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An ecological assay on the serpulid Polychaete *Ficopomatus enigmaticus* (Fauvel, 1923) in the Lower Warnow Estuary

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Abstract

The rapid expansion of geopolitics and international trade has facilitated the global spread of alien invasive species. These species spread and reproduce in foreign ecosystems, damaging their function, biodiversity, species composition, and environmental parameters and thereby posing risks to humans. Among these invaders, *Ficopomatus enigmaticus* (Fauvel, 1923), a cosmopolitan serpulid polychaete, was recently introduced into the Lower Warnow Estuary. Given its unprecedented population explosion in 2021, an investigation into its population size, biomass, production rate, succession rate, and possible impacts onto the local system and its inhabitants is needed. To address these concerns, metal plates were attached to a rope and placed at two different depths in the Warnow waters. Over a six-month period, six plates were collected and subjected to analysis on a monthly base. During this investigative phase, a peak abundance was recorded in September with 132663 ± 13728 ind./m^2, and a peak biomass in October with 1054.62 ± 248.63 g/m^2 for the bottom plates. Conversely, the population on the surface plates exhibited significantly lower figures, with a peak abundance of 4121 ± 1495 ind./m^2 and a peak biomass of 21.95 ± 18.84 g/m^2. Production and succession rates peaked between August and September before declining. *F. enigmaticus* first settled in July, which predicts reproduction and larval development in June. After the first settlement in July a recession in the daily colonisation was observed. However, the weight of individual worms kept increasing till October. The much smaller population on the surface plates can be attributed to abiotic factors, alongside potential competition for space with *Amphibalanus improvisus*. High production and succession rates are achieved due to high filtration and ingestions rates. Food concentrations are high in the Baltic Sea and its estuaries during summer, which grants a rapid growth and development. Despite the biomass peak in October, which is predicted to even increase more, a recession in almost all biotic parameters was observed. This is mainly due to lack of space on the plates and a recession in larval abundance. Food depletion might be a factor as well but in controversially discussed.

1. Introduction

Since the rapid rise in globalization and therefore increasing geopolitics regarding trade and tourism a sharp increase in biological invasions by non-native species can be observed (Hellrigl, 2006). Habitat degradation and loss, overexploitation and pollution as well as the increasing impact of climate change in recent years compromised ecosystem integrity, which makes them even more prone for biological invasions (Dudgeon *et al.*, 2006; Halpern *et al.*, 2015). Non-native species - so-called alien species - overcome biogeographical barriers such as oceans, mountains, deserts, or rivers due to anthropogenic activity (Richardson et al., 2000; Pyšek *et al.*, 2004). Private and commercial shipping, deliberate release or escape from captivity, and anthropogenic corridors are possible distribution pathways (Hulme et al., 2008; Pyšek *et al.*, 2020). Vascular plants (van Kleunen *et al.*, 2015; Pyšek *et al.*, 2017), invertebrates (Ojaveer *et al.*, 2010; Capinha *et al.*, 2015; Zettler and Zettler, 2017), and vertebrates (Blackburn *et al.*, 2008; Dawson *et al.*, 2017) circulate all around the world especially affecting Europe, North-America, and Australia (Pyšek *et al.*, 2020). In order to colonise an ecosystem, at least temporarily (casuals) (Pyšek *et al.*, 2004), abiotic and biotic barriers of an habitat must be overcome (Richardson et al., 2000). While 'casuals' must be reintroduced repeatedly to persist, others can establish fully functional populations in an alien ecosystem. To do so, they need to reproduce regularly over a certain period of time and spread within the system and between systems (Richardson et al., 2000). If one of the established species has a ± negative or positive impact on the newly colonised ecosystem, it is classified as invasive (Carlton, 2002). Invasive species can interfere with the entire system in many ways. They can disrupt the food web (Beisner *et al.*, 2003; Townsend, 2003), overgrow, infect native species (Beltrán-Beck *et al.*, 2012; Etchegoin *et al.*, 2012), compete with latter for resources (Hrabik *et al.*, 2001), shift biodiversity and species composition (Barton *et al.*, 2005), alter nutrition cycles, water quality (Davies *et al.*, 1989) and other ecosystem processes (Parker *et al.*, 1999; Andersen *et al.*, 2004; Wołowicz *et al.*, 2007). Additionally, they can affect economic sectors such as agriculture, forestry, or fisheries and thus harm humans (United States. Congress. Office of Technology Assessment, 1993; Pimentel *et al.*, 2000; Crowl *et al.*, 2008). Aquatic systems are particularly sensitive to biological invasions. The world's oceans are highly migratory due to higher shipping frequency, shorter transit times and increasing geopolitics, displacing species quite easily. Moreover, climate change is altering physical and chemical properties, that favours dispersal (Occhipinti-Ambrogi and Galil, 2010). However, coastal areas, with their many ports and their function as natural corridors, are particularly affected by invasive alien species (Reise *et al.*, 2006). In fact, fresh and brackish waters already show a high loss of biodiversity due to anthropogenic use, which is exacerbated by biological invasions and provides space and ecological niches for colonisation (Ricciardi, 1998; Ricciardi and Rasmussen, 1998, 1999). Brackish waters in general are particularly affected by invasive species. On the one hand, a wide range of salinities allows the colonisation of salt-tolerant species, which means that both euryhaline freshwater and saltwater species can colonise and reproduce in the brackish water of estuaries (Paavola *et al.*, 2005). Nonetheless, a strong salinity gradient can function as a limiting parameter (Baltic Sea, 2-30 PSU), which affects biodiversity and species richness and increasingly favours the settlement of new invasive alien species with a broad abiotic tolerance (Wolff, 1998; Leppäkoski and Olenin, 2000). On the other hand, estuary inhabitants are affected by high ecological stress due to unstable environmental conditions, including changes in salinity, temperature, oxygen saturation and substrate type caused by elevated hydrodynamics, wind forces, tidal forces, or seasonal variations, which also induce mechanical stress (Winkel, 2003; Wołowicz *et al.*, 2007). Finally, estuaries are heavily used by humans and their ports. Euryhaline species are transported in the ballast water or on the hulls of ships and released back into the system at their destination (Carlton, 1996; Wolff, 1998; Wołowicz *et al.*, 2007). One species that has travelled around the world on ship hulls and strongly changes local habitats is *Ficopomatus enigmaticus* (Fauvel, 1923) (Figure 1, **A**-**D**).

