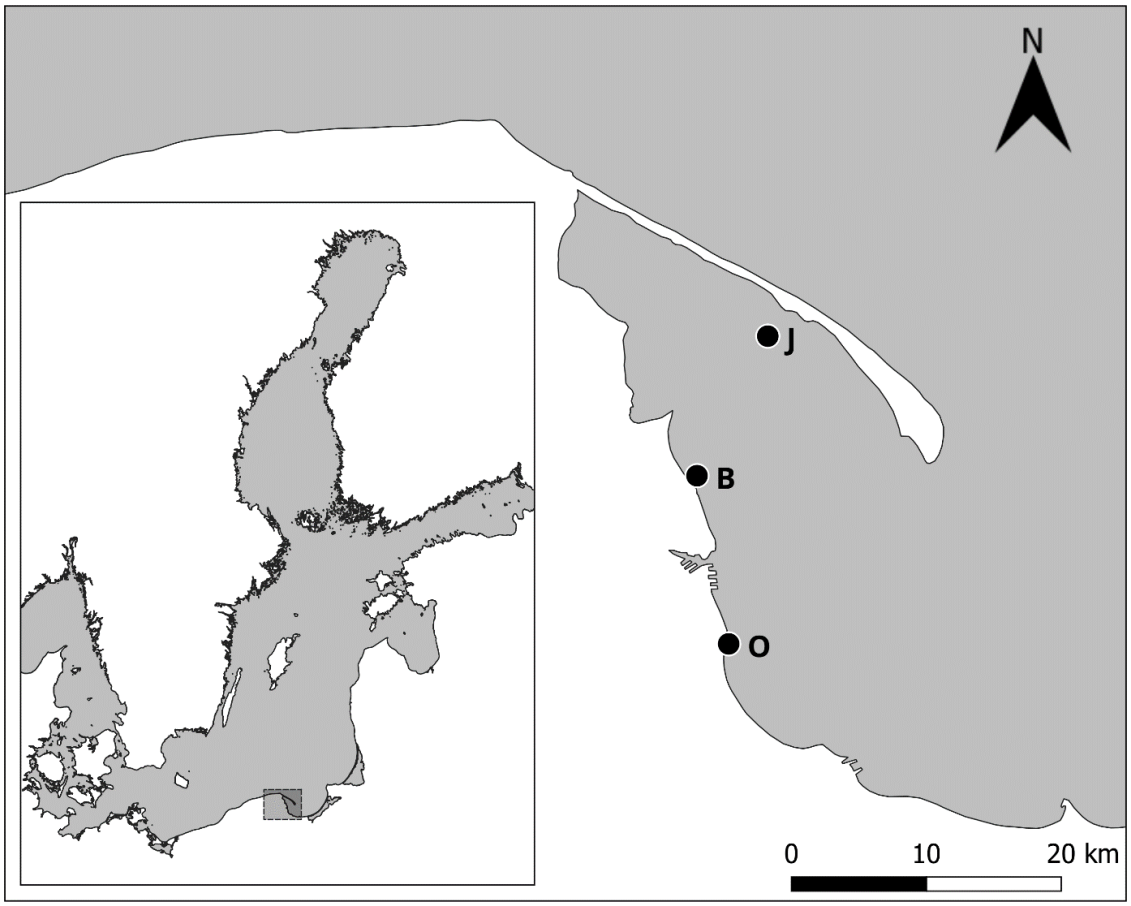

Fig. 5. Locations of study sites.

Assemblages associated with natural rocky bottom were sampled at sites B and O. Communities inhabiting artificial hard substrate were sampled at site B and J. Samples of soft bottom macrofauna were collected at site B. The natural hard substrate at sites B and O was represented by boulders (up to 2 m in diameter) elevated up to 1 m above the sandy seabed (fig. 7). The boulders originate from the eroded cliffs at the western coast of the Gulf of Gdansk. The artificial substrate at sited B and J was represented by concrete remains of two 70-year-old offshore structures that were part of a torpedo testing complex constructed during World War II. Both structures at sites B and J provide a vertical, smooth hard surface that extends from the seabed up to 1 m above the water surface. The structure at site B is 17 m long, 7.5 m wide and lies at a depth of 8 m (fig. 6). The structure at site J is 9 m long, 4 m wide and lies at 4 m depth. Soft sediment at site B was identified as medium and coarse sand.

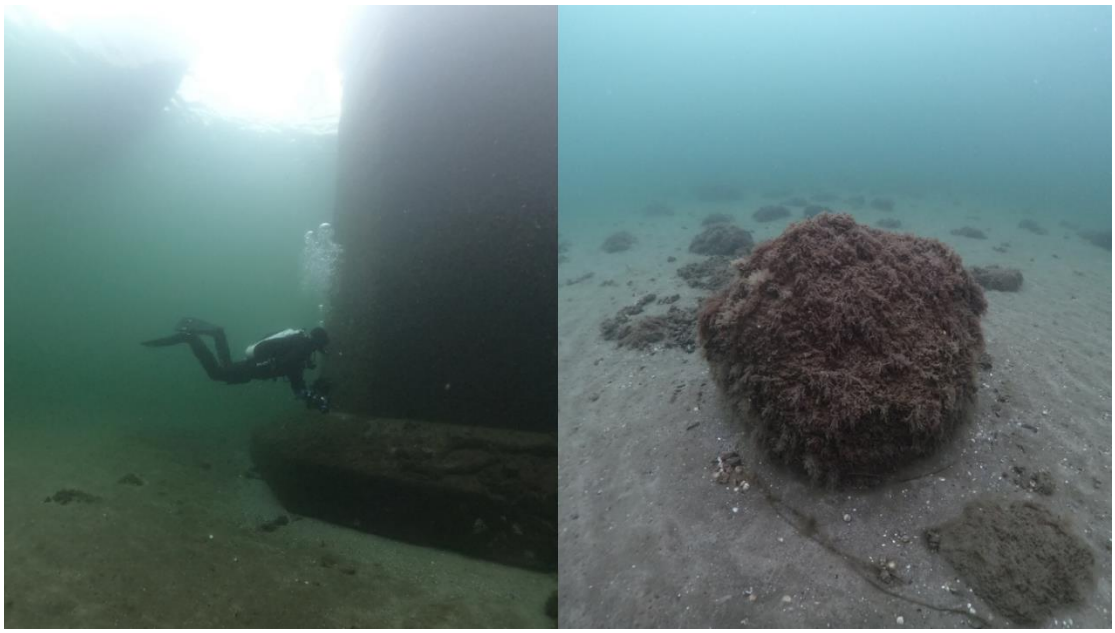

Fig. 6. Man-made structure (left) and natural boulders (right) at site B (photographs by R. Brzana).

Samples from hard substrate were collected at several depths ranging from the surface up to 8 m depending on the location and substrate type. In order to compare natural and artificial substrate assemblages, samples were collected only at vertically oriented surfaces, as it has been reported that surface orientation is significant for the structure of biofouling communities (Van Volkom et al., 2023). Sampling was performed by SCUBA divers using a modified Kautsky net that consisted of a metal 20 cm x 20 cm frame (0.04 m^2 catch area) mesh sleeve and swappable mesh bags (Andrulewicz et al. 2004). In order to collect a single replicate the frame was placed upon a hard surface covered by macrobenthic epifauna. The organisms within the frame were scraped off with spatula and fell into a bag attached to the frame. The bag was then closed and replaced with an empty one before collecting subsequent samples (fig. 7).

Sandy bottom assemblages were sampled at site B in November of 2015, 2016 and 2017. Samples were collected 1, 7 and 50 meters away from the structure in southeastern direction. The distance and direction were measured underwater by the divers using a marked reel line and a diving compass. Samples were collected at each distance using a Hydro-Bios Ekman-Birge bottom sampler (15 cm x 15 cm, 0.0225 m^2 catch area) operated by a diver directly at the bottom. Each replicate was transferred to a separate mesh bag underwater. Sediment cores were collected using PVC cylinders (3 cm

diameter, 10 cm height) to determine organic matter content, mean grain size and sediment type at each distance in November 2017.

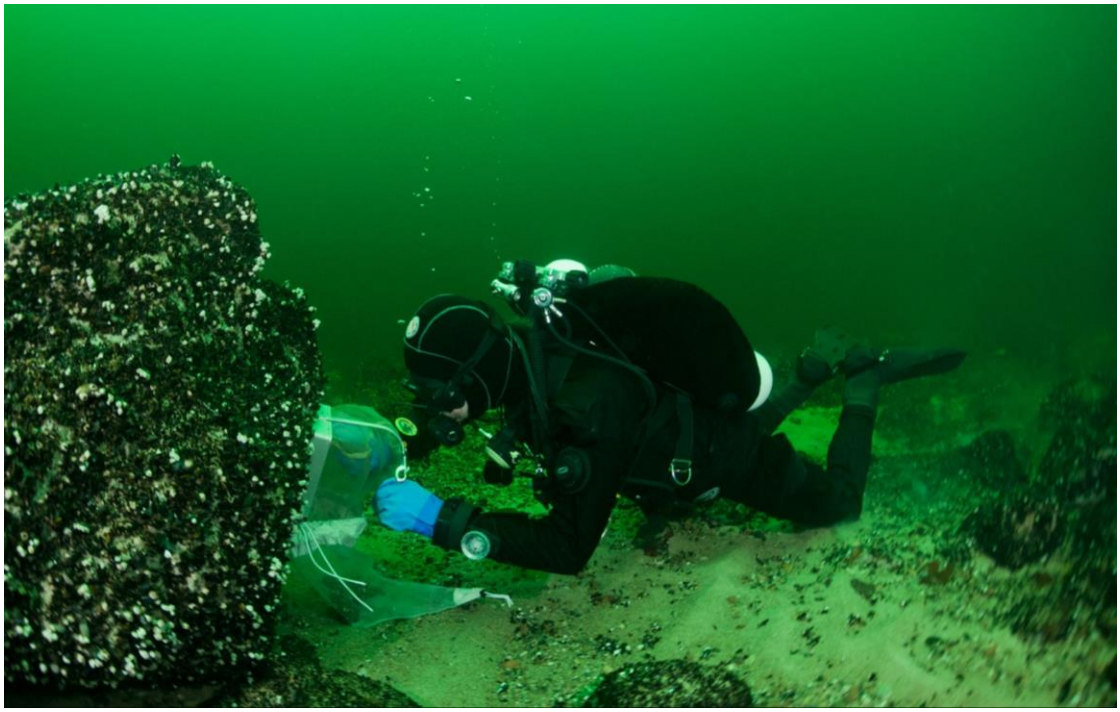

Fig. 7. SCUBA diver collecting macrobenthic sample using a modified Kautsky sampler (photograph by P. Bałazy).

Temperature, salinity and oxygen concentration were measured with a use of data loggers (HOBO U24 and HOBO U26). The loggers set to collect data in 1 hour intervals were attached to steel pole anchored with concrete paving slab (fig. 8). A set of loggers gathered data 1 m away from the structure from August to November 2015 and from July 2016 to October 2016. From July to November 2017 the parameters were measured at all three distances. Each macrobenthic sample was sieved (1 mm mesh size) and preserved with 4% solution of formaldehyde. During the laboratory analysis macrobenthic organisms found in samples were sorted, identified to the lowest possible taxonomic level, counted and weighed (wet mass) with the exception of colonial hydrozoans and bryozoans, which were assessed as present or absent.

Statistical analyses were performed using MS Excel, R Studio and PRIMER 6 with PERMANOVA add-on. The Shannon diversity *H'* and Pielou evenness *J'* indices were calculated. The functional diversity was assessed using biological traits analysis (BTA). Forty modalities among nine biological traits (maximum size, body flexibility, body shape, longevity, sociability, living habit, biodeposition and dispersal habit) were

selected for the analysis. Functional diversity expressed by the RAO index was calculated using an MS Excel file and instructions created by Lepš et al. (2006).

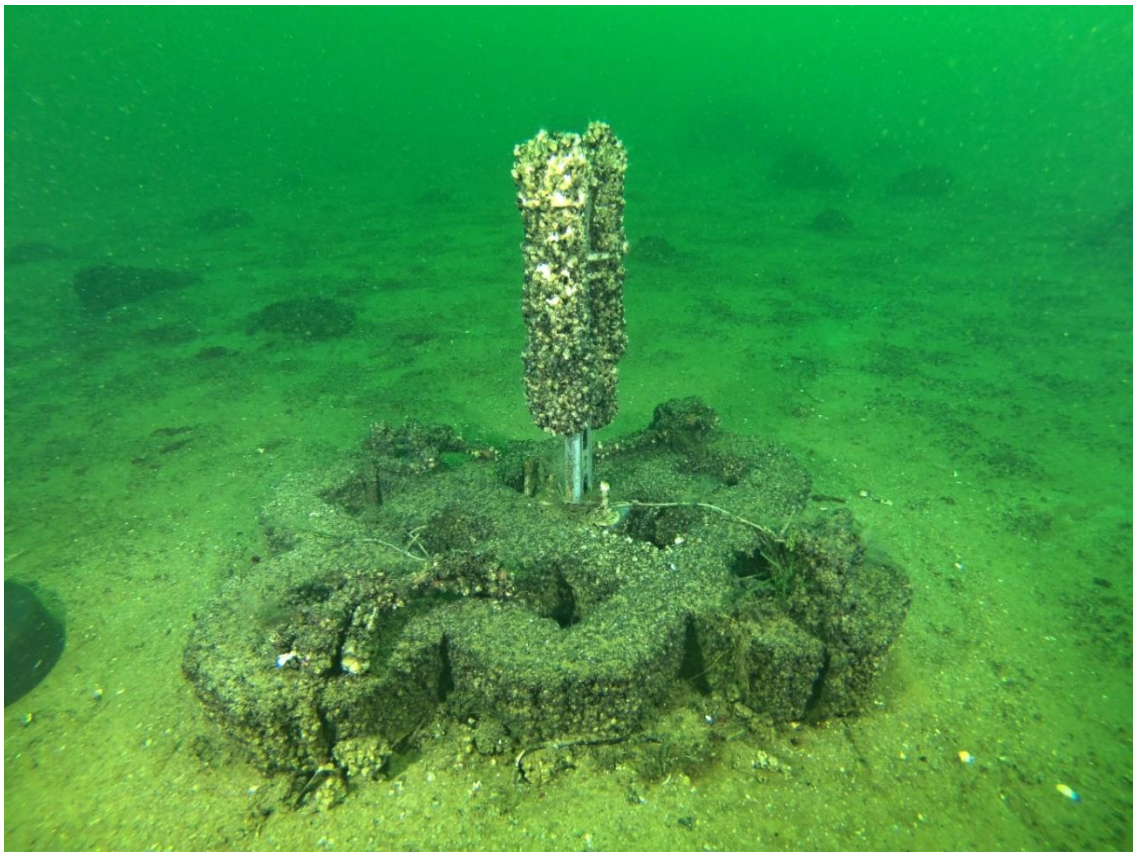

Fig. 8. Data loggers deployed at site B (photograph by R. Brzana).

Mann-Whitney U test and Kruskal Wallis test were used for comparing abundance, biomass, taxonomic richness and diversity indexes. PERMANOVA based on Bray–Curtis similarity between assemblages was used for multivariate analyses. SIMPER analysis was used to calculate the contribution of individual taxa to similarity between the groups. MDS and PCO plots were used to visualise level of similarity between samples.

Results and general discussion

In total 40 macrozoobenthic taxa were recorded during the research. Thirty eight taxa were recorded at hard substrates and 23 taxa were recorded at sandy bottom. Thirty seven taxa were recorded at artificial substrate, while 33 were present at natural rocky bottom. Nine of the recorded taxa are considered non-indigenous to the Baltic Sea region. No new non-native species were recorded during the research. The taxonomic

composition was typical for communities associated with the hard substrate and shallow sandy bottom in the Gulf of Gdańsk.

Taxonomic richness was significantly higher at boulders (18 taxa on average) than at concrete substrate at the same depth (13 taxa on average), which is consistent with reports of other authors (Wilhelmsson and Malm, 2008; Sedano et al., 2019; Hill et al., 2021). On the contrary biomass was significantly higher at artificial substrates (0.6 kg · m^{-2} against 0.2 kg · m^{-2} median). The abundance and biomass of macrofauna were particularly high at artificial structure closer to the water surface exceeding a median of 95 000 individuals and 7.8 kg per square meter respectively. Similar to Andersson and Ohman (2010), slight vertical zonation of the assemblage was observed at the artificial structure expressed mainly by varying proportion of the dominant filter feeders *M. trossulus* and *A. improvisus*.

The biological traits expressed by the studied assemblages were strongly affected by taxonomic composition and biomass of individual taxa, which is typical for species-poor systems where some trait modalities may be represented by single species (Włodarska-Kowalczuk et al., 2010). The higher species richness resulted in significantly higher number of trait modalities at natural substrate (38 against 34 on average). Despite that overall functional diversity did not differ between the compared assemblages and was relatively low. It was caused by strong domination of the trait modalities expressed by dominant sessile filter-feeding species. Functional diversity of associated mobile fauna (excluding dominant sessile species) was significantly higher at natural substrate. PERMANOVA revealed, that both taxonomic and functional structure of the macrobenthic assemblage differ significantly between natural and artificial hard substrate. Interestingly PCO plots demonstrated that the two dominant species *M. trossulus* and *A.improvisus* and their trait modalities were among the ones that contributed the most to the differences between the assemblages.

The average richness and relative abundance of non-native species was higher at natural substrate than at artificial structure. Although natural and artificial substrate assemblages differed significantly based on abundance of particular taxa (including native taxa), no such differences were observed based on the composition of non-indigenous fauna, meaning that both substrate types supported similar groups of non-native species. It is worth noting that the contribution of NIS to the total species richness and abundance on both types hard substrate was relatively high: 31 and 33 % on average.

In comparison NIS accounted for an average of 17 % of the total species richness and 6 % of the total abundance on soft bottom in the Puck Bay (Janas & Kendzierska; 2014).

An important feature of offshore structures is that unlike natural hard bottom they can span through the entire water column (Ruiz et al., 2009; De Mesel et al., 2015). In fact a closer look at abundance of individual NIS revealed their preferences for substrate type at particular depths. Most of the recorded NIS were the most abundant at depth ranging from the surface up to 4 m. Several species were present almost exclusively on artificial substrate: rockpool shrimp *Palaemon elegans*, amphipod *Melita nitida* and dreissenid *Mytilopsis leucophaeata*. The abundance of mud crab *Rhithropanopeus harrisii* was also higher on artificial substrate. The abundance of *A. improvisus* and *Sinelobus vanhaareni* was similar on natural and artificial substrates at a depth of 8 m, but the highest abundance of these species was observed at smaller depths on artificial substrate. Soft-shell clam *M. arenaria* was less abundant on artificial substrate at a depth of 8 m, but its abundance at depths of 4 m and 2 m was close to that observed on natural substrate. Only two out of nine recorded NIS were more abundant at natural substrate – the New Zeland mud snail *Potamopyrgus antipodarum* and spionid *Marenzelleria* spp.

Significant differences in oxygen concentration among different distances away from the structure were observed with no difference in temperature. The five-month average at 1 m was 0.6 mg · L^{-1} lower compared to 7 and 50 m away from the structure. The monthly average was lower at 1 m compared to the two other sites by up to 1.0 mg · L^{-1} in September, October and November). The highest observed difference in single measurements between 1 m and the other sites was 3.7 mg · L^{-1} at the beginning of November 2017. Oxygen-stressed conditions (2.0–4.0 mg · L^{-1}) and hypoxic events (<2.0 mg · L^{-1}) were observed in 2016 at a distance of 1 m from the structure. In 2016, the average was below 4.0 mg · L^{-1} in August and September and the minimum was below 1.0 mg · L^{-1} in July, August and September. However, as the site at 1 m distance was the only one with associated oxygen concentration readings that year it is uncertain, whether the conditions were related to artificial structure. In 2015, 2017, no hypoxic events were observed with the oxygen concentration dropping to 4.5 mg · L^{-1} and 2.1 mg · L^{-1}, respectively. There were few instances of oxygen stressed conditions in 2017.