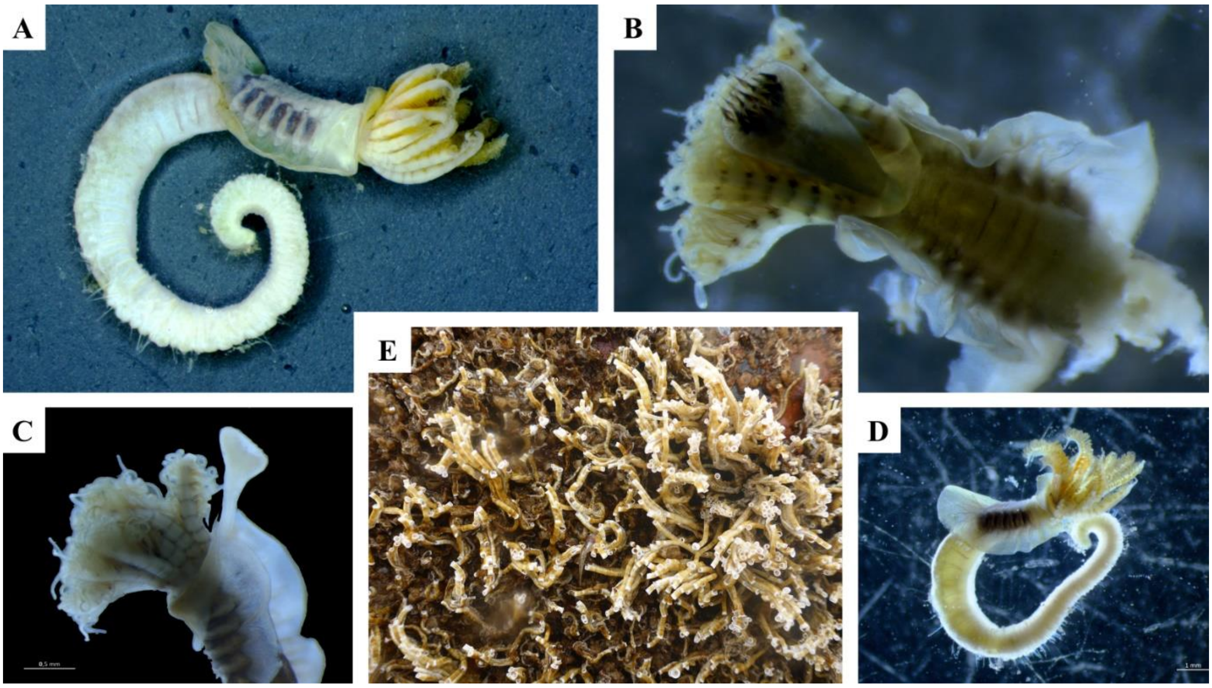

Figure 1: Habitus of the serpulid polychaete *Ficopomatus enigmaticus* (**A**-**D**). The aggregation of the calcareous tubes, which form the reef-like structures (**E**).

The serpulid polychaete *Ficopomatus enigmaticus*, also known as Australian Tubeworm, is an euryhaline alien invasive species with a cosmopolitan appearance. It functions as an ecosystem engineer (Schwindt *et al.*, 2004a, 2004b) by building up cone-shaped aggregations of calcareous tubes, which form reef-like structures in depths of 0.5-4.5 m (Figure 1, **E**) (Bianchi and Morri, 1996; Hille *et al.*, 2021). These structures can reach sizes, which cover enormous areas with 70,000 to 180,000 worms/m^2 but strongly varies on prevalent circumstances (Dittmann *et al.*, 2009). However, there is a lack of data monitoring their growth rate and succession velocity. Furthermore, several studies investigated reef growth (Fornós *et al.*, 1997; Schwindt *et al.*, 2004a) , tube aggregation (Thorp, 1994), or filtration rate (Davies *et al.*, 1989), but little is known of the diversity and species composition among the reefs. Thomas & Thorp (1994) investigated species that thrived alongside *F. enigmaticus* in a millpond in the UK and were able to identify individual species that benefitted from *F. enigmaticus*. Moreover and since *F. enigmaticus* alters ecosystem structures, it is highly expectable that biodiversity and species composition are as well affected (Katsanevakis *et al.*, 2014). The length of this polychaete depends on environmental conditions, such as water depth or food concentration and is controversially discussed. The animals length ranges between 4-50 mm (Dittmann *et al.*, 2009; Kopiy *et al.*, 2022; Obenat *et al.*, 2006b), whereas the tubes can exceed the length of the polychaete by 1.7 to 3 times (Straughan, 1972; Weitzel, 2021; Kopiy *et al.*, 2022). *F. enigmaticus* feeds on detritus and phytoplankton with particle size ranging from 2-16 µm (Davies *et al.*, 1989). It can clear an entire water column in ± a day, depending on food concentrations and population size, and therefore is to be considered crucial in maintenance of water quality (Davies *et al.*, 1989; Bruschetti *et al.*, 2008). However, by displacing other species such as mussels and its filtration capacity, it can change water properties by affecting water storage, food availability, ocean nourishment and species composition (Katsanevakis *et al.*, 2014). Adult tubeworms mature with a length of 4-8 mm (Straughan, 1972; Obenat *et al.*, 2006a) and release sperms and eggs into the water column. For reproducing itself, certain abiotic preconditions are required. The gamete release generally needs temperatures of 14-18 °C (Dixon, 1981; Bianchi and Morri, 1996; Obenat *et al.*, 2006a), but may be lower at 10 °C (Thorp, 1994). After fertilisation, a vagile trochophore larvae stage, succeeded by a Metatrochophore larvae stage develops (Gabilondo *et al.*, 2013). Metamorphosis begins after approximately three weeks, and they start to search for a suitable place to settle. The larvae of *F. enigmaticus* settle on inorganic hard substrate such as debris, rocks, ropes, and stakes, as well as on organic substrates such as shells of mussels or on barnacles (Straughan, 1972). Due to ship hulls being *F. enigmaticus'* distribution pathway it also settles on artificial substrates, such as anchors, sheet pile walls, or rudders. After settling, tube building is initiated. The tubes are divided into an inner thin organic membrane and an outer calcareous layer. The calcareous layer is composed of small crystals of aragonite and calcite (Aliani *et al.*, 1995) and is produced by the paired glands located on the collar (Dittmann *et al.*, 2009). The tubes can grow to a length of 100 mm and form those reef-like structures. Tube thickness varies depending on environmental conditions. High mechanical stress in lower depths or the substrate type can lead to thinner or thicker tubes (Kopiy *et al.*, 2022).