The negative impact on oxygen concentration close to the structure was not reflected in soft bottom macrobenthic assemblage. Taxonomic richness, abundance and biomass of benthic macrofauna were generally similar or higher at the two sites close to the structure compared to 50 m away. Various effects were observed for individual taxa.

Several species were found in large numbers near the structure, including species typical of the Baltic hard seabed – sessile species like the mussel *M. trossulus*, the barnacle *A. improvisus* and the hydrozoan *Gonothyraea loveni* as well as mobile species like small crustaceans: the amphipod *Leptocheirus pilosus*, the isopod *Jaera ischiosetosa* and the non-indigenous tanaid *Sinelobus vanhaareni*. Larger number of oligochaetes was found close to the structure which can be explained by organic enrichment.

Some species typical for the sandy bottom were also positively affected by the structure, including the bivalves *M. arenaria* and *Cerastoderma glaucum*, and the polychaete *H. diversicolor.* As all these species feed on suspended and deposited organic matter particles, their increased abundance in the vicinity of the structure may have resulted from the enhanced food supply due to organic enrichment (Scaps, 2002; Malham et al., 2012). Potential adverse effects of the artificial structure were observed only in the case of the corophid amphipod *Corophium multisetosum*. This crustacean was present in large numbers at a distance of 7 m and 50 m, but only a few individuals were observed at a distance of 1m. This may be due to sediment fining and higher organic matter content close to the structure.

Fig. 9. Mussel bed at the base of the structure at site B.

Conclusions

Benthic communities at artificial substrate differ from communities at natural substrates even 7 decades after construction in the low-diversity brackish environment of the Gulf of Gdańsk. Most importantly, the assemblage at artificial structure was characterized by lower taxonomic richness compared to the community at natural substrate at the same depth. Functional diversity is also higher at natural substrates with higher heterogeneity among biological traits of the associated mobile species. The positive effect of artificial structure on benthic species richness and diversity would probably be observed in species-poor environments, i.e. silty bottom in deep waters affected by hypoxia and anoxia. In other areas, an increase in the density of few taxa should be expected, leading to a significant increase in biomass of few filter-feeding species and free living crawlers/swimmers (mainly crustaceans).

Direct comparison of fully developed benthic communities on natural and artificial substrates at the same depth did not confirm that artificial hard substrate is a more favourable habitat for NIS than natural hard substrate. However, artificial substrate extending throughout the entire water column can form a specific habitat that may support exceptionally dense populations of some NIS compared to natural boulders. As both types of hard substrates contained more NIS than reported for soft bottom, the construction of artificial structures in an environment dominated by soft sediments should be perceived as a risk to facilitate the further spread of some NIS.

Study included in the thesis has demonstrated that oxygen concentration can be significantly lower in the immediate vicinity of artificial structures. However, other effects have a greater impact on the benthic assemblage, leading to increased taxa richness, abundance and biomass in the direct vicinity of the structure.

In summary the impact of man-made structure on macrobenthic assemblages was reflected mainly by their enhanced density and biomass on the structure itself and at nearby soft bottom. A positive impact on biodiversity is debatable as the community was heavily dominated by few species and did not provide a surrogate for natural hard substrate assemblage. Moreover the provision of suitable habitats for non-native species particularly at lower depths is a potential threat for biodiversity. High density of macrofauna on the structure resulted in an oxygen depletion in its vicinity, but not to such an extent, that would negatively affect the macrofaunal assemblage.

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Biodiversity and functioning of benthic macrofauna associated with natural and artificial hard substrate in the Gulf of Gdańsk (Baltic sea)

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1. Introduction

With increasing human activity in the seas, both in the coastal zone and in the offshore areas, artificial structures have become an integral element of the marine environment in many regions of the world. A particularly significant increase in the number of artificial structures in the seas has been observed for the last few decades due to the rapid development of the offshore wind energy industry. There are currently over 5000 operational wind turbines within the European waters, with the majority located in the North Sea (Walsh et al., 2020). Another important European sea, the Baltic Sea, currently has a much smaller number of such structures, with only a few wind farms operating in its waters. However, there are plans for massive wind energy development in the Baltic Sea in the coming decades (Purta et al., 2016; Walsh et al., 2020).

The increasing presence of artificial structures in the marine environment raises a question about their impact on marine organisms. This includes benthic macrofauna, which is an important ecological component of marine systems. The most apparent impact of man-made structures on benthic communities is the replacement of natural substrate with artificial substrate and the provision of new habitat (Petersen and Malm, 2006; Andersson and Öhman, 2010; Vaissière et al., 2014; Wilhelmsson and Langhamer, 2014). In areas where the seabed is dominated by soft sediments, i.e. sand or silt, such transformation of the substrate leads to a significant change in key characteristics of benthic habitats and the communities they support (Petersen and Malm, 2006; Andersson and Öhman, 2010; Bałazy et al., 2019). In general, the soft bottom provides a habitat for organisms that burrow into the sediment, but does not provide a suitable surface for permanently attached filter feeders. Hard surfaces, on the other hand, are impossible for most organisms to burrow into, but provide a stable surface for sessile filter feeders to attach to (Henseler et al., 2019).

Both artificial and natural hard substrates are believed to support particularly rich benthic communities (Zintzen et al., 2006; Grzelak and Kukliński, 2010; Langhamer, 2012; Šiaulys and Bučas, 2015; Bałazy et al., 2019). Sessile, usually filter-feeding organisms, such as mussels and barnacles, are the main component of these communities. They create a complex three-dimensional structure on otherwise featureless flat, hard surfaces (Alvarado and Castilla, 1996; Guiñez and Castilla, 1999; Coolen et al., 2018). The structure formed by sessile fauna is home to numerous species of crustaceans, polychaetes and other organisms (Ragnarsson and Raffaelli, 1999; Norling and Kautsky, 2007, 2008; Wilhelmsson and Malm, 2008; Grzelak and Kukliński, 2010). Given such diversity, the introduction of artificial structures into a marine environment with predominantly soft bottom is often considered to have a mostly positive effect on the local benthic macrofauna (Coolen et al., 2019).

Although it is known that benthic communities at artificial structures are significantly different from soft-bottom communities, it is not clear as to what exactly artificial structures bring to areas where hard substrate already exists in the natural form of rocks and boulders. However, several previous studies are consistent in that artificial substrate is not a

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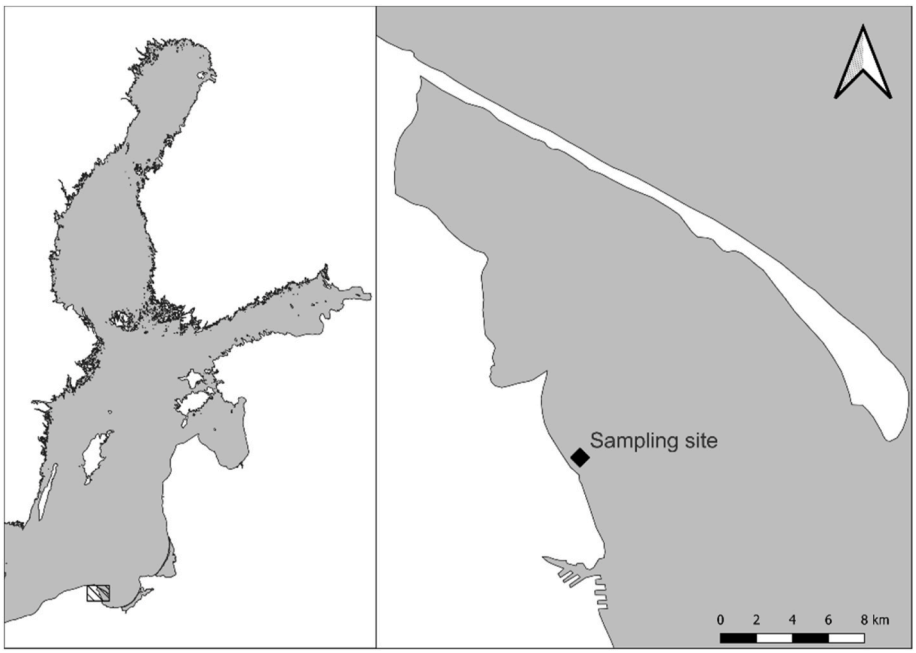

Fig. 1. Location of the sampling site in the Gulf of Gdańsk (Baltic Sea).

substitute for natural hard substrate and significant differences in macrobenthic communities on these different substrates are to be expected (Connell and Glasby, 1999; Petersen and Malm, 2006; Wilhelmsson and Malm, 2008; Kerckhof et al., 2017, 2019; Sedano et al., 2019).

Another issue concerning hard-bottom macrofaunal communities, which has not yet been thoroughly investigated is the functional aspect of their biodiversity. The functioning of benthic communities has been extensively studied, also in the Baltic Sea, but the majority of these studies focused on the soft-bottom fauna (Bonsdorff and Pearson, 1999; Darr et al., 2014; Törnroos et al., 2015; Weigel et al., 2016). There are relatively few studies that have addressed the functioning of hard-bottom communities (Kerckhof et al., 2017; Franz et al., 2019; Henseler et al., 2019).

Most studies addressing the impact of offshore structures on benthic fauna have been conducted in the North Sea, where the offshore wind farm industry is much more developed. Although some of these observations can be applied to other regions, it should be emphasized that the Baltic Sea is characterized by some important distinguishing features. High freshwater input and limited seawater exchange with the North Sea result in a salinity gradient in the Baltic Sea ranging from 2 to 20 PSU (Gogina et al., 2016). Salinity in the Baltic Proper ranges from 5 to 8 PSU, which has been described as particularly challenging conditions for both marine and freshwater organisms and leads to relatively low species richness and diversity (Remane, 1934; Zettler et al., 2014). Consequentially biota in the south-eastern Baltic Sea is represented by opportunistic organisms with high potential for adaptation, that include euryhaline marine species from the North Atlantic as well as brackish and freshwater organisms (Sokołowski et al., 2017). In relation to benthic communities it leads to an absence of some influential groups such as echinoderms, megafaunal decapods and sessile cnidarians.

This study provides one of the few direct comparisons of benthic communities on natural and artificial hard substrates. In both cases, fully developed communities were studied as the artificial substrate was sampled at an offshore structure that has been present in this environment for over seven decades. This is also one of the few attempts to study functional diversity of hard substrate benthos and compare the functioning of natural and artificial hard-bottom communities.

The objective of this study was to answer the question whether artificial and natural hard substrates support the same taxonomic and functional diversity as well as abundance and biomass of macrozoobenthos. By comparing assemblages found on artificial substrate and those of natural hard substrate in different seasons and at different depths we tested the following hypotheses.

1. Natural hard substrate supports different assemblages than artificial hard substrate in terms of their taxonomic richness, abundance, biomass and structure.
2. Assemblages at natural and artificial hard substrate represent different biological traits leading to differences in their role for ecosystem functioning.
3. Assemblages at natural and artificial hard substrate undergo different seasonal changes.

2. Material and methods

Samples were collected by SCUBA divers in the Gulf of Gdańsk, the southern Baltic Sea, at a site located off the coast of Gdynia (54.594487°N; 18.543944°E; Fig. 1).

There were three sampling events: in July 2015, April and November 2016. Samples were collected at two types of hard substrates: artificial and natural. The artificial substrate was represented by the concrete foundation of an offshore structure that was part of a torpedo test complex during World War II. The structure is located 900 m offshore. The base of the structure is 17 m long and 7.5 m wide. The concrete walls extend from the base at a depth of 8 m up to 1 m above the water surface. Bottom sediment around the structure is mainly coarse sand (Brzana et al., 2020; Sokołowski et al., 2021). The natural substrate was located approximately 100 m away from the structure. It was represented by boulders (up to 1 m in diameter) elevated up to 0.5 m above the sandy seabed. Similarly to other natural hard substrates in the Gulf of Gdańsk, the boulders at the study site originate from the eroded cliffs and are represented by granitoids, gneisses, sandstones, porphyry and quartzites (Grzelak and Kukliński, 2010; Kowalewska, 2020; Sokołowski et al., 2021).

Samples at the artificial structure were collected at several depths – at the water surface in the splash zone, and at depths of 2 m, 4 m and 8 m in order to compare assemblages at different depths. Sampling was

Table 1
Description of traits and trait modalities included in the analysis. The listed labels and trait initials refer to Figs. 6 and 7.

Trait	Trait modality	Trait modality label	Relevance for processes and functions
Maximum size (mm)	1–5	vS	Secondary production, habitat forming
	5–10	S	
	10–50	M	
	50–100	L	
	>100	vL	
Body flexibility (degrees)	<10	<10	Habitat forming,
	10–45	10–45	
	>45	>45	
Body shape Trait initials: BS	Encrusting	enc	Secondary production, habitat forming,
	Bushy	bus	
	Turbinate	tur	
	Conical	con	
	Bivalved	biv	
	Wormlike	wor	
	Articulate	art	
Longevity/life cycle (years)			
Trait initials: L	<1	<1	Secondary production
	1–2	1–2	
	2–5	2–5	
	5–10	5–10	
	>10	>10	
Sociability	Solitary	Sol	Habitat forming
	Gregarious	gre	
	Colonial	col	
Living habit/ mobility Trait initials: LH	Permanently attached	pat	Import/export of organic matter from system, habitat forming
	Temporary attached	tat	
	Burrower	bur	
	Tube builder	tub	
	Free living crawler	cra	
	Free living swimmer	swi	
Feeding habit	Surface deposit feeder (incl. grazer)	sur	Import/export of organic matter from system, nutrient cycling
	Sub-surface deposit feeder	sub	
	Filter/suspension feeder	sus	
	Predator (opportunistic scavenger)	pre	
Biodeposition	Surface deposition	sde	Import/export of organic matter from system, nutrient cycling, habitat forming
	Surficial transport	str	
	Conveyor belt transport	con	
	Reverse conveyor belt transport	rcon	
Dispersal habit	Non dispersal (no larval stage)	non	Secondary production, import/export of organic matter from system
	Local (short larval period)	loc	
	Long distance (long larval period)	lon	

performed at the wall facing the nearest shore to ensure minimal impact of waving. Samples from the natural substrate were collected at a depth of 8 m in order to compare assemblages from different substrate types at the same depth. Temperature and salinity were measured at a depth of 8 m.

Benthic samples at both substrate types were collected only at vertically oriented surfaces using a modified Kautsky sampler (0.04 m^2 catch area; Andrulewicz et al., 2004). Four replicates were collected at each depth and each type of substrate during each sampling event, except for a depth of 2 m at the artificial substrate in July 2015. The collected samples were sieved (1 mm mesh size) and preserved in 4% solution of formaldehyde for further analysis. Organisms found in the samples were sorted and identified to the lowest possible taxonomic level. Individuals of most taxa were counted and weighed (wet mass, $g \bullet m^{-2}$). The exceptions were colonial hydrozoans, which were only weighed, and colonial bryozoans, which were neither counted nor weighed.

Nine biological traits with a total of 40 modalities were selected to analyze the functioning of the studied communities. We included the most basic traits such as body shape, life and feeding habit, and others (Table 1). Fuzzy coding was applied, with values ranging from 0 to 3, with 0 representing no affinity and 3 representing full affinity to the trait modality. If a taxon had affinity to more than one trait modality within the same trait, it was coded up to 2.

Functional diversity (FD) expressed by the RAO index was calculated using an MS Excel file and instructions created by Lepš et al. (2006). Functional identity of communities was presented as community weight means of trait modality expression (CWM). Statistical comparisons were performed separately for different substrate types at 8 m depth and for artificial substrate at different depths. Statistical differences between communities in species richness, total abundance, total biomass, total number of trait modalities and FD were tested using R Studio (Mann–Whitney *U*, Kruskal–Wallis and Dunn's tests). Primer 6 with PERMANOVA add-on was used to test differences between communities in biomass of particular taxa (square root transformed data) and trait modalities (not transformed data) and the relevance of substrate type (natural and artificial at depth 8 m), depth and season (for artificial substrate) to those differences. Two-way permutational multivariate analysis of variance (PERMANOVA), based on Bray Curtis similarity metrices, with 999 unrestricted permutation of raw data, sums of squares type III were used. Post hoc pairwise permutation *t*-test were used to identify differences between levels of significant factors (Anderson et al., 2008).

Sample sets from a depth of 2 m were not included in the statistical analysis as they lacked data for July 2015. Some analyses were performed excluding sessile fauna, leaving only mobile (associated) fauna. Sessile fauna included permanently attached organisms (hydrozoans, barnacles) and organisms that attach to the surface via byssi (i.e. mussels). Data visualization was performed in Statistica 13 (boxplots), RStudio (Venn diagram) and Primer 6 with PERMANOVA add-on (PCO).

3. Results

Temperature ranged from 5.3 °C in April to 20.1 °C in July 2015. Salinity ranged from 6.8 in November to 7.2 in April 2016. The highest algal biomass was observed at artificial substrate at depths of 0 and 2 m. At a depth of 8 m, algal biomass was higher at the natural substrate than at the artificial substrate (Fig. 2). The most contributing groups were filamentous algae and *Enteromorpha* (Chlorophyta) close to the surface, and *Vertebrata* (Rhodophyta) close to the seabed.

A total of 35 zoobenthic taxa were observed, with almost half (17) of them belonging to Crustacea. Thirty three taxa were found at artificial substrate and 29 taxa at natural substrate. Seven taxa were observed in each sampling season at both substrate types and each depth: sessile *Amphibalanus improvisus*, *Mytilus trossulus*, *Gonothyraea loveni* and *Einhornia crustulenta*, and mobile *Gammarus salinus*, *Heterotanais oerstedi*

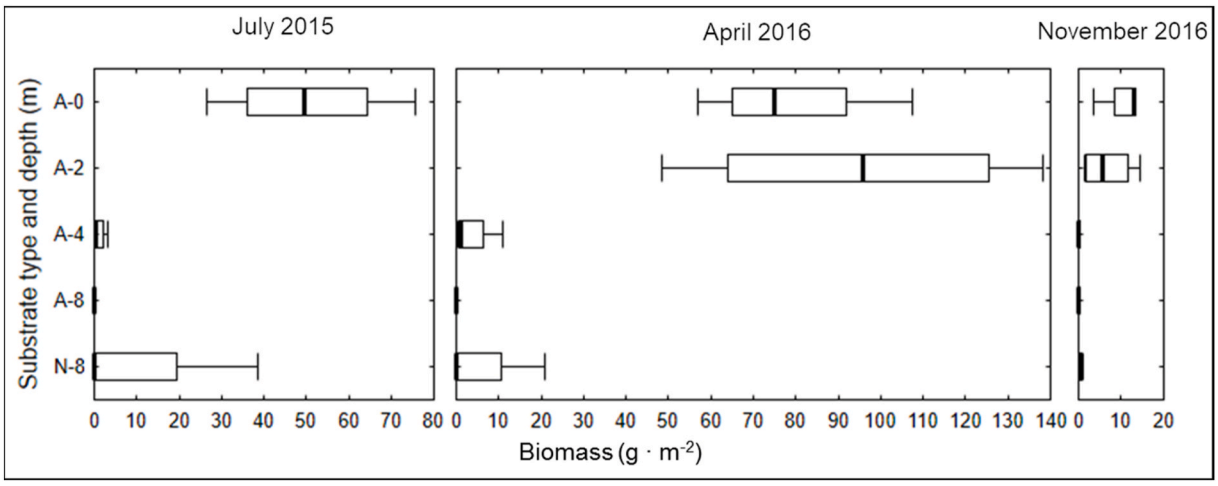

Fig. 2. Algal biomass at different depths at the study site in different months. N on the X (vertical) axis refers to natural substrate and A refers to artificial substrate. Bold lines represent median, boxes represent 25–75th percentile, whiskers extend between the minimum and maximum.

and *Sinelobus vanhaareni*. When analyzing specific depths separately, the overall taxonomic richness was generally higher at the natural substrate (Table 2).

Pooled data from all three sampling seasons revealed higher overlap in taxonomic composition. The largest overlap was observed between natural substrate and artificial substrate at a depth of 4 and 8 m (24 and 23 taxa respectively). Relatively few taxa were unique to specific sample sets (0–2; Fig. 3).

Taxonomic richness was significantly higher at natural substrate compared to artificial structure in all seasons. No significant differences were found between specific depths at artificial substrate (Fig. 4, Table 3).