Ficopomatus enigamticus origin is unknown (Ten Hove and Weerdenburg, 1978). However, Dittman et al. (2009) predicted the Indian Ocean and the coastal waters of Australia in the Southern hemisphere as the area of origin. Supporting the hypothesis, Styan et al. (2016) considers Australia to be the origin of the polychaete. His study revealed that there are three genetically distinct groups, despite no morphological differences. In recent decades, *F. enigmaticus* has continuously invaded estuaries on all continents (except Antarctica). Although it prefers temperate or warm-temperate areas, it can also be found in subtropical to tropical water (Styan *et al.*, 2017). Despite its wide salinity tolerance (8-40 PSU), it thrives best in brackish water (10-30 PSU) and needs temperatures of above 16 °C for reproduction, growth, and maturation. Slow currents and shallow depths favour their colonisation and development success (Dittmann *et al.*, 2009). Therefore, it successfully spread in estuaries of southern Australia and New

Zealand (Read and Gordon, 1991; Hewitt *et al.*, 2004; Styan *et al.*, 2017), North- and South America (Hoagland and Turner, 1980; Cohen and Carlton, 1995; Bruschetti *et al.*, 2008; Heiman *et al.*, 2008; Pernet *et al.*, 2016; Tovar-Hernández *et al.*, 2022), Africa (Hill, 1967; Davies *et al.*, 1989; McQuaid and Griffiths, 2014; Bezuidenhout and Robinson, 2020), Asia (Gugel, 1996; Yu *et al.*, 2021; Kobayashi *et al.*, 2023) and Oceania (Straughan, 1969). In Europe it was first recorded in northern France (1921) and London (1922) (Conservation *et al.*, 1997), but has since spread across the entire continent. *F. enigmaticus* settled in the Black Sea (Micu and Micu, 2004; Kopiy *et al.*, 2022), the Mediterranean Sea (Bianchi and Morri, 1996; Fornós *et al.*, 1997; Cukrov *et al.*, 2010; Shumka *et al.*, 2014; Oliva *et al.*, 2020), the Sea of Marmara (Çinar *et al.*, 2008), the Caspian Sea (Read and Gordon, 1991), on the European Atlantic coast (López and Richter, 2017; Charles *et al.*, 2018), and the North Sea (Brockmann, 2020). From 2020 on *F. enigmaticus* mass occurred in the Lower Warnow, an estuary of the Baltic Sea, even despite the abiotic requirements which were revealed by Dittman et al. (2009). Prior*, F. enigmaticus* could only be detected sporadically (Hille *et al.*, 2021). The Baltic Sea is characterised by a strong salinity gradient. The western Baltic Sea is attributed by euhaline properties, whereas the east is more brackish or even freshwater. Johanna Weitzel (2021) already investigated in her Bachelor thesis *F. enigmaticus* regarding its distribution, morphology, and ecology in the Warnow Estuary. However, there are no data concerning (1) growth rate, (2) succession stages, (3) biodiversity, (4) species composition and (5) possible influences of *Ficopomatus enigmaticus* on the local system of the Lower Warnow Estuary. To cope the lacking data artificially exposed substrate in form of metal plates were placed in two depths of the Lower Warnow river water in order to analyse abiotic and biotic parameters of this tubeworm.

2. Material and Method

In order to determine the full extent of the occurrence and the associated impact of *Ficopomatus enigmaticus* on the ecosystem of Lower Warnow, and to further gain an appropriate insight into the successional status of these waters, metal plates were used as an artificial substrate. This methodological approach proved to be optimal to observe biotic factors like settlement of the larvae, diversity, abundance, biomass, species composition and succession.

2.1. Study area

The Lower Warnow estuary in Mecklenburg-Vorpommern, a federal state in northern Germany, was identified to be a suitable location for studying autecological aspects *of Ficopomatus enigmaticus*.

The Lower Warnow which is approximately 15 km (kilometres) long is a eutrophic river that runs from Mühlendamm, a weir in the south that limits freshwater drainage from the Upper Warnow, to the estuary in the north (Figure 2). The mean water depth is 5.6 m (metre), with a total depth of 15 m in the shipping channels. These channels extend up to 6 km into the Bay of Mecklenburg and connect the ambient seawater with the estuary (Lange *et al.*, 2020). Moreover, 74 % of the shoreline is artificially fortified (Schernewski *et al.*, 2019). According to Schernewski et al. (2019), 37 % of the water is occupied by harbours, jetties, and shipping lanes. The Warnow waters are increasingly affected by tourism and shipping – with 2.7 million passengers and 21.5 million tons of freight shipped in 2022 (*Hansestadt Rostock*, 2023) – indicating a significant anthropogenic impact whatsoever.

The circulation and stratification mechanisms in the Warnow estuary are primarily governed by buoyancy forces and wind forces, whereas tidal forces play a minor role due to its microtidal nature (amplitude of 8 cm) (Lange *et al.*, 2020). The high saline bottom water is transported upstream into the estuary where it is transformed (e.g. mixed) into a near-surface downstream flow (Winkel, 2003; Geyer and MacCready, 2014). However, the salinity gradient is highly dependent on the salinity in front of the estuary which is influenced by both the Baltic Sea and the North Sea. This can lead to an inverted estuarine circulation as remarked by Lange et al. (2020). Furthermore, strong winds and associated water level fluctuations in the Baltic Sea may cause changes in current conditions and support a reversed salinity gradient (Winkel, 2003). Lange et al. (2020) also revealed average salinity values of 7.5 PSU (Practical Salinity Unit) in the south and 15 PSU in the north for bottom waters. Surface water salinities ranged from 5 PSU near Mühlendamm to 13 PSU at the mouth. However, in the period of investigation, the measured average salinity values near Mühlendamm were at 2 PSU for surface waters and 3 PSU for bottom waters, with a total low of 0.1 PSU. The temperature varies between 0 °C and 22 °C with an average of 12.5 °C ± 8 °C throughout the year.

A floating dock located approximately 9 km from the mouth of the estuary (54.107622 N, 12.094162 E) was selected for sampling (Figure 2, **C**). The dock is situated on the *Smart Ocean Technologies (SOT)* campus site which is a working group of the *Frauenhofer Gesellschaft*. The floating dock was located near the shore about 30 m away from the land and was approximately 12 m long. It was easily accessible and proved to be well-suited for the installation of an artificial substrate like metal plates (Figure 4).

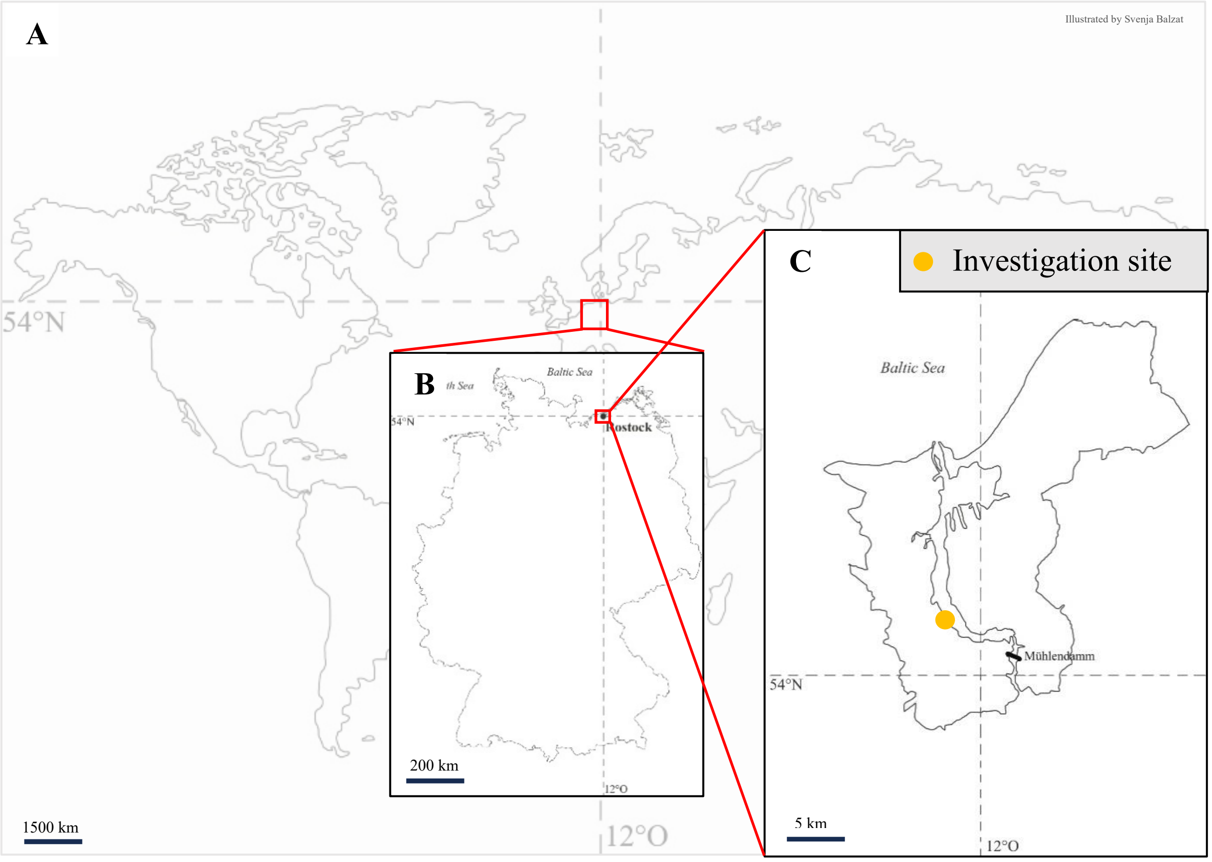

Figure 2: Maps of (**A**) the world, (**B**) Germany and (**C**) the Lower Warnow estuary in Rostock. The investigation site is marked on the map of the Lower Warnow.