The highest average abundance and biomass were observed in November at a depth of 2 m. In contrast to taxa richness, biomass at the natural substrate was significantly lower than at the artificial substate at the same depth, but no difference in abundance was observed. There were also significant differences in biomass between 4 m and 8 m at the artificial substrate with no difference in abundance (Fig. 5, Table 3).

The highest median number of trait modalities was determined at the natural substrate and was significantly higher than that at the artificial substrate. There were no significant differences in the overall functional diversity, but functional diversity of mobile fauna was significantly higher at the natural substrate (Table 3; Fig. 6).

Results of two-way PERMANOVA test demonstrated that at a depth of 8 m the type of substrate and season led to a significant differences between communities for both biomass and functional structure ($p = 0.001$ for the factors substrate type and month and of their interaction, except for differences in functional structure between months where $p > 0.05$). The differences were also found at artificial substrate between seasons and depths for both taxonomic and functional structure ($p = 0.001$ for the factors month and depth and of their interaction).

Taxonomic and functional structure at natural substrate differed significantly from artificial substrate at 8 m (Table 4). There were also several instances of significant differences in taxonomic structure between assemblages from artificial substrate at different depths (Table 5). We observed significant seasonal variability in community structure and functioning for all depths on artificial substrate while no significant differences were observed for assemblages from natural substrate (Tables 4 and 5).

The PCO plot based on community structure showed a clear distinction between natural and artificial substrate. Samples collected from artificial substrate in different seasons created 3 separate clusters. *Fabricia stellaris, M. trossulus, P. antipodarum* and *A. improvisus* where the most correlated with variables vectors (Fig. 7).

Samples collected in November 2016 from artificial substrate at depth of 4 an 8 m were also relatively tightly coupled.

On the PCO plot based on functional structure of assemblages from different substrate types only a slight overlap was observed between natural and artificial substrate. The first ordination axis explained 95.7% of the total variation. The trait modalities, that where best correlated with this axis were associated with the two dominant sessile filter feeder species: *M. trossulus* (body shape: bivalved; living habit: temporary attached; longevity: >10) and *A. improvisus* (body shape: conical; living habit: permanently attached; longevity: 1–2) (Fig. 8). These differences are also reflected on a plot demonstrating functional structure of particular assemblages (Fig. 9). On the PCO plot created for functional structure at artificial substrate at different depths the first ordination axis also explained over 90% of the total variation. The trait modalities, that where best correlated with this axis were also associated with the two dominant sessile filter feeder species. However the collected samples did not create distinct groups except for samples collected in July 2015 at the surface (Fig. 8).

Regarding the associated mobile fauna functional identity, higher heterogeneity was observed at the natural substrate, especially in the case of body shape, body flexibility, longevity and life habit of organisms. Mobile fauna at the artificial structure was dominated by annual species, especially in the surface zone where the community was exposed to more disturbance. The artificial substrate supported mainly free living crawlers/swimmers with a small proportion of tube builders. Organisms at the natural substrate exhibited much lower propensity to swim, with crawlers and burrowers being the most abundant. The natural substrate also exhibited much higher diversity of shapes and higher percentage of animals with long life cycles (Fig. 9).

4. Discussion

The obtained results showed that the studied fully developed zoobenthic communities at artificial hard substrates differed significantly from those found on natural hard substrates, even when both communities developed at the same depth in the same area. The observed similarities and differences were consistent with some of those reported by other authors. The taxonomic composition in a broad sense was typical for communities associated with the hard substrate in the Baltic Sea. Assemblages consisted of four ubiquitous sessile taxa (*M. trossulus*, *A. improvisus*, *E. crustulenta* and hydrozoans) accompanied by varied mobile fauna represented predominantly by crustaceans (Andrulewicz et al., 2004; Qvarfordt et al., 2006; Grzelak and Kukliński, 2010; Brzana and Janas, 2016; Sokołowski et al., 2017; Bałazy et al., 2019). As

Table 2
Taxonomic composition and mean biomass of taxa at each site and depth; + indicates presence of a taxon that was not weighed; empty cells indicate the absence of taxa.

	Month and year	July 2015				April 2016					November 2016				
Substrate type (A – artificial, N – natural)		A	A	A	N	A	A	A	A	N	A	A	A	A	N
	Taxa	0	4	8	8	0	2	4	8	8	0	2	4	8	8
	Oligochaeta	0.05			<0.01	0.01	0.01	<0.01		0.01	<0.01	<0.01	<0.01		<0.01
Platyhelminthes	*Planaria torva*				0.33			0.15		0.25		5.63		0.56	3.39
Polychaeta	*Fabricia stellaris*			<0.01	0.01	<0.01	<0.01			0.02		<0.01			0.02
	Hediste diversicolor	0.17	0.02	<0.01	0.04	<0.01	0.23	0.03		0.50			0.01	<0.01	0.01
	Manayunkia aestuarina	<0.01													
	Marenzelleria spp.				0.01				<0.01	0.02		<0.01		0.02	0.02
	Pygospio elegans				<0.01										
Crustacea	*Amphibalanus improvisus*	803.64	45.07	85.64	221.17	103.62	244.30	236.58	201.69	175.50	16.50	607.94	183.20	248.99	169.54
	Apocorophium lacustre	<0.01	0.01		0.02		0.01	<0.01	0.01	0.21		<0.01		<0.01	0.07
	Corophium multisetosum													<0.01	
	Gammarus locusta	3.91	0.19	0.12			0.42							0.38	
	Gammarus oceanicus											0.20			
	Gammarus salinus	1.86	1.18	1.00	0.51	0.35	0.28	0.27	0.34	0.10	0.11	6.90	0.91	0.41	0.11
	Gammarus zaddachi	32.98	0.16	0.47	0.55	1.48	3.14	1.15	1.43		1.12	32.96	1.97	1.41	0.08
	Melita nitida						<0.01		<0.01			0.27		0.01	
	Jaera ischiosetosa	0.87	0.02	0.10	0.06	1.12	0.18	0.30	0.78		0.03	0.96	0.01	0.25	0.02
	Leptocheirus pilosus	<0.01	0.63	0.07	0.36	0.02	0.74	0.63	0.43	0.54		0.84	0.04	0.87	0.53
	Cyathura carinata				<0.01					<0.01		<0.01	<0.01		<0.01
	Idotea chelipes										0.01		0.03	0.03	0.16
	Praunus flexuosus									0.02					
	Rhitropanopeus harrissii		0.15	1.62	0.15	0.05	0.47		0.08	0.03		1.03	0.21		
	Palaemon elegans		5.95							0.18		3.75	6.59	1.66	
	Heterotanais oerstedi	<0.01	0.08	<0.01	0.01	<0.01	0.02	0.03	0.01	0.02	<0.01	0.02	0.01	<0.01	0.01
	Sinelobus vanhaareni	0.43	0.71	0.03	0.01	0.22	0.77	0.43	0.14	0.12	0.02	0.20	0.04	0.03	0.06
Gastropoda	*Peringia ulvae*				0.29			0.01		0.07					0.12
	Potamopyrgus antipodarum				2.38					0.69		0.01	0.01	0.01	0.84
	Tenelia adspersa	<0.01													
Bivalvia	*Cerastoderma glaucum*	<0.01	0.10	0.02	<0.01							1.12	<0.01		
	Macoma balthica			<0.01	0.35		<0.01			0.07					<0.01
	Mya arenaria		0.025		0.16		0.39			0.22		0.53	0.03	<0.01	0.02
	Mytilopsis leucophaeata		0.59		0.01							4.70	0.53		
	Mytilus trossulus	411.07	450.47	278.69	118.58	193.31	401.01	384.76	353.28	83.96	171.27	6576.78	3845.00	2154.73	42.84
Insecta (larvae)	Chironomidae	0.03	0.01	0.01	0.01	0.27	0.02	<0.01	<0.01	0.17	<0.01				0.01
Hydrozoa	*Gonothyraea loveni*	12.74	16.50	4.66	0.06	1.24	0.41	1.93	14.18	2.17	3.27	0.25	+	1.67	3.41
Bryozoa	*Einhornia crustulenta*	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	TOTAL NUMBER OF TAXA	18	19	17	26	15	20	16	15	23	12	24	20	21	23

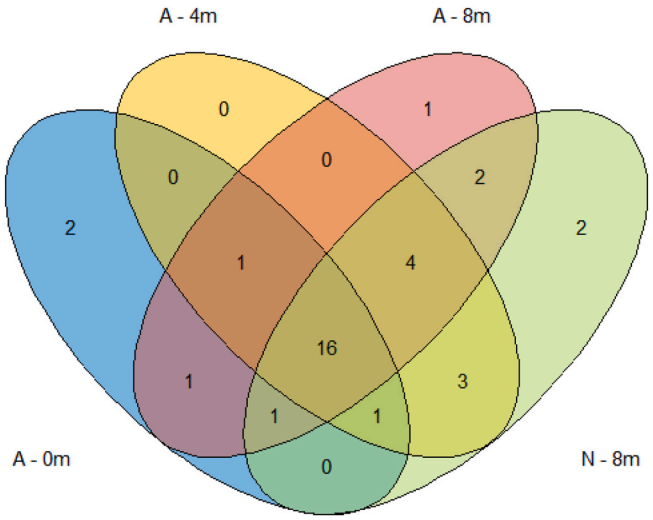

Fig. 3. Venn diagram showing the number of taxa unique or common to different types of substrates and depths. N refers to natural substrate and A refers to artificial substrate.

expected, total and average numbers of observed taxa were lower than reported in the North Sea (Zintzen et al., 2006; Zintzen et al., 2008; Kerckhof et al., 2017; Rumes et al., 2021). It is worth noting, that in the North Sea sessile and mobile epifauna can be represented by equally high numbers of species, whereas in the Baltic Sea few sessile species are accompanied by relatively diverse mobile fauna (Zintzen et al., 2008; Rumes et al., 2021).

Clear differences in the taxonomic composition of the communities occurring at the two types of substrates were observed across months, with some taxa absent at the artificial substrate but present at natural boulders and vice versa. The total number of taxa was higher at the artificial substrate, but it should be noted that the artificial substrate was sampled more extensively (more different depths resulted in more replicates collected). When comparing the natural substrate with the artificial substrate at each depth, in most cases the natural substrate supported higher species richness, which is consistent with some of the previous reports (Wilhelmsson and Malm, 2008; Kerckhof et al., 2017; Sedano et al., 2019; Hill et al., 2021).

The pooled results from three sampling periods showed a great overlap in the taxonomic composition between the communities at the two types of substrates and at different depths. Only a few taxa remained unique to a specific depth or substrate type over a broader time scale. Taxa unique to the natural substrate include the polychaete *Pygospio elegans*, which is a typical soft bottom species, and the nektobenthic mysid *Praunus flexuosus*. Species that were present at the artificial structure but absent at the rocks included mainly amphipods: *Gammarus locusta*, *Corophium multisetosum*, and non-indigenous *Melita nitida*. It should be assumed that macrofauna on the natural and artificial hard substrates in the Baltic Sea may have nearly identical taxonomic composition when compared over a longer period of time. Such similarity should be expected in a brackish, low-diversity system inhabited by highly tolerant, eurytopic species with opportunistic strategies, such as the Baltic Sea (Rumohr et al., 1996; Włodarska-Kowalczuk et al., 2010; Węsławski et al., 2013).

The differences between the studied communities did not result from the presence/absence of particular taxa but from different proportions between certain species. Similar to Qvarfordt et al. (2006) and Wilhelmsson and Malm (2008), we observed that despite the differences in the taxonomic composition, it was the two dominant sessile species, ubiquitous in all samples (*M. trossulus* and *A. improvisus*), that contributed to the differences between the studied communities. The biomass of *M. trossulus* was always higher at the artificial substrate than at the natural substrate. Moreover, the proportion between *M. trossulus* and

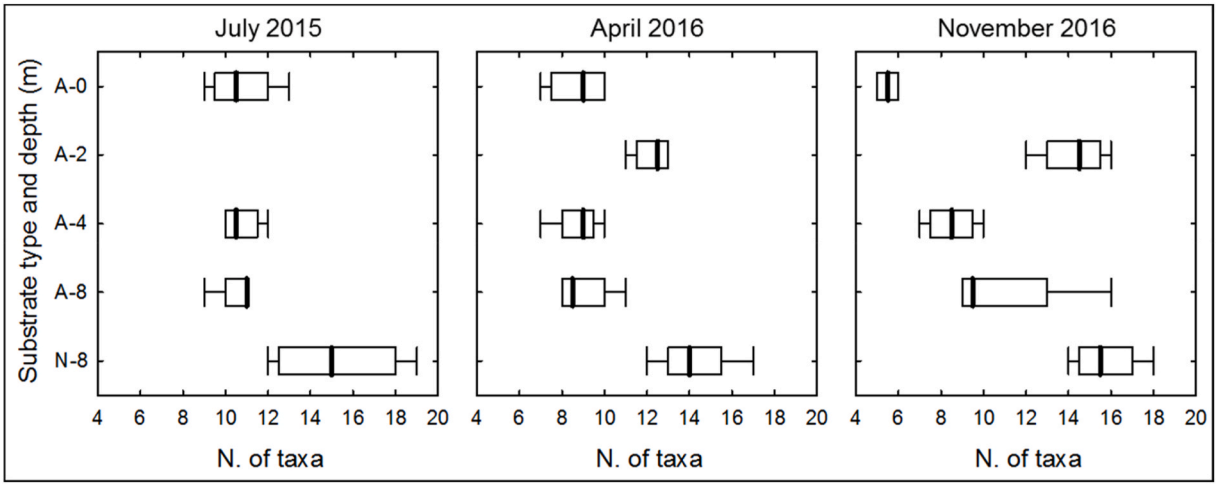

Fig. 4. Taxonomic richness at specific depths at the study sites in different months. N on the X (vertical) axis refers to natural substrate and A refers to artificial substrate. Bold lines represent the median, boxes represent 25–75th percentile, whiskers extend between the minimum and maximum.

Table 3
P values obtained by Mann–Whitney *U* test between different substrate types (natural or artificial) and Dunn's pairwise test between different depths at artificial substrate using samples collected in all three seasons. Bold values indicate significant differences ($p < 0.05$ for Mann–Whitney *U* test, $p < 0.025$ for Dunn's test). Missing values indicate, that no significant differences were observed in Kruskal–Wallis test.

Pair	N° of taxa	Abundance	Biomass	N° of trait mod.	FD	FD (mobile fauna)
Natural & Artificial	**0.0002**	0.1571	**0.0007**	**0.0007**	0.0782	**<0.0001**
8 m & 4 m			**0.0168**			1.0000
8 m & 0 m			0.1041			**0.0007**
4 m & 0 m			1.0000			0.0630

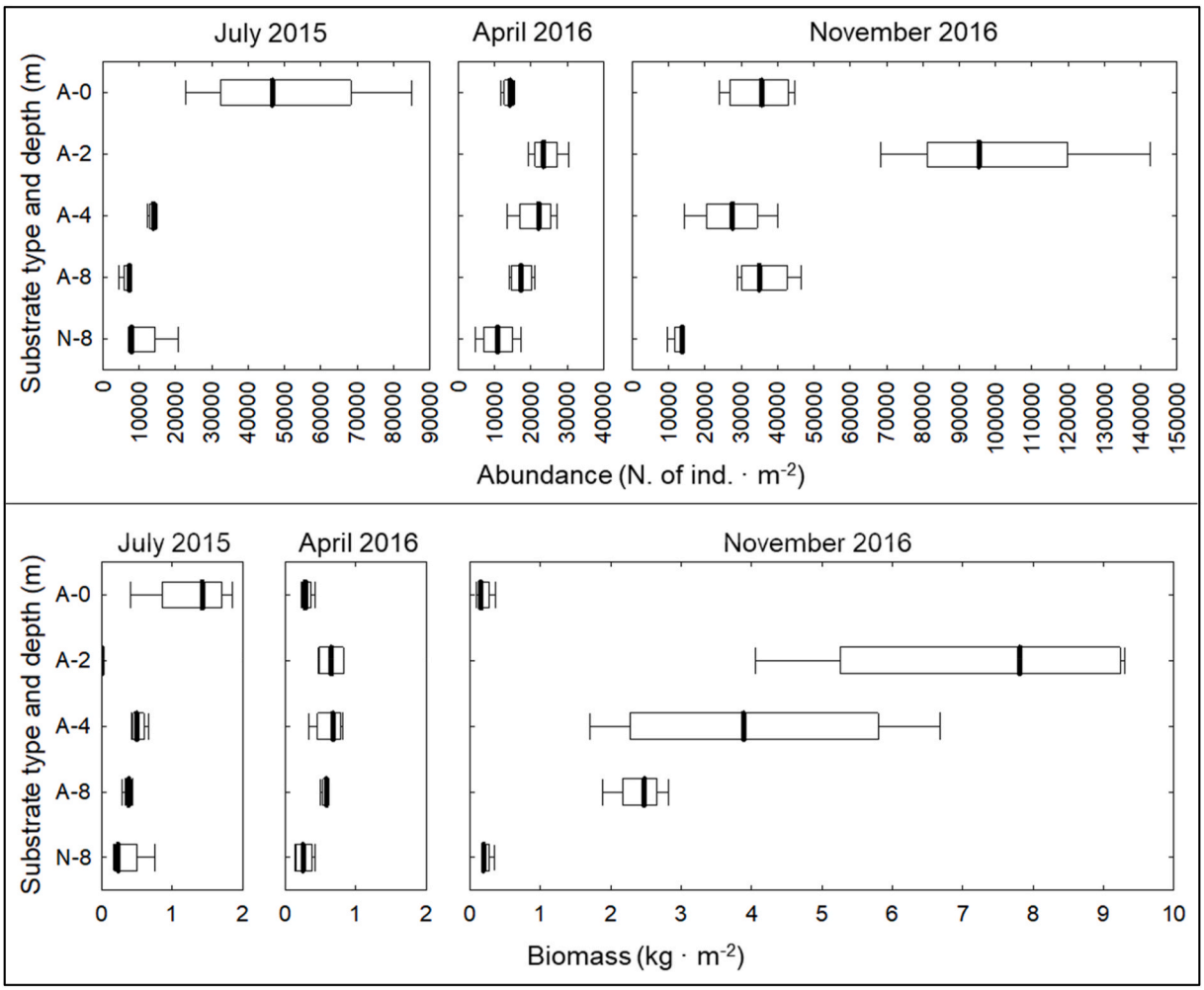

Fig. 5. Abundance (top) and biomass (bottom) at each depth and each site in different months. N on the X (vertical) axis refers to natural substrate and A refers to artificial substrate. Bold lines represent the median, boxes represent 25–75th percentile, whiskers extend between the minimum and maximum.

A. improvisus was different at the two types of substrates. *M. trossulus* had a higher proportion at the artificial substrate, while *A. improvisus* dominated at the natural substrate. Such an inverted proportion between the two species was not reported by other authors who compared natural and artificial hard-bottom benthic communities in the Baltic Sea (Qvarfordt et al., 2006; Wilhelmsson and Malm, 2008). On the other hand, Grzelak and Kukliński (2010), who studied communities at the rocky seabed in another part of the Gulf of Gdańsk, also observed the dominance of *A. improvisus* at the natural substrate in relation to *M. trossulus*.

The varying biomass of filter feeders is likely the result of different hydrodynamics around the artificial structure that extends across the water column or natural boulders elevated only up to 0.5 m above the seabed. These differences may lead to a varying amount of food particles and resuspension of sediments, which has been indicated to be a key factor affecting filter feeders (Pearson and Rosenberg, 1978; Kautsky, 1982; Wildish and Kristmanson, 1984; Fréchette et al., 1989; Dolmer and Frandsen, 2002; Whomersley and Picken, 2003). Higher amount of *M. trossulus* at artificial substrate when compared to boulders at the same depth may be explained by the fact, that mussels are semi-mobile organisms. It has been previously reported, that mussels colonize the artificial substrate in the shallow subtidal zone first and then move downwards (Kerckhof et al., 2019).

Mussels from *Mytilus* genus are an important element of sessile macrofauna on artificial hard ssubstrates in the North Sea as well, however they do not have as strong dominant position as in the Baltic Sea (Kerckhof et al., 2019; Rumes et al., 2021). This can be due to higher competition from other sessile species. For example in the North Sea plumose anemone *Metridium senile* has been described as a successful competitor of *Mytilus* on artificial substrate leading to co-dominance of mussels and anemones (Kerckhof et al., 2019; Rumes et al., 2021). On the other hand the only major competitor of *Mytilus* in the Baltic Sea is barnacle *A. improvisus*, which has been reported to be outcompeted by mussels on artificial substrate (Dürr and Wahl, 2004). Another reason for the stronger dominance of mussels on artificial hard substrate in the Baltic Sea may be the absence of megafaunal predators. Even in the western Baltic Sea species like starfish *Asterias rubens* and shore crab *Carcinus maenas* can significantly reduce mussel population, but they do not occur in the Baltic Proper (Reusch and Chapman, 1997; Enderlein and Wahl, 2004).

Interestingly, although mussel biomass was up to 100 times higher at the artificial substrate, the species richness of the associated mobile fauna was lower at the artificial structure. This in a way contradicts some of the reports about dense populations of mussels supporting particularly rich benthic communities (Suchanek, 1985; Tsuchiya and Nishihira, 1985; Lintas and Seed, 1994; Rumes et al., 2021). The associated fauna in communities with high mussel biomass was relatively homogenous, with abundant gammarids and decapods. Higher species richness was observed in samples with lower biomass of *M. trossulus*, especially at the natural substrate. This follows the observations of Dürr and Wahl (2004), who found, that high densities of *Mytilus* can negatively affect the recruitment of other sessile species and tube-building

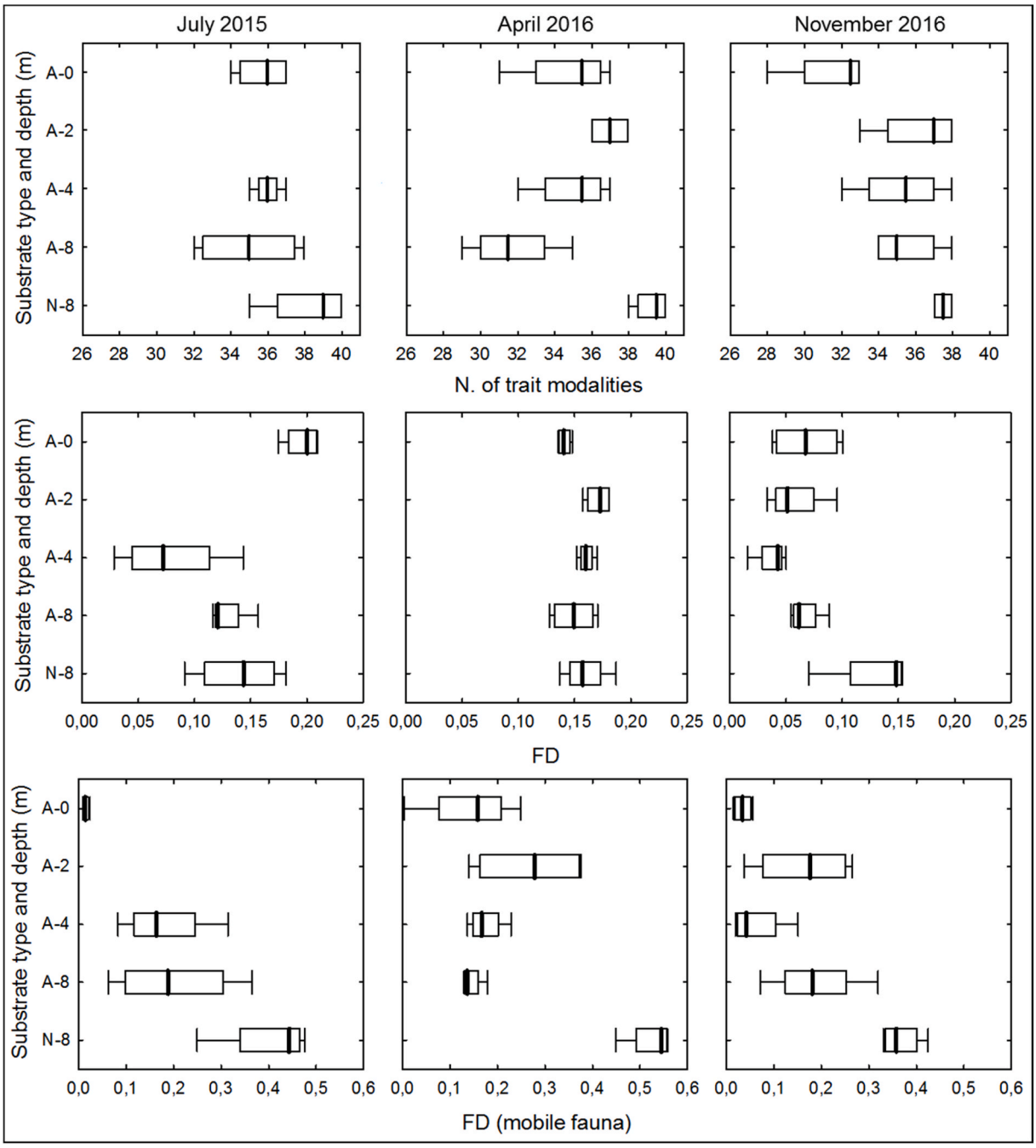

Fig. 6. Total number of trait modalities, FD of the entire assemblages and FD of associated mobile fauna at each depth and each site in different months. N on the X (vertical) axis refers to natural substrate and A refers to artificial substrate. Bold lines represent the median, boxes represent 25–75th percentile, whiskers extend between the minimum and maximum.

polychaetes and crustaceans.

Similar to Andersson and Öhman (2010), we observed slight vertical zonation of the community at the artificial structure. Of all depths at the artificial substrate, the splash zone was characterized by the highest percentage of *A. improvisus* and gammarids. As the substrate in this zone may have been exposed by water for long periods of time due to changing sea level, barnacles were more competitive. Gammarids were also reported to inhabit such communities in greater numbers (Brzana and Janas, 2016). Smaller differences were observed between the remaining depths at the structure. As in other reports, the zonation was mainly expressed in higher biomass of *M. trossulus* at a depth closer to the surface.

We observed high seasonal variability at the structure, but not at the natural substrate, where no significant differences were observed between the seasons. The most variable zone was the splash zone, which is to be expected in an environment that can be periodically exposed and re-covered by water. It is also worth mentioning that defining the splash zone during the sampling was not always a simple task due to a relatively high wave during some seasons. The other depths were easy to locate due to visible footprints on the wall left from previous sampling, which made the sampling more consistent.

Seasonal changes were once again related to varying biomass of *M. trossulus* and *A. improvisus*. Particularly high seasonal variation in biomass was observed in the case of mussels at a depth of 2 m, with an increase from over 400 g m^{-2} in April to over 6500 g m^{-2} in November the same year. This variation at lower depths may be explained by the

Table 4
Results of two-way PERMANOVA pair-wise tests for differences in the taxonomic and functional structure in relation to substrate type and season at depth of 8 m.

Factor	Group	Pair	*p* values for pairwise comparisons	
			Taxonomic structure	Functional structure
Month	July 2015	Natural, Artificial	**0.026**	**0.038**
	April 2016	Natural, Artificial	**0.021**	0.056
	Nov. 2016	Natural, Artificial	**0.022**	**0.034**
Substrate type	Natural	Jul., Apr.	0.182	0.373
		Jul., Nov.	0.150	0.231
		Nov., Apr.	0.100	0.065
	Artificial	Jul., Apr.	**0.020**	0.087
		Jul., Nov.	**0.032**	**0.020**
		Apr., Nov.	**0.030**	**0.033**

Table 5
Results of two-way PERMANOVA pair-wise tests for differences in the taxonomic and functional structure in relation to depth and season at artificial substrate.

Factor	Group	Pair	*p* values for pairwise comparisons	
			Taxonomic structure	Functional structure
Month	July 2015	8 m, 4 m	**0.040**	**0.032**
		8 m, 0 m	**0.019**	**0.028**
		4 m, 0 m	**0.037**	**0.040**
	April 2016	8 m, 4 m	0.468	0.511
		8 m, 0 m	**0.028**	0.748
		4 m, 0 m	0.076	0.559
	Nov. 2016	8 m, 4 m	0.157	**0.024**
		8 m, 0 m	**0.023**	1.000
		4 m, 0 m	**0.018**	0.109
Depth	0 m	Jul., Apr.	**0.038**	0.125
		Jul., Nov.	**0.023**	**0.030**
		Nov., Apr.	**0.025**	**0.031**
	4 m	Jul., Apr.	**0.026**	**0.030**
		Jul., Nov.	**0.034**	**0.021**
		Apr., Nov.	**0.042**	**0.023**
	8 m	Jul., Apr.	**0.022**	0.095
		Jul., Nov.	**0.029**	**0.028**
		Apr., Nov.	**0.030**	**0.025**

removal of mussels due to wave action during storms. This may be related to the impaired ability of *Mytilus* to form byssus threads under low salinity conditions (Allen et al., 1976; Young, 1985; Andersson and Öhman, 2010). The increase in biomass in November may be explained by the fact that mussels can double their weight just before the spawning, which can occur also autumn (Kautsky, 1982).

The overall functioning identity of benthic communities from both natural and artificial hard substrates may be described as highly homogenous, with a strong emphasis on sessile or semi-sessile suspension feeders. This is different than observations of Henseler et al. (2019), who compared rocky bottom benthic assemblages with the ones associated with sandy bottom and macrophytes. The difference is probably a result of different approaches to calculating CWM, primarily the fact, that we used biomass instead of abundance in our calculations.

It should be noted that although the communities were characterized by similarly high percentage of filter feeders, the higher biomass at artificial structures may lead to a significantly higher import of organic matter from pelagic zone (Rönnbäck et al., 2007).

The functional diversity of the studied communities was strongly affected by taxonomic composition and biomass of individual taxa, which is typical for species-poor systems where some trait modalities may be represented by single species (Włodarska-Kowalczuk et al., 2010). As *M. trossulus* and *A. improvisus* accounted for up to 95% of the total biomass, they were also responsible for shaping the overall functional identity of the studied communities. Therefore, the differences in the composition of biological traits reflected the varying proportions between the two species and were observed only in the case of traits for which the two taxa were affiliated to different modalities. This included living habit/mobility, longevity and body shape.

The above mentioned differences may affect functions such as habitat forming and productivity. Probably the most important trait distinguishing the two dominant sessile species is the degree of attachment to the substrate. Barnacles are attached permanently via biological adhesives (Liang et al., 2019). This means that even after the death of organism it's six shell plates will remain attached to the substrate. It may be important for the function of habitat forming as some species have been observed to find shelter in empty *A. improvisus* shells (personal observations, Fig. 10).

On the other hand *M. trossulus* is attached to the substrate via byssus and is more susceptible to being detached from the surface during environmental disturbances. It is also unlikely for the organism's shell to remain attached after its death (Allen et al., 1976; Young, 1985). As a result, the assemblages dominated by *A. improvisus* may be more reliable

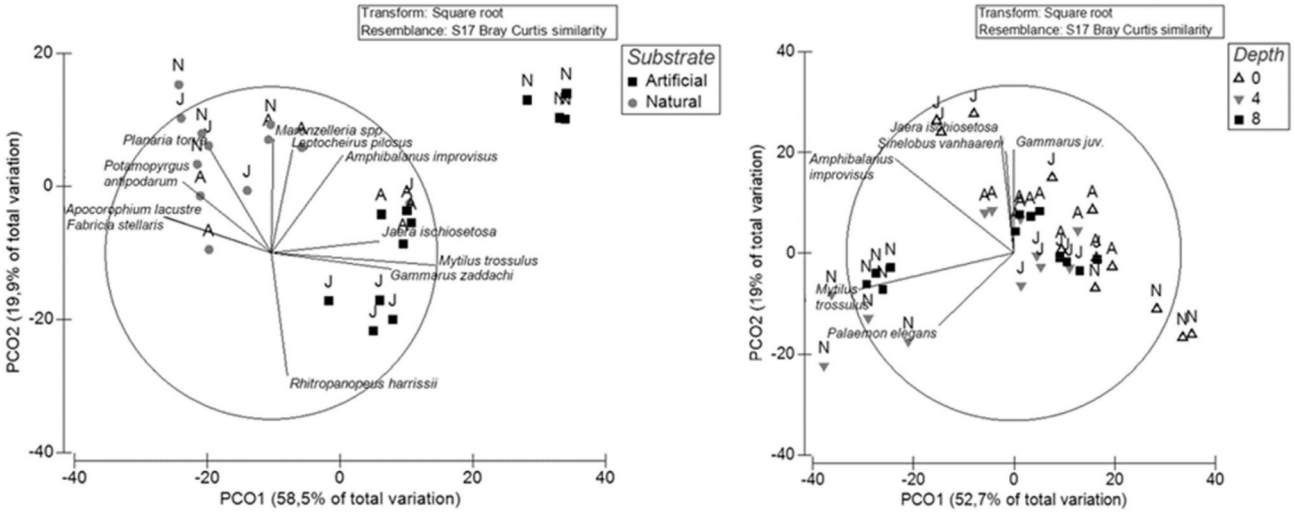

Fig. 7. PCO plots of taxonomic composition of benthic communities at natural and artificial substrates (left) at different depths (right) in particular months (J – July, A – April, N – November). Vector overlay shows species that are best correlated (Spearman correlation >0.6) with the observed multivariate pattern.

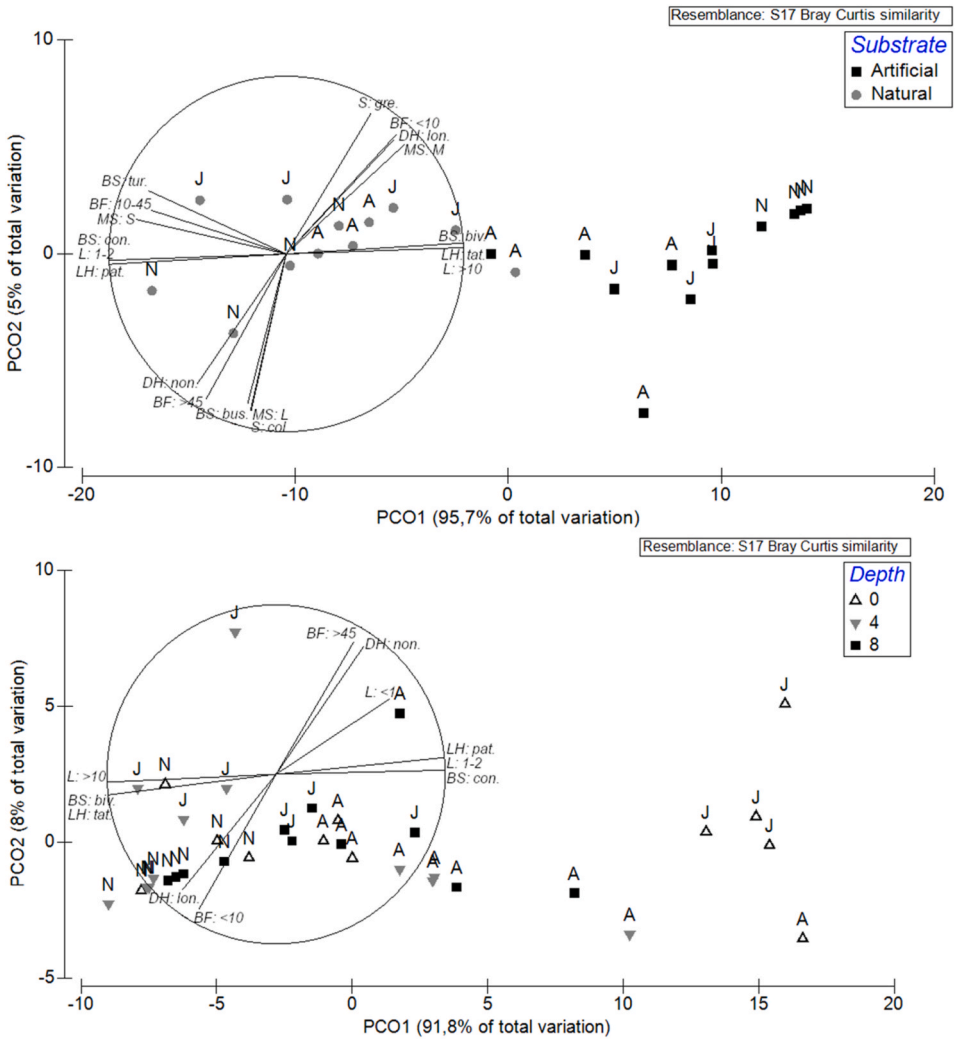

Fig. 8. PCO plots of biological traits of benthic communities at natural and artificial substrates (upper) at different depths (lower) in particular months (J – July, A – April, N – November). Vector overlay shows species and trait modalities that are best correlated (Spearman correlation >0.8) with the observed multivariate pattern. Categories and modalities labels refer to Table 1.

in contributing to habitat forming function. In fact, the functioning identity of assemblages from natural substrate did not differ significantly between the studied months, while significant seasonal variability was observed for artificial substrate.

5. Conclusions

Our results are consistent with the reports that benthic communities at artificial structures are not substitutes for communities at natural substrates. Most importantly, the artificial structure does not support a higher taxonomic richness compared to the natural substrate. On the contrary, natural hard substrate should be considered as equally or more diverse than artificial substrate. Functional diversity is also higher at natural substrates, indicating higher heterogeneity among biological traits of the associated mobile species. They are also less susceptible to seasonal variation.

The positive effect of artificial structure on benthic species richness and diversity would probably be observed in species-poor environments, i.e. silty bottom in deep waters affected by hypoxia and anoxia. In other areas, an increase in the density of specific taxa should be expected, leading to a significant increase in biomass of some filter-feeding species and free living crawlers/swimmers (mainly crustaceans). The identification of artificial structures as biodiversity hotspots should therefore be approached with greater caution.

CRediT authorship contribution statement

Radosław Brzana: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Marta Beata Peschke:** Writing – review & editing, Visualization, Software, Formal analysis, Data curation. **Urszula Janas:** Writing – review & editing, Supervision, Software, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

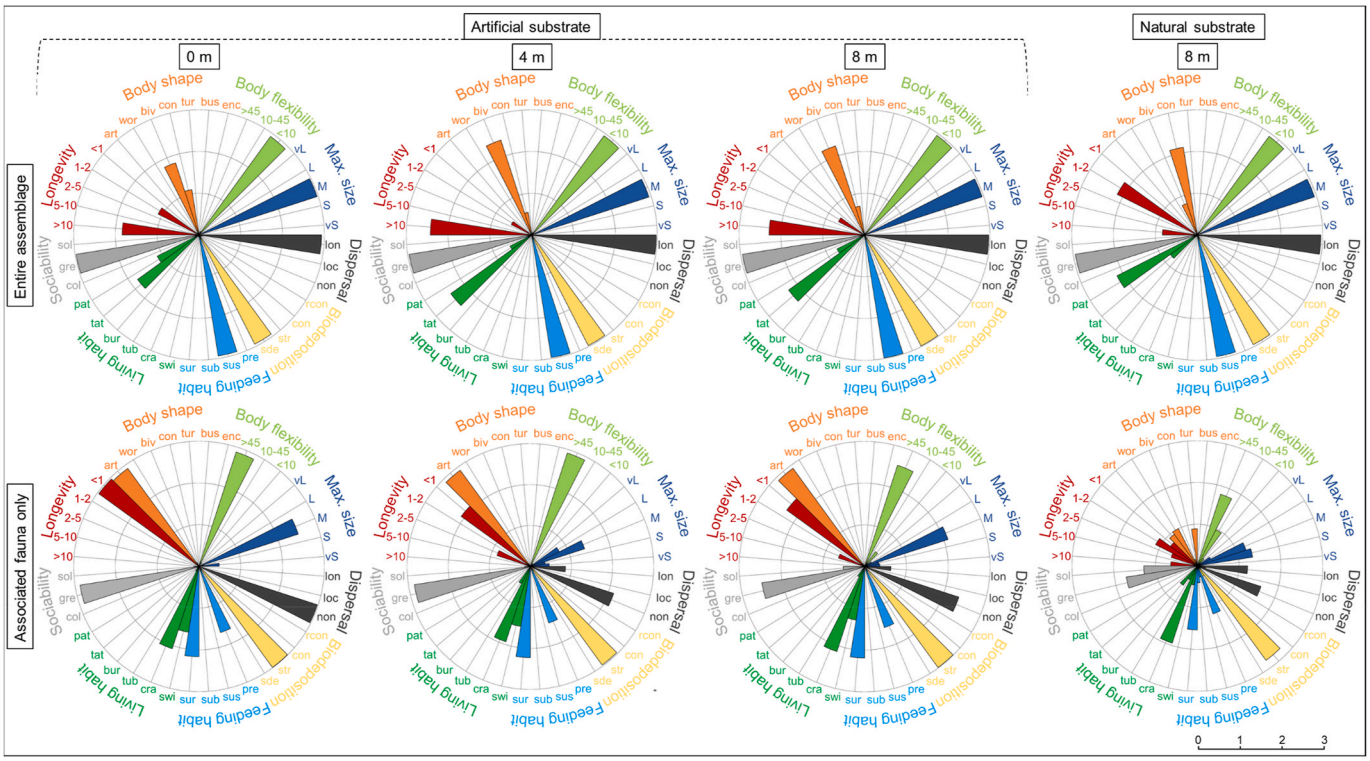

Fig. 9. Community weighted means of trait modality expression (CWM) across depths and substrate types. Trait modalities labels refer to Table 1.