2.2. Abiotic

During the six-month investigation period, four abiotic values were measured monthly to provide environmental context for the biotic data. The relevant factors were temperature (°C), salinity (PSU), oxygen saturation (mg/l), and water depth (m), with salinity being particularly important. Temperature and salinity were measured in both surface waters and bottom waters using the portable conductivity meter *Cond 1970i* from the manufacturer *WTW* (serial: 09510828). The portable 2-channel multimeter *HQ40d multi* from the manufacturer *HACH* (serial: 99.201000) was used to measure oxygen saturation below the water surface. Two values were obtained and then averaged. The water depth was measured with the *Cond1970i* probe attached to a cable reel.

2.3. Biotic

To provide an optimal environment for the serpulid polychaete *Ficopomatus enigmaticus*, which settles and thrives on hard substrates, pairs of 20x20 cm uncoated, abrasive metal plates (0.08 m^2) were attached to a rope. This size of a metal plate constituted a manageable experimental unit regarding construction, deployment, and taxonomic analysis. The first plate was attached approximately 50 cm below the water and the second installed 2 m away from the first plate near the bottom (Figure 4). This approach was carried out to observe succession at varying water depths. The metal plates each had two small holes in opposite corners that served as connection points for the ropes. 36 strings, each with two metal plates, were prepared and tied to the floating dock. Every month, three strings (which means six plates: three bottom water, three surface water) were consecutively taken out of the water in a pseudo-randomized manner which reduced biases due to different distances of the strings to the shore and therefore minimized associated abiotic differences. Afterwards, the growth on each side of each plate was scraped off and collected in vats (Figure 3).

Figure 3: Pictures of the sampling process at the floating dock.

The biomass was then transferred to labelled Kautex containers (Kautex Textron Inc.) (seen in Figure 6) which are highly resistant to chemicals such as formaldehyde (to be used later for organism fixation) and are commonly utilized for sample storage (Smith, 1992). Formaldehyde (short: Formol) from the manufacturer *VWR Chemicals* was used due to its low price and its effectiveness of producing strong cross-linking bonds between tissue proteins. These bonds significantly reduced tissue degradation (Leong and Gilham, 1989). Throughout the entire process, pictures of the plates, the epibenthos and the labelled containers were taken with the *Tough! TG-5* by *OLYPMPUS.*