Fig. 10. Isopods from genus *Lekanesphaera* using empty *Amphibalanus improvisus* shells as shelter at artificial substrate in Puck Bay. Photographs taken by the first author.

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Gdynia, 26.09.2025

Radosław Brzana

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Natural hard substrate and 70-year-old artificial offshore structures as habitats for non-indigenous species in the brackish environment of the Baltic Sea☆,☆☆

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1. Introduction

Human-mediated introductions of non-indigenous species (NIS) are considered to be one of the major threats to marine biodiversity and ecosystem functioning (Halpern et al., 2008; Butchart et al., 2010; Occhipinti-Ambrogi, 2021). The main vectors responsible for the introduction and spread of NIS include marine transport, recreational boating and aquaculture (Carlton, 1985, 1994; Rotter et al., 2020; Outinen et al., 2021). In addition to the modes of NIS transportation, a suitable habitat matching the species preferences at the place of arrival is also an important factor that may affect successful introduction, the subsequent establishment of a stable population and secondary spread in the area (Faasse and van Moorsel, 2003; Seebens et al., 2016). As many of the first records of NIS originate from heavily urbanized areas in the coastal zone around the world, man-made structures are believed to facilitate the introduction and spread of macrobenthic NIS (Glasby et al., 2007; Ruiz et al., 2000, 2009). Furthermore, the relation between NIS introduction and marine man-made structures is gaining importance due to the increasing urbanization in offshore areas as well (Kerckhof et al., 2011; Bugnot et al., 2021).

Shortly after construction, artificial structures provide a free surface available for benthic epifaunal species to settle in a highly disturbed environment (Glasby et al., 2007). They also often form specific habitats that have no natural counterparts in the area (Faasse and van Moorsel, 2003; Kerckhof et al., 2011). Indigenous species are generally less competitive in such artificially created environments than NIS, which are generally tolerant to a wider range of environmental conditions and disturbances (Cohen and Carlton, 1998; Piola and Johnston, 2008; Lenz et al., 2011). While highly competitive NIS can be expected to have an advantage over native species on a newly created artificial surface, the question remains if the artificial substrate will remain an equally attractive habitat for NIS decades after the construction, with a developed benthic community inhabiting its surface.

Due to low salinity values, the Baltic Sea ecosystem is characterized by low biodiversity (Leppäkoski, 1994; Leppäkoski et al., 2002; Kniebusch et al., 2019). The total number of NIS recorded in the Baltic Sea is also several times lower than in European marine waters (European Environment Agency, 2023; Galanidi et al., 2023; HELCOM, 2023). However with the low number of native species and unsaturated niches and habitats, each introduction of NIS to the Baltic Sea is even more significant (Leppäkoski, 1994; Leppäkoski et al., 2002; Streftaris et al., 2005; Reise et al., 2006).

Since the Baltic region has yet to experience significant offshore wind industry development, it is important to study the role of artificial hard substrate for the spread of NIS in the area. Some of the most recent introductions to the Baltic Sea have included benthic macrofaunal species associated with hard bottom: dreissenid mussel *Mytilopsis leucophaeata*, amphipod *Melita nitida* and tanaid *Sinelobus vanhaareni* (Dziubińska, 2011; Normant-Saremba et al., 2017; Brzana et al., 2019). *Sinelobus vanhaareni* in particular, given its relatively recent introduction, has been found to dwell on hard substrates in large numbers (Brzana et al., 2019).

The following study focuses on macrobenthic NIS living on hard substrates, both artificial and natural, in the Gulf of Gdańsk in the southern Baltic Sea. The two types of substrates were compared at several different depths to identify areas that are most likely to host NIS. The main objective of the study was to answer the question of whether the artificial hard substrate supports a higher number and abundance of NIS than the natural hard substrate even seven decades after the construction of a given structure. We also looked for any correlation (positive or negative) between the number and abundance of indigenous and non-indigenous species. We paid particular attention to most recently introduced NIS.

☆ The authors declare that the data supporting the findings of this study are available within the paper. Should any raw data files be needed in another format they are available from the corresponding author upon reasonable request.☆☆ The authors declare that this work was funded completely by University of Gdańsk.

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2. Material and methods

Samples of macrozoobenthos were collected in the Gulf of Gdańsk, the southern Baltic Sea, at three different sites. Two sites (B and O) were located off the western coast of the gulf and one site (J) was located off the northeastern coast of the gulf. The majority of samples were collected at site B (Babie Doły), which was located 900 m offshore and more than 6 km from the nearest harbor in Gdynia. Site O (Orłowo) was located 320 m offshore and 4.5 km away from harbor in Gdynia. Site J (Jastarnia) was located over 2.17 km offshore and 18 km away from Gdynia (Fig. 1).

Samples were collected from two types of hard substrates: artificial (sites B and J) and natural (sites B and O). The artificial substrate was represented by concrete remains of two 70-year-old offshore structures that were part of a torpedo testing complex constructed during World War II. Both structures at sites B and J provide vertical, smooth hard surface that extends from the seabed up to 1 m above the water surface. The structure at site B is 17 m long, 7.5 m wide and lies at depth of 8 m. The structure at site J is 9 m long, 4 m wide and lies at 4 m depth. Bottom sediment around the structures consists mainly of sand and coarse sand (Brzana et al., 2019; Sokołowski et al., 2021).

The natural substrate at sites B and O was represented by boulders (up to 2 m in diameter) elevated up to 1 m above the sandy seabed. At site B the boulders lie at 8 m depth approximately 100 m away from the artificial structure. Depth at site O is 5 m. The boulders at the study sites originate from the eroded cliffs at the western coast of the Gulf of Gdańsk. They are represented by granitoids, gneisses, sandstones, porphyry and quartzites (Grzelak and Kuklinski, 2010; Kowalewska, 2020; Sokołowski et al., 2021).

Samples were collected during three sampling events: in July 2015, April and November 2016. Samples at sites J and O were collected only in April 2016. Samples at the artificial structures were collected at several depths – at the water surface in the splash zone, and at depths of 2 m, 4 m and 8 m. Samples from the natural substrate were collected at a depth of 8 m (site B) and 5 m (site O).

Samples from both substrate types were collected by scraping epifauna within 20 cm × 20 cm quadrats only at vertically oriented surfaces. A modified Kautsky sampler (0.04 m^2 catch area) consisting of a metal frame, mesh sleeve and replaceable collection bags was used for sample collection (Andrulewicz et al., 2004). Four replicates were collected at each depth and each type of substrate during each sampling event. The collected samples were sieved (1 mm mesh size) and preserved in 4 % solution of formaldehyde for further analysis. Organisms found in the samples were sorted and identified to the lowest possible taxonomic level. Individuals of all taxa were counted. Colonial hydrozoans and bryozoans were counted as one individual if present in a sample.

The abundance of selected NIS was compared with that of their indigenous counterparts – taxonomically related species with similar biological traits. We decided to include only the results obtained for *S. vanhaareni*, as it is one of the most recently introduced species and occurred in relatively large numbers. The species can be described as a small (less than 5 mm), tube-building tanaid crustacean (Gagnon et al., 2022). Other crustacean species that matched these characteristics included a tanaid *Heterotanais oerstedii* and two corophiids *Apocorophium lacustre* and *Leptocheirus pilosus* (Krodkiewska et al., 2021; Gagnon et al., 2022; Van Den Neucker et al., 2023).

Statistical analysis was performed using R Studio and PRIMER 6. Differences in richness, abundance and relative abundance (proportion in total abundance) of NIS at site B between the substrate types, depths

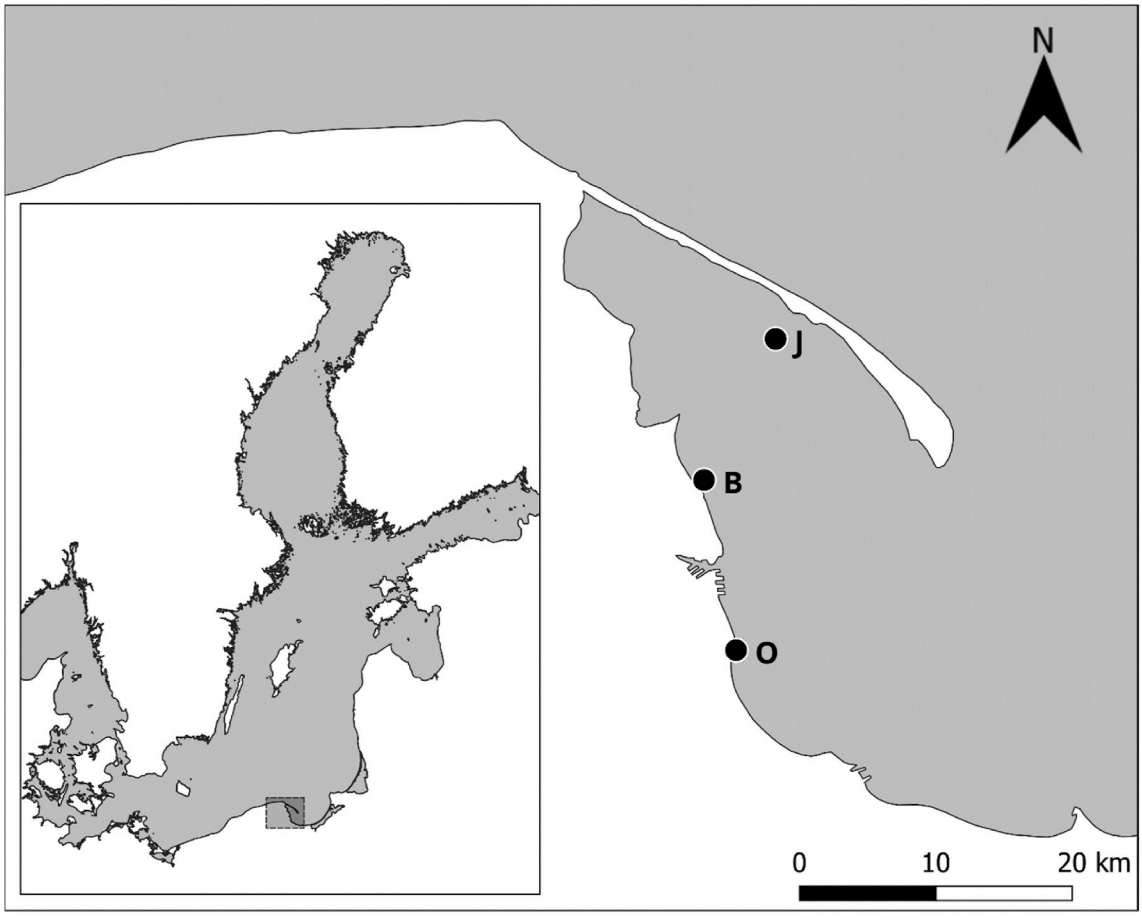

Fig. 1. Location of sampling sites in the Gulf of Gdańsk (Baltic Sea).

Table 1
Taxonomic composition and abundance (N. of ind. · m^{-2}, average ± SD) of macrofaunal NIS at particular sites in different months.

Month and year	July 2015					April 2016								Nov. 2016					
Site	B	B	B	B	B	B	B	B	B	J	J	O	B	B	B	B	B	B	B
Substrate type (A – artificial, N – natural)	A	A	A	N	A	A	A	A	N	A	A	N	A	A	A	A	A	A	N
Taxa Depth (m)	0	4	8	8	0	2	4	8	8	2	4	5	0	2	4	8	8	8	8
Marenzelleria spp.				38 ± 32				6 ± 13	56 ± 52					6 ± 13		50 ± 20	69 ± 13		
Amphibalanus improvisus	11,184 ± 5334	2206 ± 737	1571 ± 591	6956 ± 4806	1144 ± 392	3924 ± 525	6575 ± 3269	3288 ± 519	4613 ± 2994	5781 ± 1646	9075 ± 1388	2969 ± 1528	375 ± 98	21,144 ± 7569	8700 ± 5469	6594 ± 387	5331 ± 2060		
Melita nitida						6 ± 13		6 ± 13			25 ± 35			894 ± 846		13 ± 25			
Rhithropanopeus harrisii		6 ± 13	56 ± 47	13 ± 14	6 ± 13	19 ± 24		19 ± 24	13 ± 14					19 ± 24	13 ± 14				
Palaemon elegans		13 ± 25							6 ± 13					19 ± 24	19 ± 13	13 ± 14			
Sinelobus vanhaareni	4281 ± 2276	3889 ± 1189	250 ± 190	63 ± 52	1650 ± 543	6244 ± 2781	3269 ± 1122	956 ± 283	431 ± 281	1031 ± 718	263 ± 159	463 ± 355	194 ± 97	1556 ± 465	369 ± 238	275 ± 74	544 ± 281		
Potamopyrgus antipodarum				525 ± 438					319 ± 302					13 ± 14	6 ± 13	13 ± 14	500 ± 239		
Mya arenaria		6 ± 13		25 ± 20		25 ± 29			88 ± 83		50 ± 46			100 ± 54	13 ± 25	6 ± 13	19 ± 13		
Mytilopsis leucophaeata		13 ± 14		6 ± 13						19 ± 24				31 ± 31	31 ± 13				
NUMBER OF NIS	2	6	3	7	3	5	2	5	7	3	4	2	2	9	7	7	5		
TOTAL NUMBER OF TAXA	18	19	17	26	15	20	16	15	23	24	27	13	12	24	20	21	23		

and seasons were tested. The differences were tested separately between artificial and natural substrate at 8 m depth (Mann–Whitney *U* test) and between different depths (0 m, 4 m and 8 m) at artificial substrate (Kruskal–Wallis test). The differences between sampling events (July 2015, April 2016, November 2016) were tested separately for artificial and natural substrate assemblages. Dunn's test with Bonferroni correction was used for pairwise comparisons. Results from site O, J and B at 2 m depth were not included in above analyses due to a significantly smaller sample size. Correlations were tested using the Spearman test. The SIMPROF test was used to test differences between benthic communities based on the abundance of individual taxa.

3. Results

A total of 38 macrobenthic taxa were identified during the study. Nine of them are considered to be non-indigenous to the Baltic Sea region. This included five crustaceans, three mollusks and one polychaete. All of the species were previously recorded in the Baltic Sea. Three of the species had been introduced relatively recently to the region – the dreissenid bivalve *M. leucophaeata,* the amphipod *M. nitida* and the tanaid *S. vanhaareni*. Few taxa were present at all sites and depths in every sampling season, including two NIS: *Amphibalanus improvisus* and *S. vanhaareni.* All NIS were recorded at both types of substrate except for *M. nitida*, which was observed exclusively on artificial substrates at sites B and J (Table 1).

The highest average number of taxa was observed at site J on artificial substrate at a depth of 4 m in April 2016 (22). The highest number of NIS (9) was observed at site B on artificial substrate at a depth of 2 m in November 2015. This was also the highest percentage of NIS in total species richness (37 %). However, in both July and April, the number of NIS was highest on the natural substrate at site B (Fig. 2a).

The total abundance of benthic macrofauna, as well as the abundance of NIS, was highest in November at site B on artificial substrate at a depth of 2 m. The percentage of NIS in total abundance was highest on the natural substrate at site B in July (70 %; Fig. 2b).

A comparison of assemblages on different substrate types at site B revealed, that NIS richness was significantly higher at natural substrate ($p = 0.002$). There was no significant difference in the abundance of NIS ($p = 0.167$), but the relative abundance was significantly higher on natural substrate ($p < 0.001$). There were several significant differences in NIS richness, abundance and relative abundance (p values < 0.001, 0.026 and < 0.001 respectively) between different depths at artificial substrate. No significant differences were observed between samples collected in different seasons from natural substrate. A significant difference ($p = 0.015$) in relative abundance on artificial substrate was observed between sampling seasons (Tables 2 and 3).

A weak positive correlation was found between key characteristics of indigenous and non-indigenous species, both for richness ($r = 0.358$, $p = 0.002$) and abundance ($r = 0.440$, $p < 0.001$; Fig. 3).

There were significant differences between depths, substrate types and seasons in taxonomic composition and abundance (SIMPROF test). Natural and artificial hard substrate samples were divided into two separate clusters based on the structure of the entire communities. On the other hand, the composition and abundance of NIS did not differ between the sites and types of substrates (Fig. 4).

Different NIS showed various preferences for substrate types at particular depths. The New Zealand mud snail *Potamopyrgus antipodarum* was present almost exclusively on natural substrate. Spionid polychaete *Marenzelleria* spp. was also more abundant and more frequent on natural substrate. On the other hand, several species occurred almost exclusively on artificial substrate: rockpool shrimp *Palaemon elegans*, amphipod *M. nitida* and dreissenid *M. leucophaeata.* The abundance of crab *Rhithropanopeus harrisii* was also higher on artificial substrate. The abundance of *A. improvisus* and *S. vanhaareni* was similar on natural and artificial substrates at a depth of 8 m, but the highest abundance of these species was observed at smaller depths on

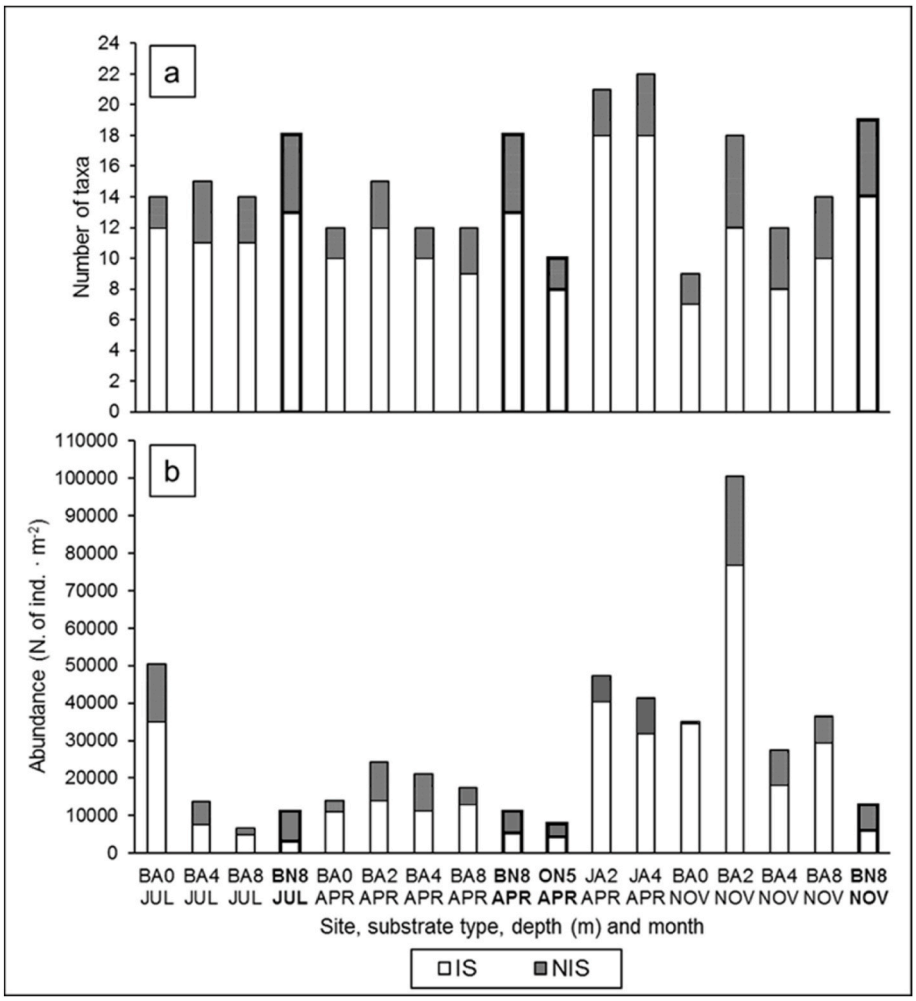

Fig. 2. Average taxonomic richness (a) and abundance (b) of indigenous species (IS) and non-indigenous species (NIS). On the X axis, the first letter indicates a site (B, O or J), the second letter stands for the type of substrate (A – artificial, N – natural) and the number indicates the depth (meters). Bold columns and labels on the X axis indicate natural substrate.

Table 2
Results obtained by Mann–Whitney *U* test and Kruskal–Wallis tests. Bold values indicate significant differences ($p < 0.05$).

Factor (Levels)	Variable	Mann – Whitney *U* Test	
		p value	W
Substrate type (Natural, Artificial)	NIS richness	**0.002**	19
	NIS abundance	0.167	47
	NIS relative abundance	< **0.001**	4

Factor (Levels)	Variable	Kruskal – Wallis Test		
		p value	Chi-squared	df
Depth on artificial substrate (0 m, 4 m, 8 m)	NIS richness	< **0.001**	13.861	2
	NIS abundance	**0.026**	7.281	2
	NIS relative abundance	< **0.001**	17.802	2
Season on natural substrate (July 2015, April 2016, November 2016)	NIS richness	0.503	1.375	2
	NIS abundance	0.878	0.261	2
	NIS relative abundance	0.116	4.308	2
Season on artificial substrate (July 2015, April 2016, November 2016)	NIS richness	0.068	5.392	2
	NIS abundance	0.789	0.475	2
	NIS relative abundance	**0.015**	8.443	2

Table 3
P values obtained by Dunn's pairwise test using samples collected at different depth and in different seasons on artificial substrate at site B. Bold values indicate significant differences ($p < 0.05$).

Factor	Pair	NIS richness	NIS abundance	NIS relative abundance
Depth	8 m & 4 m	1.000	0.086	**0.003**
	8 m & 0 m	**0.001**	1.000	1.000
	4 m & 0 m	0.0220	**0.042**	< **0.001**
Season	Jul. & Apr.	–	-	0.913
	Jul. & Nov.	–	-	**0.012**
	Apr. & Nov.	–	-	0.197

artificial substrate. Soft-shell clam *Mya arenaria* was less abundant on artificial substrate at a depth of 8, but its abundance at depths of 4 m and 2 m was close to that observed on natural substrate (Fig. 5).

The range of abundance of particular NIS is indicated below their names (N. of ind. · m^{-2}).

Compared to the other small tube-building crustaceans included in the analysis (*H. oerstedii*, *A. lacustre* and *L. pilosus*), *S. vanhaareni* was virtually the only species of the four that occurred in the surface zone. It was also the most abundant species at a depth of 4 m. Near the bottom, on both natural and artificial substrates, *L. pilosus* predominated (Fig. 6).

There was no correlation ($p > 0.05$) between the abundance of *S. vanhaareni* and *H. oerstedii.* There was a positive correlation between the abundance of *S. vanhaareni* and the total abundance of indigenous

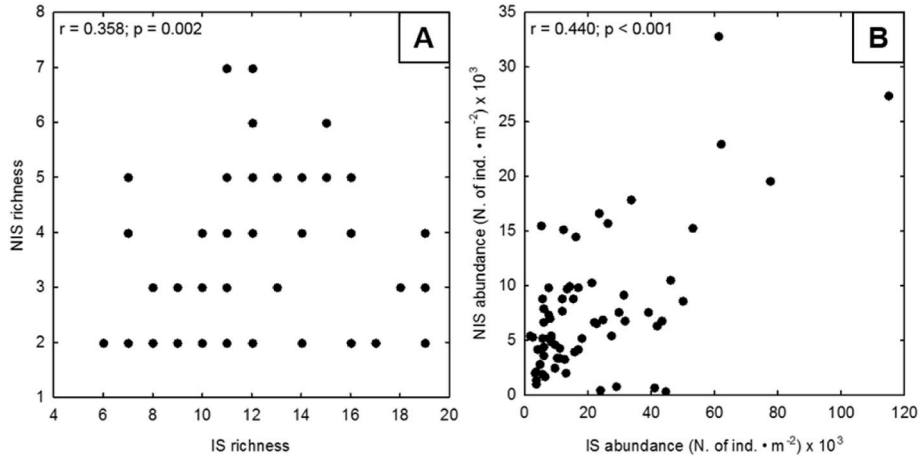

Fig. 3. Relationship between richness (a) and abundance (b) of non-indigenous species (NIS) and indigenous species (IS).

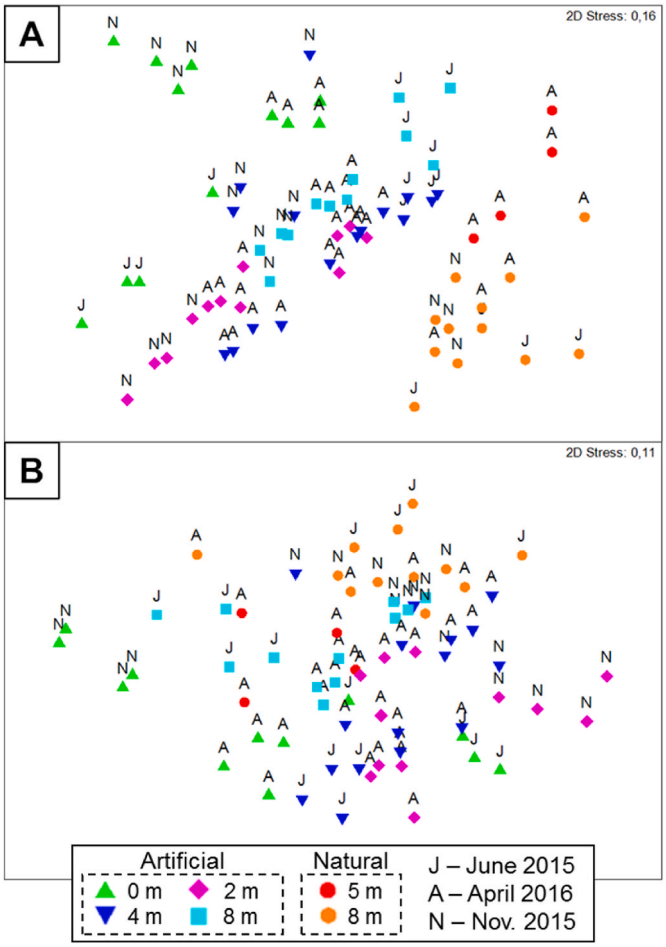

Fig. 4. MDS based on the abundance of individual taxa (Bray–Curtis similarity, square root). A – analysis with all taxa, B – NIS only.

small tube-building crustaceans ($p < 0.05$; Fig. 7).

4. Discussion

The results of the direct comparison between artificial and natural hard substrates at the same depth are not consistent with the widely accepted view that artificial substrate attracts more NIS, both in terms of their richness and abundance. On the contrary, we observed that, on average, more NIS were present on the natural substrate and there were no differences in their abundance between the two types of substrates at different depths. It is worth noting, however, that the relative abundance of NIS on the natural substrate was higher and in some cases they were more abundant than native species. This, however, was mainly due to the high abundance of the barnacle *A. improvisus*, which is one of the two dominant sessile taxa associated with hard substrate habitats in the Baltic Sea (Qvarfordt et al., 2006; Grzelak and Kuklinski, 2010; Brzana et al., 2024).

As mentioned earlier, these results in some ways contradict the reports of several other authors who carried out studies both on temporarily submerged experimental substrate and older structures with well-established benthic communities. For example, Tyrrell and Byers (2007) observed similar NIS richness on various types of experimental artificial and natural hard substrates, but a significantly higher abundance on artificial substrate. Glasby et al. (2007) reported higher NIS richness on various types of artificial substrates compared to natural substrate, with the exception of the sandstone seawall, which was the only type of substrate sampled at a similar depth as the natural reef, compared to wooden and concrete pilings and pontoons, which were sampled closer to the water surface. In our study, the number of NIS was generally higher on natural substrate than on artificial substrate at any studied depth. The results obtained by Glasby et al. (2007) may be more an effect of different types and materials of substrates (for example a floating pontoon versus a stable seawall). The results in the current study may also be due to the opportunistic nature of many species in the brackish environment of the Baltic Sea. Unlike the truly marine environments studied by other researchers, there are very few species living exclusively on a certain type of substrate in the Baltic Sea, resulting in small differences in taxonomic composition (Węsławski et al., 2013). The lack of a significant intertidal zone may also be a factor, as some authors point to artificial structures as those that provide unique habitats in this particular zone (Kerckhof et al., 2011; De Mesel et al., 2015). As a result, many of the Baltic native species may prove to be equally competitive as some of the NIS, for example, *Mytilus trossulus*, which is the main competitor of *A. improvisus* and was actually far more abundant on artificial than natural substrate. It is worth noting that the inhibitory effect of *Mytilus* on the recruitment of other fauna, including non-indigenous *A. improvisus*, has been reported in the past (Dürr and Wahl, 2004). Also since the natural and artificial hard substrates at site B were located quite close to each other (approximately 100 m apart), the question arises whether the high number of NIS on boulders could be due to the proximity of the man-made structure.

In general, we observed more NIS than reported in other works related to hard substrate in Polish waters (Dziubińska and Janas, 2007; Sokołowski et al., 2017; Bałazy et al., 2019; Witalis et al., 2021). It is

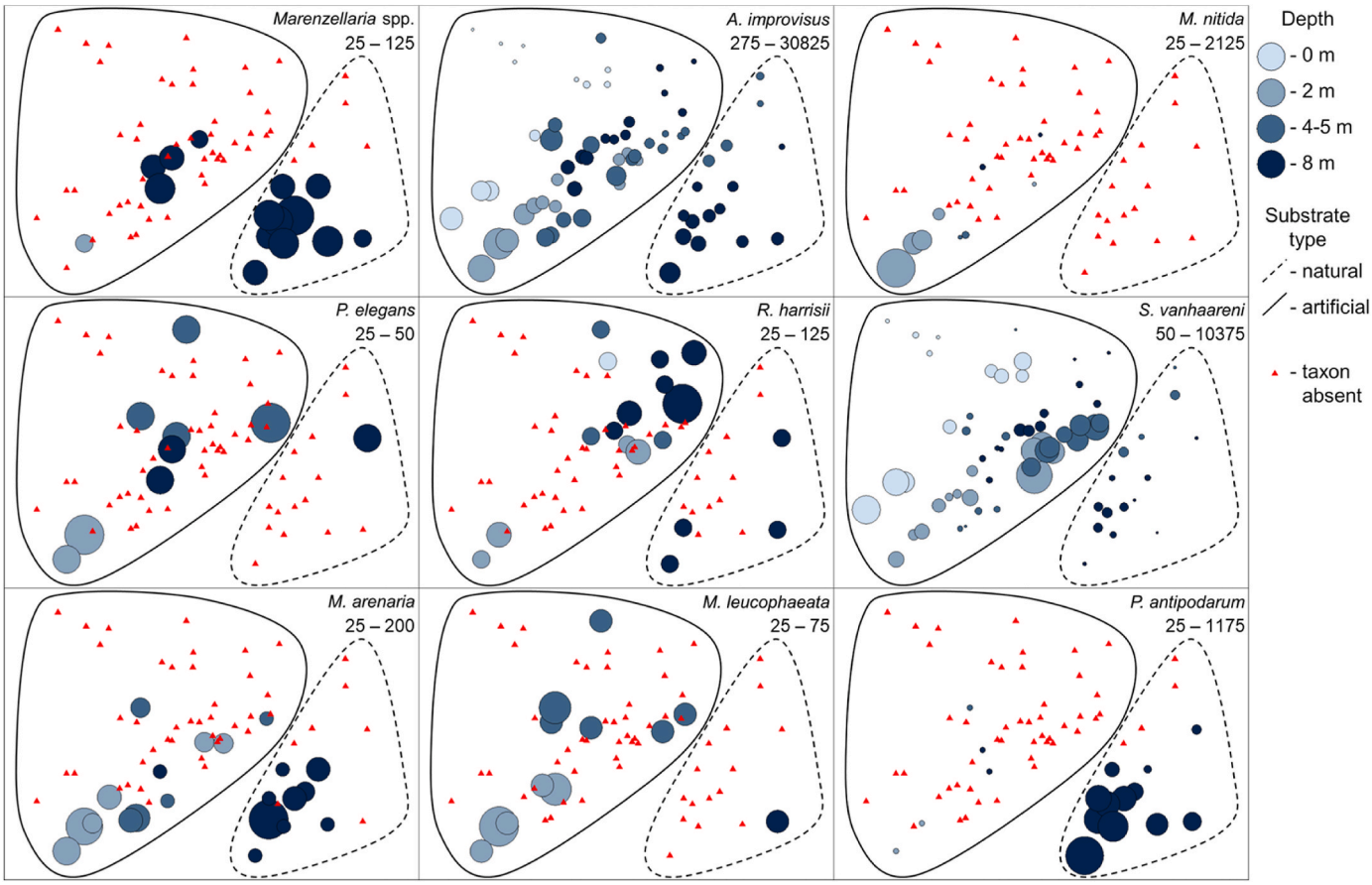

Fig. 5. Bubble graphs presenting the abundance of specific NIS in all samples. The scaling for bubbles is different for every species.

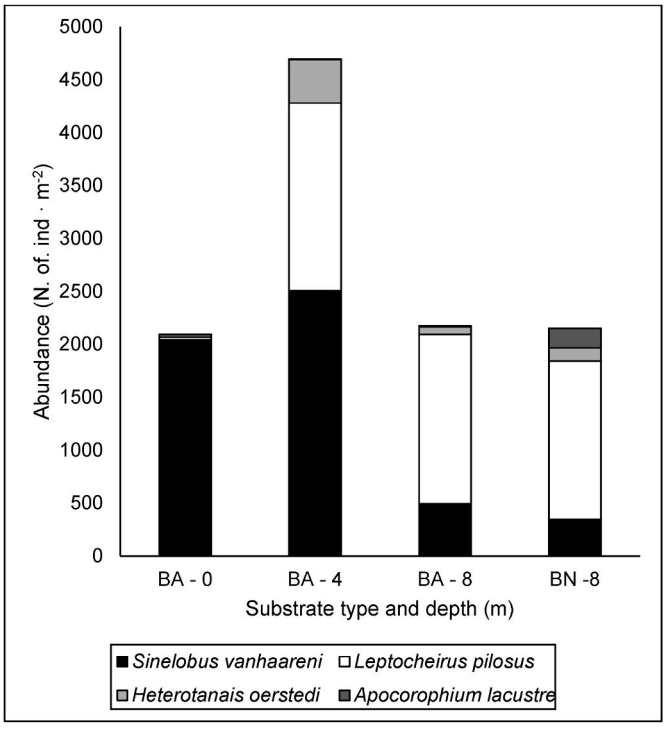

Fig. 6. Average abundance of small tube-building crustaceans at site B at different substrate types and depths. On the X axis, the second letter in each label stands for the type of substrate (A – artificial, N – natural) and the number indicates the depth (meters).

worth noting, however, that these studies focused on ecological succession and used experimental hard substrate. This, however, reveals an importance of including substrates with well-established macrobenthic communities in research and monitoring aimed at detecting NIS.

A closer examination of specific NIS reveals a more significant role of artificial substrate for the introduction and spread of NIS, especially when looking at some of the species that have been recorded in the area relatively recently. *Melita nitida* was recorded only at artificial structures, and both *S. vanhaareni* and *M. leucophaeata* were present in larger numbers at artificial structures, especially at depths where natural substrate was not present. This was also true for several other NIS that had been recorded in the area for a longer time: *A. improvisus*, *P. elegans* and *R. harrisii.* On the other hand, several NIS showed a clear preference for natural substrate, including taxa more closely associated with soft bottom: *Marenzelleria* spp. and *P. antipodarum* (Janas and Kendzierska, 2014). Interestingly, one of the NIS observed on vertical, concrete surface was soft-shell clam *M. arenaria*, which is an infaunal species typical for sandy bottom (Ledoux et al., 2023). It is worth noting, that the species was represented only by juvenile individuals (<10 mm), that had been previously reported to occur embedded in hard bottom fouling communities (Carlton, 1999; Brzana and Janas, 2016). Study by Brzana et al. (2020) revealed, that *M. arenaria* was far more abundant at soft bottom in direct vicinity of man-made structure compared to 200 m away from the structure. This suggests that an artificial structure may indirectly affect abundance of some NIS associated with soft bottom. Overall the results reveal the importance of the ability of artificial structures to provide specific habitats with no natural counterparts, such as shallow (near surface) hard substrate located offshore, which is consistent with the findings of several other studies (Ruiz et al., 2009; De Mesel et al., 2015).

Three of the observed NIS were introduced to the Gulf of Gdańsk

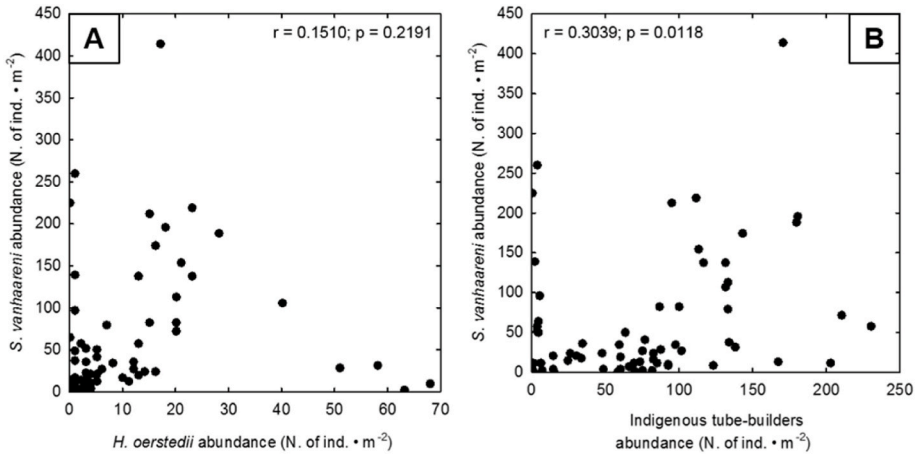

Fig. 7. Relationship between the abundance of *S. vanhaareni* and the abundance of *H. oerstedii* (a) and all native small tube-building crustaceans (b).

relatively recently, i.e. after 2010. These include *M. leucophaeata*, *M. nitida* and *S. vanhaareni* (Dziubińska, 2011; Normant-Saremba et al., 2017; Brzana et al., 2019). *Mytilopsis leucophaeata* was found in large numbers in port basins (Brzana et al., 2017; Outinen et al., 2021). Outside the ports, its abundance is much lower compared to indigenous species with a similar mode of life, i.e. *M. trossulus*. It is worth noting, however, that this is the first time the species was recorded on natural hard substrate. The only previous records of *M. nitida* in the Polish waters came from the Port of Gdynia in 2014 (Normant-Saremba et al., 2017). The current study shows that in 2016 the species spread outside the port, even to locations approximately 18 km away.