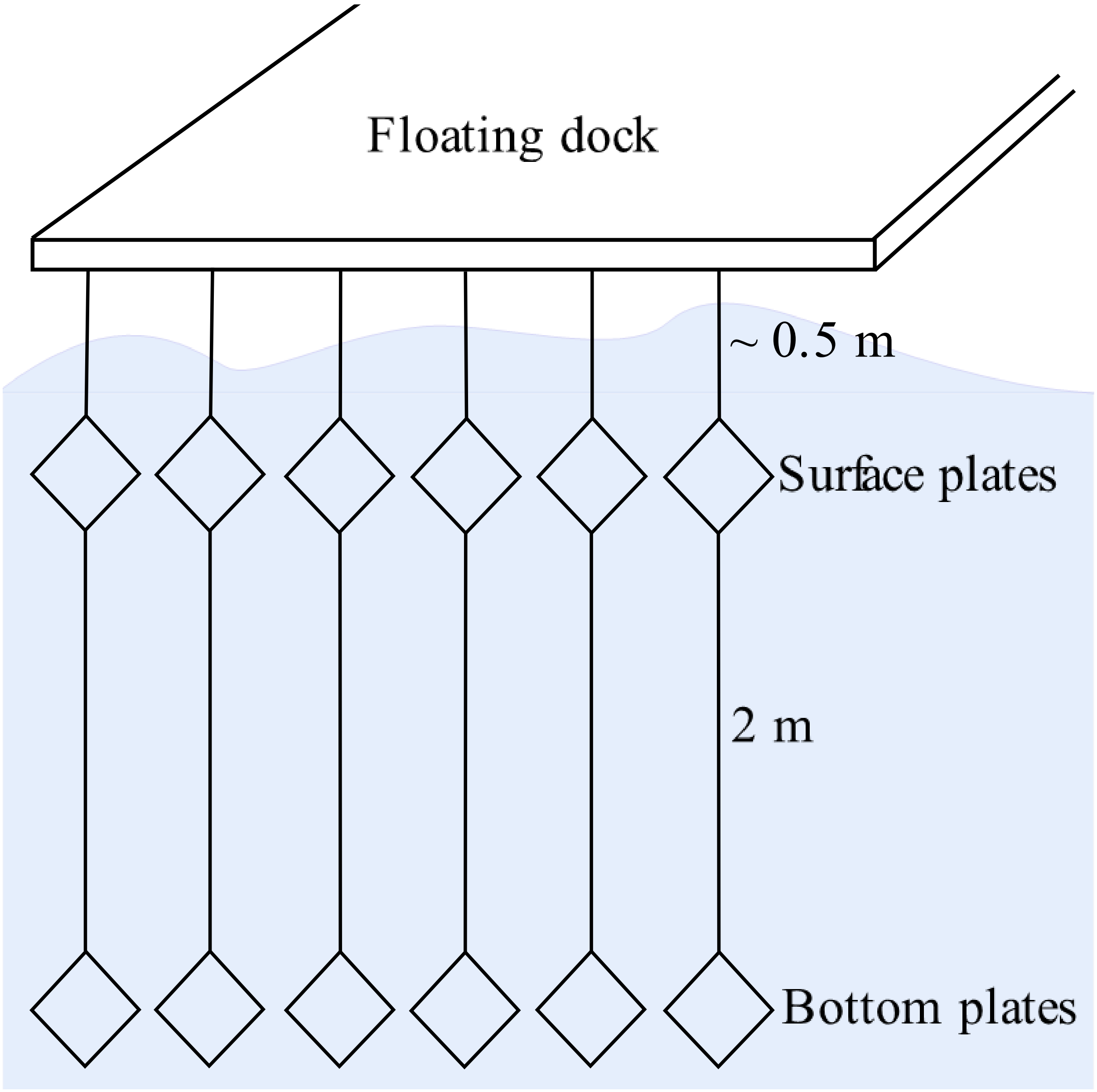

Figure 4: Schematic illustration of the experimental setup.

2.4. Analysis

The samples were analysed at the laboratory of the *Leibniz Institute for Baltic Sea Research Warnemünde*. Each animal on every plate was sorted, identified, and counted using the binocular *SteREO Discovery V8* (*Zeiss*) and further weighed (wet weight, without tubes) with the *CUBIS sartorius* (*CUBIS,* serial: 25602250). The values of resulting abundance and biomass for each plate were extrapolated to one m^2. Mean values and the corresponding standard deviations for surface plates and bottom plates of each month were calculated and analysed. The data had been truncated to two decimal places for clarity which happened to result in a biomass of zero even if species were present. *Ficopomatus enigmaticus* is the main organism of this study. It is separately listed in the following results, even though it belongs to the phylum Annelida. Taxonomy was done with the World Register of Marine Species (WoRMS) database on 2024-03-14. Pictures of *F. enigmaticus* were done by using the *AxioCam ICc 3* (ZEISS) attached to the binocular. Additionally, the Shannon-Wiener-Index (H') (Shannon, 1948) and the Evenness (E) (Pielou, 1966) were calculated for each depth of each month (Figure 5). These values provided insights into the species' biodiversity and the distribution of individuals.

$$\boldsymbol{H'} = -\sum p_i \ln(p_i) \qquad\qquad \boldsymbol{E} = \mathrm{H'}/\ln(i)$$

Figure 5: Shannon-Wiener-Index (*H')* and Evenness (*E*) formula modified after Shannon (1948) and Pielou (1966). p_i = relative abundance of each organism, ln = natural logarithm, i = number of species.

3. Results

3.1. Abiotic

To investigate the potential correlation between the colonisation, growth, and succession of *Ficopomatus enigmaticus* in the Lower Warnow as well as abiotic factors, the following parameters were monthly determined: temperature (°C), salinity (PSU), oxygen saturation (mg/l) and water depth (m). Both surface and bottom water temperature and salinity were recorded.

The temperature of surface waters varied seasonally with a maximum of 21.1 °C in July 2023 and a minimum of 0.8 °C in January 2024. There was a sharp increase in temperature from April to May (+ 36.9 %) and from May to June (+ 31.4 %). The mean temperature during the summer months (June-September) of 2023 was constant at 20.2 ± 1 °C (mean ± SD). Naturally, temperatures were decreasing between October and December (- 71.3 %) reaching their lowest point in January 2024. The seasonal pattern of the bottom water was similar to that of the surface water, with both lower total and average temperatures. The hottest month recorded is September 2023, with a temperature of 19.5 °C, while the lowest temperatures could be observed in January 2024, reaching 2.8 °C (Table 1).

The lowest salinity value in surface waters was measured in January 2024, with 0.4 PSU, which coincided with the lowest temperature (0.8 °C). Despite some inconsistencies, salinity increased with rising water temperature. The highest salinity was recorded in October 2023, with 13.1 PSU and a temperature of 15.7 °C. During the warmer months in summer (June-September), salinity ranged between 9.1-11.1 PSU (average: 10 ± 1.1 PSU). The salinity of surface waters varied with temperature whereas bottom waters had a consistent salinity ranging from 10.5 PSU in June 2023 to 14.8 PSU in December 2023, with an average of 12.8 ± 1.4 PSU (Table 1).

Oxygen saturation was measured only in surface waters. It reached its maximum in September 2023 with 12.32 mg/l and decreased to its minimum in October 2023 at 6.31 mg/l. On average, no seasonal difference had been observed (9.2 ± 1.7 mg/l) (Table 1).

The water level remained relatively constant at 3.4 ± 0.3 m throughout the observation period. The highest water level was recorded in September 2023 with 3.9 meters (Table 1).

Table 1: The abiotic parameters of the Lower Warnow at the investigation site for each month. Temperature [°C] and salinity [PSU] for surface and deep waters, O_2-saturation [mg/l] for surface waters and water depth [m]. The months of biotic investigation are underlined in grey. **S**: Surface, **B**: Bottom.