Sinelobus vanhaareni had remarkably high success in colonizing the habitats at the study sites, compared not only to *M. nitida* and *M. leucophaeata*, but also to the majority of other NIS recorded during the study. Although we did not observe a negative correlation between the abundance of *S. vanhaareni* and similar native species, a comparison with previous research by Brzana and Janas (2016) suggests that it may have a negative impact on the native tanaid *H. oerstedii* and tube-building corophiid *L. pilosus*. The research was conducted in a similar area and involved sampling at an artificial structure at a depth of 5 m in September 2012. At that time, *S. vanhaareni* was not recorded on the structure. *Heterotanais oerstedii* was the only tanaid present at the site and accounted for an average of over 25 % of the total abundance of mobile macrofauna, while *L. pilosus* was the most abundant among mobile epifaunal species (73 % of the total abundance of mobile macrofauna). The presented results show, that three years later in 2015, at a similar depth (4 m) and with a similar type of substrate, *S. vanhaareni* became a significant contributor to the total abundance of mobile macrofauna with an average contribution of 25–49 %, depending on the season. At the same time, both *H. oerstedii* and *L. pilosus* became significantly less abundant (5–9 % and 15–38 % on average respectively). It is uncertain, however, if this is the result of *S. vanhaareni* competing with native species. The relationship between *S. vanhaareni* and similar native species may be worth conducting further research under experimental conditions.

Our study revealed the importance of hard substrate, both artificial and natural, in the Gulf of Gdańsk for the spread of NIS. Despite the relatively small spatial and temporal scale of the study, we recorded many NIS that have been reported to occur in the area. The proportion of NIS in the total species richness and abundance at the study sites was relatively high: 31 and 33 % on average, respectively. The study by Janas and Kendzierska (2014), which focused mainly on soft-substrate benthos in the Bay of Puck, reported that NIS accounted for an average of 17 % of the total species richness and 6 % of the total abundance in the study area.

5. Conclusions

Direct comparison of fully developed benthic communities on natural and artificial substrates does not indicate that artificial hard substrate is a more favorable habitat for NIS than natural hard substrate at the same depth. Nevertheless, artificial substrate located in the surficial zone (e.g., buoys) or extending throughout the entire water column (e.g., windmill foundations) can form a specific habitat that may support exceptionally dense populations of some NIS. As both types of hard substrates contained more NIS than reported for soft bottom, the deployment of artificial structures into an environment dominated by soft sediments should be perceived as a risk to facilitate the further spread of some NIS in the area.

CRediT authorship contribution statement

Radosław Brzana: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Urszula Janas:** Writing – review & editing, Supervision, Software, Methodology, Funding acquisition.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107222.

Data availability

Data will be made available on request.

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Gdynia, 26.09.2025

Radosław Brzana

OŚWIADCZENIE

Oświadczam, że w pracy:

Brzana, R., & Janas, U. (2025). Natural hard substrate and 70-year-old artificial offshore structures as habitats for non-indigenous species in the brackish environment of the Baltic Sea. *Marine Environmental Research*, 209. 107222

mój udział polegał na współtworzeniu koncepcji artykułu, opracowaniu metodyki, zbiorze i analizie prób makrozoobentosu, przygotowaniu danych do analiz statystycznych, przeprowadzeniu analiz statystycznych, przygotowaniu przeglądu literatury, przygotowaniu wszystkich części manuskryptu, przygotowaniu tabel i grafik, korekcie artykułu zgodnie z uwagami współautorów, wysłaniu artykułu do czasopisma naukowego oraz korekcie artykułu zgodnie z uwagami recenzentów.

Radosław Brzana

Gdynia, 26.09.2025

Urszula Janas

Pracownia Bioróżnorodności i Funkcjonowania Bentosu

Katedra Ekologii Morza

Wydział Oceanografii i Geografii

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mój udział polegał na współtworzeniu koncepcji artykułu, opracowaniu metodyki, zapewnieniu finansowania badań, przeprowadzeniu analiz statystycznych, edycji manuskryptu oraz przesłaniu uwag do artykułu pierwszemu autorowi.

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Podpisano przez:

Urszula Janas
Uniwersytet Gdański

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Effects of a 70-year old artificial offshore structure on oxygen concentration and macrobenthos in the Gulf of Gdańsk (Baltic Sea)

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ABSTRACT

Artificial structures with dense benthic assemblages on their surfaces are likely to affect the adjacent soft bottom and the communities that live there. In this study, we investigated environmental and benthic parameters in the vicinity of a 70-year old offshore concrete structure in the Gulf of Gdańsk, in the southern part of the Baltic Sea. Samples were collected at three distances from the structure in autumn of 2015, 2016 and 2017. Each year, temperature and dissolved oxygen loggers were deployed 4–5 months prior to the collection of benthic samples. The obtained results revealed a significant impact of the structure on several parameters. The average oxygen concentration at 1 m distance was 0.6 mg L^{-1} lower than at 7 m and 50 m distance from the structure. We registered hypoxic events that lasted up to 4 days, with the oxygen concentration dropping to 0.57 mg L^{-1}, and this is the first report on hypoxia in the coastal zone (depth < 8 m) of the Gulf of Gdańsk. Despite the decrease in the oxygen concentration, no adverse effects on the benthos were observed. The highest values of the taxa richness, abundance and biomass were generally recorded at sampling sites located close to the structure.

1. Introduction

Biofouling is a common phenomenon observed on most artificial hard substrates found in the marine environment (Wolfson et al., 1979; Forteath et al., 1982; Stachowitsch et al., 2002; Dziubińska and Janas, 2007; Andersson et al., 2009). Hard substrates in particular provide favourable habitats for sessile filter feeders such as mussels *Mytilus* spp. (Leewis et al., 1994; Wilhemsson & Malm, 2008; Joschko et al., 2008; Krone et al., 2013; Brzana and Janas, 2016). Dense populations of these ecosystem engineers form three-dimensional structures that provide shelter and food for many other invertebrates (Suchanek, 1980; Tsuchiya and Nishihira, 1985; Norling and Kautsky, 2008). As a result, the replacement of soft sediment with artificial substrate leads to significant changes in taxonomic composition as well as an increase in the total abundance and/or biomass of benthic assemblages (Steimle et al., 2002; Zettler and Pollehne, 2006; Wilhemsson & Malm, 2008; Raoux et al., 2016).

Large aggregations of mussels and associated fauna on artificial structures are likely to affect the adjacent natural bottom and benthic assemblages that live there. Observed effects include sediment fining and organic enrichment (Coates et al., 2014; Wilding, 2014; Dannheim et al., 2019; Lefaible et al., 2018). Large organic debris (i.e., dead organisms) sink to the bottom in the immediate vicinity of the structure and smaller particles may be transported and dispersed over a larger distance and surface (Chamberlain et al., 2001; Maar et al., 2009; Dannheim et al., 2019). In addition, the beds of mussels and their empty shells near the structure cause further accumulation of organic material in the sediment (Norling and Kautsky, 2008; Wilding, 2012; Wilding and Nickell, 2013; Janas et al., 2019). Previous studies have estimated the range of significant organic matter enrichment and sediment fining at less than 50 m from the structure (Coates et al., 2014; Colson et al., 2017; Lefaible et al., 2018).

The organic enrichment related to artificial structures has been reported to have neutral, positive as well as negative impact on the benthic fauna of natural substrates. For instance, it enhances the food supply for organisms and leads to a local increase in biomass and abundance of benthos (Maar et al., 2009; Ysebaert et al., 2009; Coates et al., 2014; Drouin et al., 2015; Lefaible et al., 2018). On the other hand, excess organic matter (not consumed by organisms) increases oxygen demand, leading to a reduction in macrofaunal abundance and/or diversity, as in the case of suspended mussel cultures (Tenore et al., 1982; Mattsson & Lindén, 1983; Jaramillo et al., 1992; Grant et al., 1995; Chamberlain et al., 2001; Wilding, 2012; Wilding and Nickell, 2013).

The Baltic Sea is exceptionally susceptible to hypoxia and anoxia due

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to its relatively low water circulation and intense eutrophication (Diaz and Rosenberg, 1995; Karlson et al., 2002). With this in mind, any effects that may be expected to exacerbate hypoxia should be investigated. The objective of this study was to determine whether an artificial structure in the southern Baltic Sea may significantly alter the oxygen concentration and lead to oxygen-stressed (2–4 mg L^{-1}) or hypoxic (<2 mg L^{-1}) conditions. We also investigated the impact of the artificial structure on the soft-bottom benthic assemblage in its vicinity.

2. Material and methods

2.1. Study area and sampling design

The study was conducted in 2015–2017 in the Gulf of Gdańsk, the southern Baltic Sea. Sampling was conducted approximately 900 m off the south–western coast of the Gulf of Gdańsk. Samples were collected at varying distances from the concrete foundations of an offshore watchtower (54.594,487°E; 18.543,944°N) – part of the torpedo testing complex during World War II. After the war, the watchtower was abandoned and has since been slowly decaying. However, the submerged elements of the building remain in good condition. The depth around the structure reaches 7–8 m and the seabed around the structure is homogeneous. The sediment is dominated by sand, but in a few places is mixed with boulders that reach 0.5 m in diameter.

Samples were collected at three sampling sites located southeast of the structure: at a distance of 1 m, 7 m and 50 m. This sampling gradient was parallel with the major current flow observed in the area (Minasiewicz et al., 2011).

2.2. Hydrometric parameters

Key hydrometric parameters were measured using pairs of conductivity data loggers. Each pair consisted of a HOBO U24 and HOBO U26 logger, which together allowed the measurement of water temperature, salinity and oxygen concentration 10 cm above the surface of sediment. Loggers were set to measure these parameters in 1 h intervals.

Data loggers were deployed during three periods of time: August–November 2015, July–October 2016 and July–November 2017. In 2015, 2016, loggers were only deployed at the site located 1 m from the structure. In 2017, pairs of loggers were deployed at each site. Due to intense biofouling, the HOBO U24 loggers stopped collecting data on salinity few weeks after their deployment. For this reason, only a small portion of data on salinity was taken into account in the analysis.

Statistical differences in temperature and dissolved oxygen concentration among sampling sites in 2017 were tested using the Kruskal–Wallis one-way analysis of variance. Pairwise comparisons were performed with Dunn's test. Tests were performed on 24-h average values in order to avoid impact of autocorrelation.

2.3. Bottom sediments

Bottom sediment samples were collected by scientific SCUBA divers on November 20, 2015 at all sampling sites. Sediment cores were collected using PVC cylinders (3 cm diameter, 10 cm height). Grain size analysis was performed after samples were dried at 110 °C. Sediment type and mean grain size were determined according to Folk and Ward (1957) using GRADISTAT (Blott and Pye, 2001). Organic matter content was measured using the method of loss on ignition at 550 °C (Dean, 1974). The amount of shell debris in the sediment was calculated as a percentage of total mass of a given sample.

2.4. Macrobenthos

Macrobenthic samples were collected at all three sampling sites by scientific SCUBA divers. Sample collection was conducted on November 20, 2015, October 30, 2016 and November 19, 2017. Five replicates were collected during each sampling event with a Hydro-Bios Ekman-Birge bottom sampler (0.0225 m^2 catch area). Only the upper 10 cm layer of sediment was collected. The collected samples were sieved (1 mm mesh size) and preserved in 4% solution of formaldehyde for further analysis. Organisms found in samples were sorted and identified to the lowest possible taxonomic level. Individuals from each taxa were counted and weighed (wet mass, g · m^{-2}). The Shannon diversity index *H'* (Shannon and Weaver, 1949) and Pielou's evenness index *J'* (Pielou, 1966) were calculated for each site in each year. Statistical tests were performed using R Studio and PRIMER 6 with PERMANOVA add-on. Statistical differences in species richness, diversity, evenness, biomass and abundance among sampling events were tested using the Kruskal–Wallis one-way analysis of variance. Pairwise comparisons were performed with Dunn's test. PERMANOVA based on Bray–Curtis similarity was used for multivariate analysis. SIMPER analysis was used to calculate the contribution of individual taxa to dissimilarity between the groups. MDS plot was used to visualise level of similarity between samples (Bray–Curtis similarity). The square root pre-treatment was applied to all data prior to any analysis in PRIMER.

3. Results

3.1. Hydrometric parameters

Salinity varied between 6.5 and 7.5, which is a typical range of values observed in the Gulf od Gdańsk. The highest average temperature (22.2 °C) was observed in August 2015 and the lowest (8.7 °C) in November of the same year. In the two following years, the highest temperature was also observed in August and the lowest in October or November. In 2017, differences in average temperature between distances were 0.2 °C or less (Fig. 1). The differences were not significant.

The highest average oxygen concentration (9.8 mg L^{-1}) was observed in November 2015 and the lowest (3.6 mg L^{-1}) in August 2016. There were significant differences in oxygen concentration among sites in September, October, November of 2017 and in the entire sampling period that year. The five-month average oxygen concentration at 1 m was 0.6 mg L^{-1} lower compared to the two other sites. The monthly average was lower at 1 m compared to the two other sites by up to 1.0

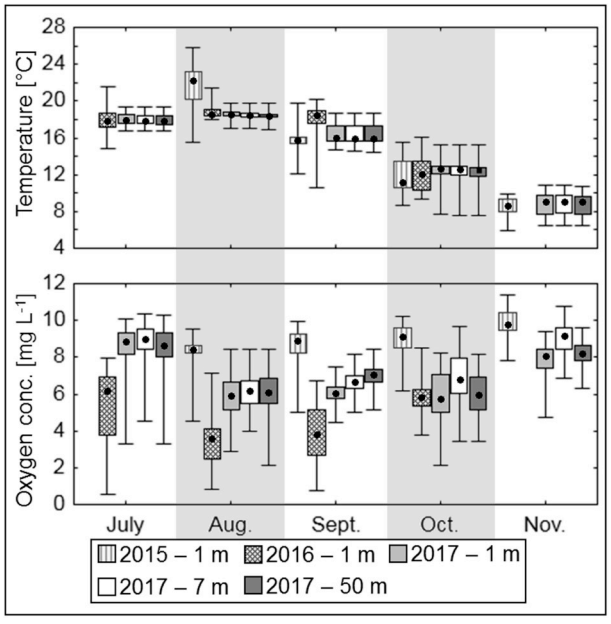

Fig. 1. Monthly temperature (top) and oxygen concentration (bottom) between August and November 2015, July and October 2016, July and November 2017. Dots show median values, boxes show interquartile range and whiskers extend to the extreme values.

mg L^{-1} in September, October and November (Fig. 1). The highest observed difference in single measurements between 1 m and the other sites was 3.7 mg L^{-1} at the beginning of November 2017.

Oxygen-stressed conditions (2.0–4.0 mg L^{-1}) and hypoxic events (<2.0 mg L^{-1}) were observed in 2016 at a distance of 1 m from the structure. In 2016, the average was below 4.0 mg L^{-1} in August and September and the minimum was below 1.0 mg L^{-1} in July, August and September. However, the site at 1 m distance was the only one with associated oxygen concentration readings that year. In 2015, 2017, no hypoxic events were observed with the oxygen concentration dropping to 4.5 mg L^{-1} and 2.1 mg L^{-1}, respectively. There were few instances of oxygen stressed conditions in 2017 (Fig. 1).

3.2. Bottom sediments

The smallest mean grain size (492.3 μm) was recorded at a distance of 1 m from the structure and increased with distance up to 590.9 μm at 50 m. Sediment at a distance of 1 m was classified as medium sand and coarse sand was observed at the two other sites. Organic matter content at 1 m distance reached 0.93%. It was nearly three times that at 7 m (0.32%) distance and four times that at 50 m distance (0.24%). The largest amount of shell debris (2.62%) was recorded at 1 m. It was 0.02% at two other sites.

3.3. Macrozoobenthos

In total, 23 macrobenthic taxa were observed during the entire study period. The largest number of taxa was observed in 2017 (18–23) and the smallest in 2016 (10–12). The taxa absent in 2015 and 2016 were mainly amphipods and decapods (Table 1).

The highest average taxa richness was observed in 2017 and the lowest in 2016. In 2017, 2015, the value was higher at sites located closer to the structure. No such trend was observed in 2016 (Fig. 2). The highest average Shannon index and Pielou's evenness index were observed in 2016 at a distance of 50 m from the structure. Similar to taxa richness, in 2015 and 2017, greater diversity and evenness were estimated for sites closer to the structure. Despite the highest taxa richness in 2017, the Shannon index was generally lower that year compared to the previous years, due to the high unevenness among the taxa, caused mainly by the high abundance of *Mytilus trossulus* Gould, 1850 (Fig. 2, Table 1).

There were no significant differences in taxa richness among the sites. In the case of diversity H' and evenness J', significant differences were observed only in 2017. More differences were detected at particular sites between different years, mainly between 2017 and two preceding years (Table 2).

Pairwise comparison revealed differences mainly between the 1 m site and the two other sites. There were mainly differences between 2017 and two preceding years, but not between 2015 and 2016 (Table 3).

The highest average abundance and biomass were estimated in 2017 (over 120,000 ind. m^{-2} and 1.4 kg m^{-2}) and the lowest in 2016. Abundance and biomass were generally greater at the sites located closer to the structure (Fig. 3). Year and distance contributed to significant differences in abundance in every tested group, but distance only significantly affected the biomass in 2017. The largest differences were observed between 2017 and the two preceding years.

Year had a greater impact on benthic assemblage than the distance, as evident from the MDS plot (Fig. 4). The 2017 samples were clearly separated from 2015 to 2016 samples, which were more similar to each other. Furthermore, the three distances were better distinguished in the 2017 group compared to 2015 and 2016.

PERMANOVA demonstrated that year, distance, and the combination of the two factors contributed to significant differences in taxonomic composition among the investigated benthic assemblages ($p < 0.01$).

Pairwise tests revealed differences between all pairs except for 7 m and 50 m in 2015 and 2016 in the 50 m group. Bray–Curtis dissimilarity was generally lower between pairs in the same year than between years at the same site. At each site, dissimilarity was higher between 2017 and the two preceding years than between 2015 and 2016. In most cases, the dominant taxa (Oligochaeta or *M. trossulus*) had the highest contribution to the dissimilarity between the pairs. Other highly contributing taxa were *Peringia ulvae* (Pennant, 1777), *Hediste diversicolor* (O.F. Müller, 1776) and *Mya arenaria* Linnaeus, 1758 (Table 4).

Table 1
Taxonomic composition and abundance (mean expressed as the number of individuals · m^{-2}) of individual taxa at the sampling sites. Empty cells represent the absence of taxa. Abbreviations in bold next to taxa name refer to Table 4.

	2015			2016			2017		
	1 m	7 m	50 m	1 m	7 m	50 m	1 m	7 m	50 m
Oligochaeta **O.**	2702	1200	1138	791	1884	364	3191	702	960
Hediste diversicolor ***HD.***	453	107	189	107	62	80	507	382	347
Marenzelleria spp.	9	44		9	9	44	89	53	133
Pygospio elegans ***PE.***	62	18	78	9		18	36	71	53
Streblospio shrubsolii ***SS.***	18	9	11	9			44	196	
Amphibalanus improvisus ***AI.***	187	9	11	533	9		62	9	80
Cyathura carinata ***CC.***	222	44	33		9	27	44	53	18
Jaera ischiosetosa ***JI.***	9		11				44	18	9
Sinelobus vanhaareni					9		338	9	27
Apocorophium lacustre							9	9	9
Corophium multisetosum ***CM.***		36			9		36	1120	222
Gammarus salinus							18		
Gammarus zaddachi							44		
Leptocheirus pilosus	9						258	151	18
Crangon crangon							9		
Peringia ulvae ***PU.***	36	373	133	107	9	44	3129	9849	5236
Potamopyrgus antipodarum ***PA.***	36	44	22	36	9	107	391	71	53
Cerastoderma glaucum ***CG.***		62					516	356	124
Limecola balthica ***LB.***	62	36	56	9	80	80	1289	1218	489
Mya arenaria ***MA.***		9	11	18		44	5707	364	169
Mytilus trossulus ***MT.***	27	9		71	9		55,822	114,204	37,920
Gonothyraea loveni							53		
Einhornia crustulenta	+			+			+		
TOTAL NUMBER OF TAXA	14	14	11	12	11	9	23	18	17

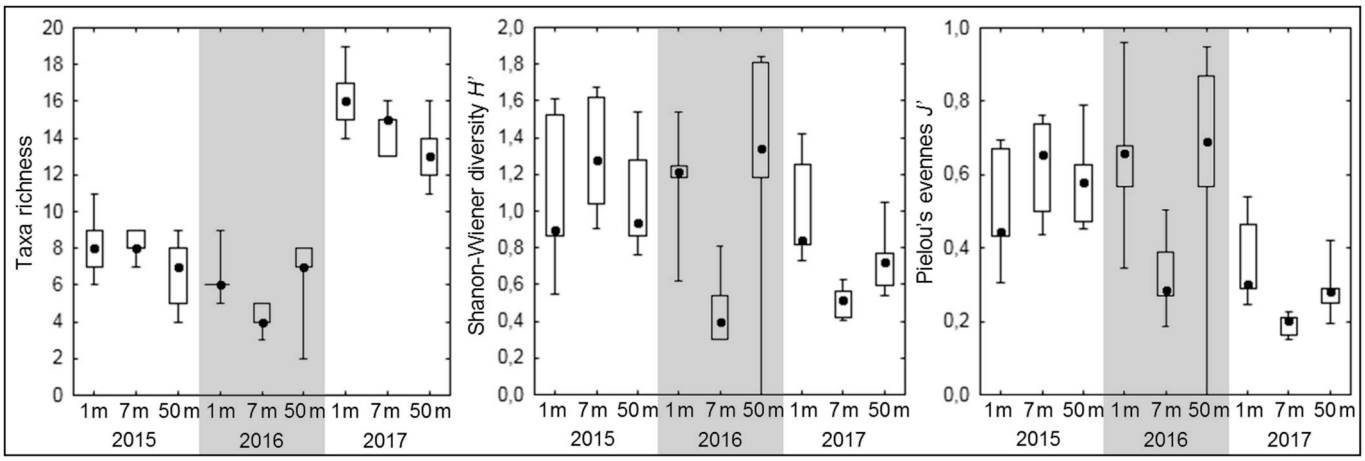

Fig. 2. Taxa richness (left). Shannon diversity index *H*' (middle) and Pielou's evenness index *J*' (right) at all sites in the studied years. Dots show median values, boxes show interquartile range and whiskers extend to the extreme values.

Table 2
P values obtained in Kruskal–Wallis one-way analysis of variance for taxa richness, Shannon diversity index, Pielou's evenness index, total abundance and biomass in different years and sites at varying distance. Bold values indicate significant differences ($p < 0.05$).

Group	Taxa richness	Shannon diversity *H*'	Pielou's evenness *J*'	Total abundance	Total biomass
2015	0.379	0.281	0.454	**0.042**	0.055
2016	0.062	0.065	0.087	**0.046**	0.932
2017	0.083	**0.009**	**0.016**	**0.024**	**0.002**
1 m	**0.005**	0.827	0.085	**0.003**	**0.008**
7 m	**0.002**	**0.008**	**0.006**	**0.009**	**0.003**
50 m	**0.009**	0.482	**0.049**	**0.008**	**0.013**

4. Discussion

Results demonstrate several significant effects of an artificial structure on hydrometric parameters, sediment properties and benthic assemblages at the adjacent natural soft bottom. Most notably a reduction in oxygen concentration was observed, but only at immediate vicinity of the structure. The average was lower by 0.6 mg L^{-1} at 1 m than at the two remaining sites and the difference between 7 and 50 m was less than 0.1 mg L^{-1} during the period of 5 months. Other observed effects - sediment fining and significantly higher organic matter content - were also restricted to the immediate vicinity of the structure.

The lower oxygen concentration at a distance of 1 m was probably due to the combined impact of several factors. The main reason was the organic enrichment that was significantly higher in close proximity. It is also likely that the mussel bed on the soft bottom adjacent to the structure contributed to the observed differences in the oxygen concentration. Although *M. trossulus* was very abundant in 2017 at every sampling site, with the highest abundance at 7 m distance, patches of large mussels (>4 cm long) were found only at 1 m distance. At two remaining sites only settled juvenile mussels (<3 mm long) were found. The results related to 7 m and 50 m distances, as well as the results of previous research (Bałazy et al., 2019) indicate that beds of adult mussels do not occur naturally in the study area. The formation of a mussel bed at a distance of 1 m was facilitated by the artificial structure. Mussel patches were probably detached from the vertical concrete wall of the structure and then sank to the adjacent soft bottom (Qvarfordt et al., 2006; Wilhelmsson and Malm, 2008).

The impact of mussel beds on oxygen concentration in the bottom water and oxygen uptake has been documented in previous studies. Jørgensen (1980) reported a decrease in oxygen concentration of 2 mg L^{-1} above the mussel bed when compared to the bare soft bottom. The same study showed that the respiration rate was ten times higher at the mussel bed than at the bare soft bottom. Janas at al. (2019) also reported higher oxygen uptake at the bottom with *M. trossulus* patches. Mussels could impact oxygen concentration directly through respiration and indirectly through the deposition of organic matter, both by living individuals and empty shells (Jørgensen, 1980; Norling and Kautsky, 2008; Wilding, 2012; Wilding and Nickell, 2013).

The mussel patches observed at the sampling site did not extend further than a few meters from the structure. However, at other locations in the Gulf of Gdańsk, i.e. shipwrecks, the beds of mussels and their empty shells have been reported to extend over greater distances (Bałazy et al., 2019; personal observations). In such cases, the impact on oxygen concentration may be expected to encompass a larger area. It should also be noted that the sediment in the study area is relatively coarse due to abrasion of the nearby cliff. Bottom sediments in other parts of the Gulf of Gdańsk are predominantly fine or muddy sands and sandy mud or mud (Zachowicz et al., 2004). It is possible that in an area with finer sediments, the effects of the structure would be more pronounced, as it would facilitate the retention of larger amounts of organic matter (Snelgrove and Butman, 1994; Janssen et al., 2005; De Backer et al., 2014).

Although numerous hypoxic events and oxygen-stressed conditions were observed in 2016 at 1 m distance, lack of data on oxygen concentration from other sites prevents us from identifying the structure as the main cause of these conditions. It is possible that oxygen concentration was low at all sampling sites that year, which could be supported by low taxa richness, abundance and biomass as well as high contribution of burrowing detritivores and a small number of crustaceans and bivalves (Diaz and Rosenberg, 1995; Villnäs et al., 2012; Jager et al., 2018). On the other hand, the longest registered hypoxic events lasted 4 days. Previous studies in the Baltic Sea have shown that such short periods of hypoxia do not affect benthic communities on a structural level (Villnäs et al., 2013).

The occurrence of hypoxia has not been previously reported in the coastal zone of the Gulf of Gdańsk. Previously published reports were restricted to deeper areas (Janas et al., 2004; Warzocha et al., 2018). The lowest oxygen concentration recorded in the coastal zone at the western coast of the Gulf of Gdańsk described by Conley et al., (2011) was between 2 and 4 (oxygen stressed) and above 4 mg L^{-1}. Our data show that the oxygen concentration in this region can episodically drop below 2 mg L^{-1} even at a depth of 8 m.

Despite the reduction in oxygen concentration, we did not observe negative effects of the artificial structure on the benthic macrofauna, as in the case of sediments affected by suspended mussel cultures (Tenore et al., 1982; Mattsson and Lindén, 1983; Jaramillo et al., 1992; Grant

Table 3
P values obtained in Dunn's pairwise test for taxa richness, Shannon diversity index, Pielou's evenness index, total abundance and biomass in different years and sites at varying distance. Bold values indicate significant differences ($p < 0.025$). Empty cells represent no differences in the Kruskal–Wallis analysis.

Group	Pair	Taxa richness	Shannon diversity H'	Pielou's evenness J'	Total abundance	Total biomass
2015	1 m & 7 m				0.033	
	1 m & 50 m				**0.008**	
	7 m & 50 m				0.286	
2016	1 m & 7 m				0.336	
	1 m & 50 m				0.028	
	7 m & 50 m				**0.010**	
2017	1 m & 7 m		**0.004**	**0.002**	0.042	0.052
	1 m & 50 m		**0.004**	0.161	0.029	**0.001**
	7 m & 50 m		0.500	0.030	**0.004**	0.033
1 m	2015 & 2016	0.142			0.069	0.262
	2015 & 2017	**0.016**			0.028	**0.010**
	2016 & 2017	**0.001**			**0.001**	**0.002**
7 m	2015 & 2016	0.038	0.038	0.045	0.500	0.052
	2015 & 2017	0.038	0.038	**0.001**	**0.004**	0.033
	2016 & 2017	**0.001**	**0.001**	0.069	**0.004**	**0.001**
50 m	2015 & 2016	0.047		0.444	0.262	0.389
	2015 & 2017	**0.004**		**0.020**	**0.010**	**0.008**
	2016 & 2017	**0.003**		**0.014**	**0.002**	**0.004**

Table 4
PERMANOVA pairwise results, average Bray–Curtis dissimilarity and taxa contribution to dissimilarity in different years and sites at varying distance. Bold numbers indicate significant differences ($p < 0.05$). Bold abbreviated taxonomic names refer to Table 1.

Group	Pair	*p*	Avg. dissimilarity	Taxa contribution (%)
2015	1 m & 7 m	**0.006**	45.64	***O.*** 18.3, ***PU.*** 14.2, ***HD.*** 10.7, ***CC.*** 8.62, ***AI.*** 8.4
	1 m & 50 m	**0.048**	43.45	***O.*** 27.7, ***HD.*** 12.6, ***CC.*** 11.4, ***AI.*** 9.9, ***PU.*** 6.8
	7 m & 50 m	0.063	44.00	***O.*** 17.4, ***PU.*** 15.8, ***CG.*** 9.0, ***HD.*** 8.3, ***PE.*** 6.9
2016	1 m & 7 m	**0.006**	54.27	***O.*** 23.4, ***AI.*** 22.4, ***PU.*** 10.5, ***LB.*** 9.4, ***MT.*** 8.1
	1 m & 50 m	**0.009**	59.77	***AI.*** 23.0, ***O.*** 17.8, ***MT.*** 9.0, ***PA.*** 8.0, ***LB.*** 7.8
	7 m & 50 m	**0.011**	58.23	***O.*** 40.4, ***HD.*** 8.3, ***PA.*** 8.1, ***LB.*** 7.2, ***MA.*** 7.2
2017	1 m & 7 m	**0.001**	32.54	***MT.*** 31.3, ***MA.*** 14.5, ***PU.*** 11.28, ***O.*** 7.5, ***CM.*** 7.3
	1 m & 50 m	**0.011**	31.71	***MT.*** 25.1, ***MA.*** 20.5, ***O.*** 7.8, ***PU.*** 6.7, ***JI.*** 4.3
	7 m & 50 m	**0.008**	27.61	***MT.*** 50.4, ***PU.*** 9.0, ***CM.*** 6.5, ***LB.*** 4.5, ***SS.*** 4.4
1 m	2015 & 2016	**0.007**	50.52	***O.*** 25.0, ***AI.*** 14.4, ***CC.*** 10.7, ***LC.*** 6.0, ***MT.*** 5.4
	2015 & 2017	**0.012**	72.35	***MT.*** 41.5, ***MA.*** 15.1, ***PU.*** 9.7, ***LB.*** 5.1, ***CG.*** 4.5
	2016 & 2017	**0.008**	79.67	***MT.*** 39.3, ***MA.*** 14.2, ***PU.*** 8.5, ***LB.*** 6.0, ***O.*** 5.6
7 m	2015 & 2016	**0.013**	46.58	***PU.*** 23.0, ***O.*** 15.1, ***CG.*** 8.8, ***HD.*** 7.8, ***LB.*** 7.7
	2015 & 2017	**0.003**	76.91	***MT.*** 58.6, ***PU.*** 13.9, ***CM.*** 5.1, ***LB.*** 5.1, ***MA.*** 3.1
	2016 & 2017	**0.008**	86.55	***MT.*** 54.7, ***PU.*** 16.0, ***CM.*** 5.3, ***LB.*** 4.0, ***MA.*** 3.1
50 m	2015 & 2016	0.648	53.74	***O.*** 27.1, ***HD.*** 11.2, ***PU.*** 9.4, ***PA.*** 9.2, ***PE.*** 8.5
	2015 & 2017	**0.003**	75.37	***MT.*** 51.0, ***PU.*** 17.6, ***LB.*** 4.7, ***CM.*** 4.1, ***O.*** 3.3
	2016 & 2017	**0.045**	78.29	***MT.*** 51.0, ***PU.*** 18.5, ***CM.*** 4.1, ***O.*** 4.1, ***LB.*** 4.0,

et al., 1995; Chamberlain et al., 2001). Quite the contrary, the highest taxa richness was generally observed at a distance of 1 m from the structure. The highest biomass and abundance were observed at a distance of 1 m or 7 m from the structure depending on the year. This is consistent with other observations of macrobenthos on soft sediment around offshore anthropogenic hard substrates (Coates et al., 2014; Lefaible et al., 2018; Bałazy et al., 2019).

We observed different effects for particular taxa present in the studied benthic community. These effects were most pronounced in 2017, when taxa richness and abundance were highest. Several taxa were found in large numbers near the structure, including species typical of the Baltic hard seabed – sessile species like the mussel *M. trossulus*, the barnacle *Amphibalanus improvisus* (Darwin, 1854) and the hydrozoan *Gonothyraea loveni* (Allman, 1859) as well as mobile species like small crustaceans: the amphipod *Leptocheirus pilosus* Zaddach, 1844, the isopod *Jaera ischiosetosa* Forsman, 1949 and the non-indigenous tanaid *Sinelobus vanhaareni* Bamber, 2014 (Grzelak and Kukliński, 2010; Brzana and Janas, 2016; Brzana et al., 2019). We also observed a larger number of oligochaetes close to the structure, which can be explained by organic enrichment (Villnäs et al., 2011).

Some species typical of the soft seabed were also positively affected by the structure, including the bivalves *M. arenaria* and *Cerastoderma glaucum* (Bruguière, 1789), and the polychaete *H. diversicolor*. As all these species feed on suspended and deposited organic matter particles, their increased abundance in the vicinity of the structure may have resulted from the enhanced food supply due to organic enrichment (Scaps, 2002; Malham et al., 2012). Moreover, juveniles of these species are most likely present on the artificial structure itself, and, although all three are described as typical of a sandy bottom, they are also found on artificial vertical hard substrates (Dziubińska, 2011; Janas and Kendzierska, 2014; Brzana and Janas, 2016). The planktonic larvae of *M. arenaria* and *Cerastoderma* spp. have been reported to settle on various hard substrata (i.e., rocks and macrophytes). Juvenile bivalves can live there attached by byssi or actively move (Kellogg, 1900; Pearson, 2003; Reise, 2003). They may later fall onto the soft bottom along with patches of mussels. These results suggest that an artificial structure may serve as an important source of important soft bottom benthic organisms that could repopulate soft sediments after disturbances such as hypoxia.

Significantly adverse effects of the structure were observed only in the case of the corophid amphipod *Corophium multisetosum* Stock, 1952. In 2017, this crustacean was present in large numbers at a distance of 7 m and 50 m, but only a few individuals were observed at a distance of 1 m. This may be due to sediment fining and higher organic matter content (Queiroga, 1990; Ré et al., 2009). Furthermore, species like *H. diversicolor*, *Limecola balthica* (Linnaeus, 1758) and *Cerastoderma*

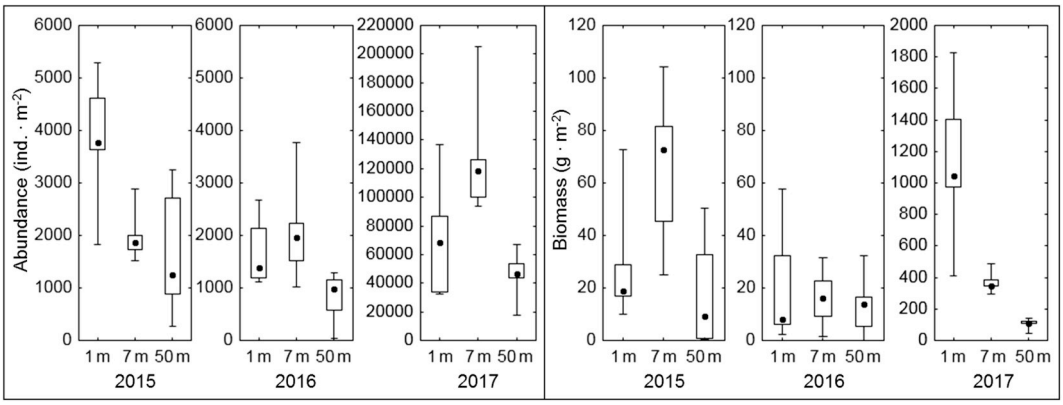

Fig. 3. Abundance and biomass of macrobenthos at all sampling sites in the studied years. Dots show median values, boxes show interquartile range and whiskers extend to the extreme values.

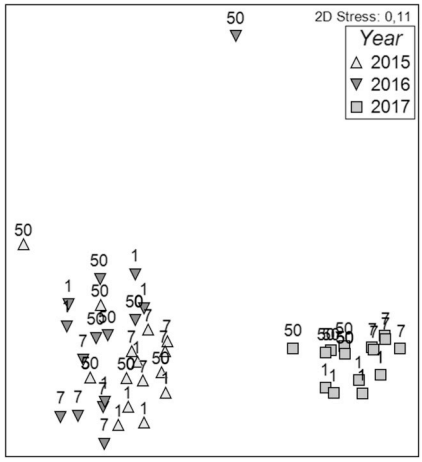

Fig. 4. MDS plot based on the Bray–Curtis similarity matrix of macrobenthic abundance data (square root transformed) at three distances in the studied years. Symbols represent sampling year; numbers represent sampling sites as distance in meters from structure.

edule (Linnaeus, 1758) have been reported to affect densities of corophid amphipods (Jensen, 1985; Bonsdorff et al., 1986; Jensen, 1988; Rönn et al., 1988; Flach, 1992; Flach and de Bruin, 1993; Jensen & Andre, 1993).

Our results showed high variability in the macrobenthic assemblage in the study area between subsequent years, with the species richness ranging from 6 to 16 and abundance ranging from 1200 ind. m^{-2} to 120,000 ind. m^{-2}. Macrobenthos was significantly more diverse and abundant in the study area in 2017 than in the two previous years. Bałazy et al. (2019) performed a study with a similar sampling design in October 2006 in the area of another artificial construction close to our sampling sites. They observed lower species richness, even compared to our reports from 2016, despite the use of a 500 μm sieve. However, the sampler used in their study had a smaller catch area. In general, their results were more in line with our results from 2015 to 2016 than with those from 2017. This indicates that relatively low species richness and abundance are probably typical of the benthic community in the study area and the status of the assemblage observed in 2017 was exceptional. This may be partly due to a large number of juvenile organisms, mainly *M. trossulus*. However, even when ignoring juveniles, the benthic assemblage in 2017 was characterised by much higher species richness, abundance and biomass than one and two years earlier.

5. Conclusions

Our study has demonstrated that oxygen concentration can be significantly lower in the immediate vicinity of artificial structures, to the extent that potentially periodic hypoxia can be observed in their close proximity. However, other effects of such structures have a greater impact on the benthic community, leading to increased taxa richness, abundance and biomass.

CRediT authorship contribution statement

Radosław Brzana: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing - original draft. **Urszula Janas:** Funding acquisition, Software, Supervision, Visualization, Writing - review & editing. **Marta Beata Tykarska:** Formal analysis, Investigation, Software, Visualization, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.106563.

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Gdynia, 26.09.2025

Radosław Brzana

OŚWIADCZENIE

Oświadczam, że w pracy:

Brzana, R., Janas, U., & Tykarska, M. B. (2019). Effects of a 70-year old artificial offshore structure on oxygen concentration and macrobenthos in the Gulf of Gdańsk (Baltic Sea). Estuarine Coastal and Shelf Science, 235, 106563

mój udział polegał na współtworzeniu koncepcji artykułu, opracowaniu metodyki, zbiorze prób makrozoobentosu i obsłudze urządzeń pomiarowych, analizie prób makrozoobentosu, przygotowaniu danych do analiz statystycznych, przeprowadzeniu analiz statystycznych, przygotowaniu przeglądu literatury, przygotowaniu wszystkich części manuskryptu, przygotowaniu tabel i grafik, korekcie artykułu zgodnie z uwagami współautorów, wysłaniu artykułu do czasopisma naukowego oraz korekcie artykułu zgodnie z uwagami recenzentów.

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Podpisano przez:

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