Date	**Temperature (°C)**		**Salinity (PSU)**		**O_2-saturation (mg/l)**	**Water depth (m)**
	Surface	Bottom	Surface	Bottom	Surface	-
12 April 2023	8.7	-	4.0	-	-	-
12 May 2023	13.8	10.0	9.0	13.4	9.72	3.5
12 June 2023	20.1	15.9	9.1	10.5	9.64	3
11 July 2023	21.1	18.3	10.5	13.6	7.18	3.2
11 August 2023	18.8	18.5	9.1	13.4	8.34	3.5
12 September 2023	20.9	19.5	11.4	13.0	12.32	3.9
11 October 2023	15.7	15.7	13.1	14.2	6.31	3
10 November 2023	9.5	9.9	11.3	12.4	9.00	3.5
11 December 2023	4.5	7.1	6.0	14.8	9.48	3.3
12 January 2024	0.8	2.8	0.4	10.9	10.66	3
12 February 2024	4.1	4.3	5.7	11.3	9.65	3.7

3.2. Biotic

3.2.1. List of species

Table 2 presents the species identified during the investigation, sorted by frequency on the plates at different water depths over 6 months. 40 species were counted including taxa not identified on the species level (Platyhelminthes, Syllidae, Chironomidae, Tubificidae, Enchytraeidae, and juvenile). Out of these, 30 species were alien or invasive species in the Lower Warnow ecosystem. The list can be divided into two parts. The first part comprises species that consistently appeared with shifting appearance within the first three months. Only 2 species, *Nais elinguis* and *Apocorophium lacustre*, were consistently found at each water level. As time went on, additional species settled on the plates. These species include *Amphibalanus improvisus*, *Paranais litoralis*, *Mya arenaria*, *Melita nitida*, *Hediste diversicolor* and *Rhithropanopeus harrisii* which first appeared in June and were present every month thereafter. Other species such as *Ficopomatus enigmaticus*, *Leptocheirus pilosus*, and platyhelminths were first observed in July. The second part of the table includes species that occurred sporadically or infrequently such as *Lekanesphaera rugicauda*, *Lekanesphaera hookeri*, *Nippoleucon hinumensis* as well as various gammarids. Species such as *Ecrobia ventrosa* or *Idotea chelipes* were only found once at a specific depth. *Hartlaubella gelatinosa* was the most found cnidarian species at various depths, occurring in 4 out of 6 months. *Einhornia crustulenta* was the most found bryozoan species appearing since June onwards.

Table 2: List of species found on all metal plates each month, sorted by frequency. **S**: Surface, **B**: Bottom.

Phylum	Species	12.05.2023		12.06.2023		11.07.2023		11.08.2023		12.09.2023		11.10.2023	
		S	B	S	B	S	B	S	B	S	B	S	B
Annelida	*Nais elinguis*	x	x	x	x	x	x	x	x	x	x	x	x
Arthropoda	*Apocorophium lacustre*	x	x	x	x	x	x	x	x	x	x	x	x
Arthropoda	*Sinelobus vanhaareni*	x		x	x	x	x	x	x	x	x	x	x
Arthropoda	*Microdeutopus gryllotalpa*		x	x	x	x	x	x	x	x	x	x	x
Arthropoda	*Amphibalanus improvisus*			x	x	x	x	x	x	x	x	x	x
Annelida	*Paranais litoralis*			x	x	x	x	x	x	x	x	x	x
Mollusca	*Mya arenaria*			x	x	x	x	x	x	x	x	x	x
Arthropoda	*Melita nitida*			x	x	x	x	x	x	x	x	x	x
Annelida	*Hediste diversicolor*	x		x	x	x	x	x	x	x	x	x	
Arthropoda	*Rhithropanopeus harrisii*			x		x	x	x	x	x	x	x	x
Annelida	*Ficopomatus enigmaticus*					x	x	x	x	x	x	x	x
Platyhelminthes	Platyhelminthes					x	x	x	x	x	x	x	x
Arhtropoda	*Leptocheirus pilosus*					x	x	x	x	x	x	x	x
Annelida	*Polydora cornuta*				x		x	x	x	x	x	x	x
Mollusca	*Mytilus edulis*						x	x	x	x	x		x
Annelida	*Alitta succinea*							x	x	x	x	x	x
Mollusca	*Mytilopsis leucophaeata*							x	x	x	x	x	x
Arthropoda	*Nippoleucon hinumensis*	x					x	x	x	x			x
Arthropoda	*Gammarus salinus*	x		x		x	x	x					
Arthropoda	Chironomidae	x		x		x	x			x			
Mollusca	*Cerastoderma glaucum*			x		x	x	x					
Annelida	Syllidae							x		x		x	x
Arthropoda	*Jaera albifrons*			x		x	x					x	
Arthropoda	*Gammarus* sp. (juv)	x	x	x									
Arthropoda	*Gammarus zaddachi*	x				x	x						
Arthropoda	*Gammarus tigrinus*					x		x					
Arthropoda	*Lekanesphaera rugicauda*								x				x
Arthropoda	*Lekanesphaera hookeri*					x	x						
Arthropoda	*Potamopyrgus antipodarum*					x	x						
Annelida	*Polydora ciliata*	x											
Arthropoda	*Diastylis rathkei*	x											
Nemertea	*Cyanophthalma obscura*			x									
Mollusca	*Ecrobia ventrosa*			x									
Annelida	Tubificidae										x		
Annelida	Enchytraeidae			x									
Arthropoda	*Idotea chelipes*										x		
Cnidaria	*Hartlaubella gelatinosa*			x	x				x		x	x	x
Bryozoa	*Einhornia crustulenta*					x		x			x	x	x
Cnidaria	*Cordylophora caspia*			x	x								
Cnidaria	*Gonothyraea loveni*		x										
Bryozoa	*Farrella repens*					x							

3.2.2. 12. May 2023

In May 2023, a total of 14 species were found on the plates which were composed of nine arthropods, two annelids, one mollusc, one nemertean, and one hydrozoan. Thereof, 12 species were found on the surface water plates and five on the bottom water. Referring to Figure 6, both metal plates were not heavily overgrown.

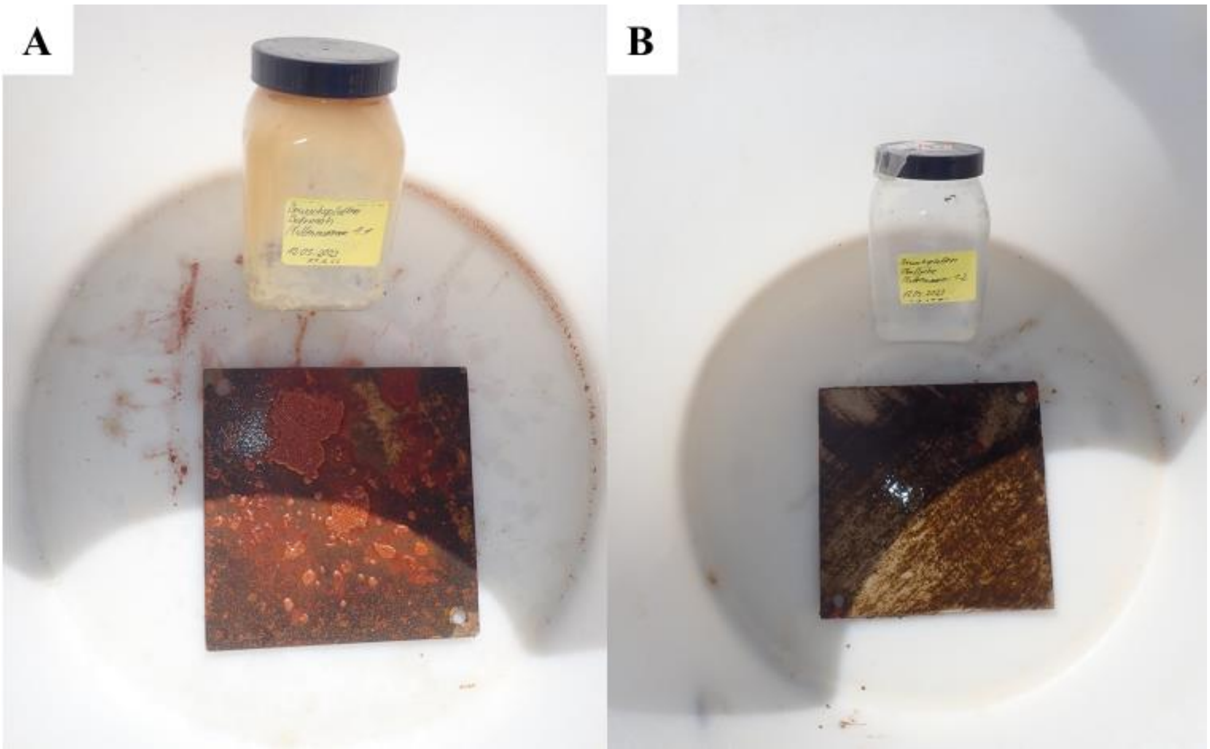

Figure 6: Metal plates of (**A**) surface water and (**B**) bottom water from 12.05.23.

The surface plates and bottom plates were inhabited by annelids and arthropods. Annelids were the most abundant phylum on the surface plates making up 87 % of the population, with *Nais elinguis* being the most abundant at 86.7 % of all individuals (679 ± 165 ind./m^2) (Table 3). However, their biomass was rather low comprising only 16 % of the total biomass. Conversely, arthropods made up 84 % of the biomass despite their relatively low numbers (12 %) (Figure 7). Additionally, the most abundant arthropod species were the gammarids, with 38 ± 54 ind./m^2 juveniles, 17 ± 19 ind./m^2 *Gammarus salinus* and 4 ± 7 ind./m^2 *Gammarus zaddachi* (Table 3). Moreover, one mollusc species (0 %) and one nemertean species (1 %) settled on the surface plates. However, due to a low individual count (4 ± 7 ind./m^2 and 4 ± 7 ind./m^2) plus a low collective (Table 3), they did not contribute to the measured biomass at all (0 %). The arthropods dominated the bottom plates making up 81 % of the population and constituting 100 % of the total biomass (Figure 7). Annelids, on the other hand, only accounted for 19 % of the population with no contribution to the total biomass. The most abundant animals at this depth were juvenile gammarids, with an average of 8 ± 7 ind./m^2 (Table 3). During this sampling no individuals of *Ficopomatus enigmaticus* were found. The Shannon-Wiener-Index indicates low levels of biodiversity for both depths with a value of *H’*=0.66 for the surface plates and *H’*=1.33 for the bottom plates. Although the distribution of individuals on the surface plates was uneven with *E*=0.27, it was relatively even on the bottom water plates with *E*=0.96.

Table 3: List of species found on surface and bottom metal plates with associated mean abundance and mean biomass per m^2 from 12.05.23.

Species	**Mean abundance/m^2**		**Mean biomass (g/m^2)**	
	Surface	Bottom	Surface	Bottom
Apocorophium lacustre	8	4	0.01	0.00
Microdeutopus gryllotalpa	-	4	-	0.00
Sinelobus vanhaareni	8	-	0.00	-
Lekanesphaera rugicauda	4	-	0.09	-
Nippoleucon hinumensis	4	-	0.00	-
Gammarus sp. (juv.)	38	8	0.01	0.00
Gammarus salinus	17	-	0.01	-
Gammarus zaddachi	4	-	0.18	-
Chironomidae	8	-	0.00	-
Hediste diversicolor	4	-	0.01	-
Nais elinguis	679	4	0.05	0.00
Ecrobia ventrosa	4	-	0.00	-
Cyanophthalma obscura	4	-	0.00	-
Gonothyraea loveni	-	x	-	-

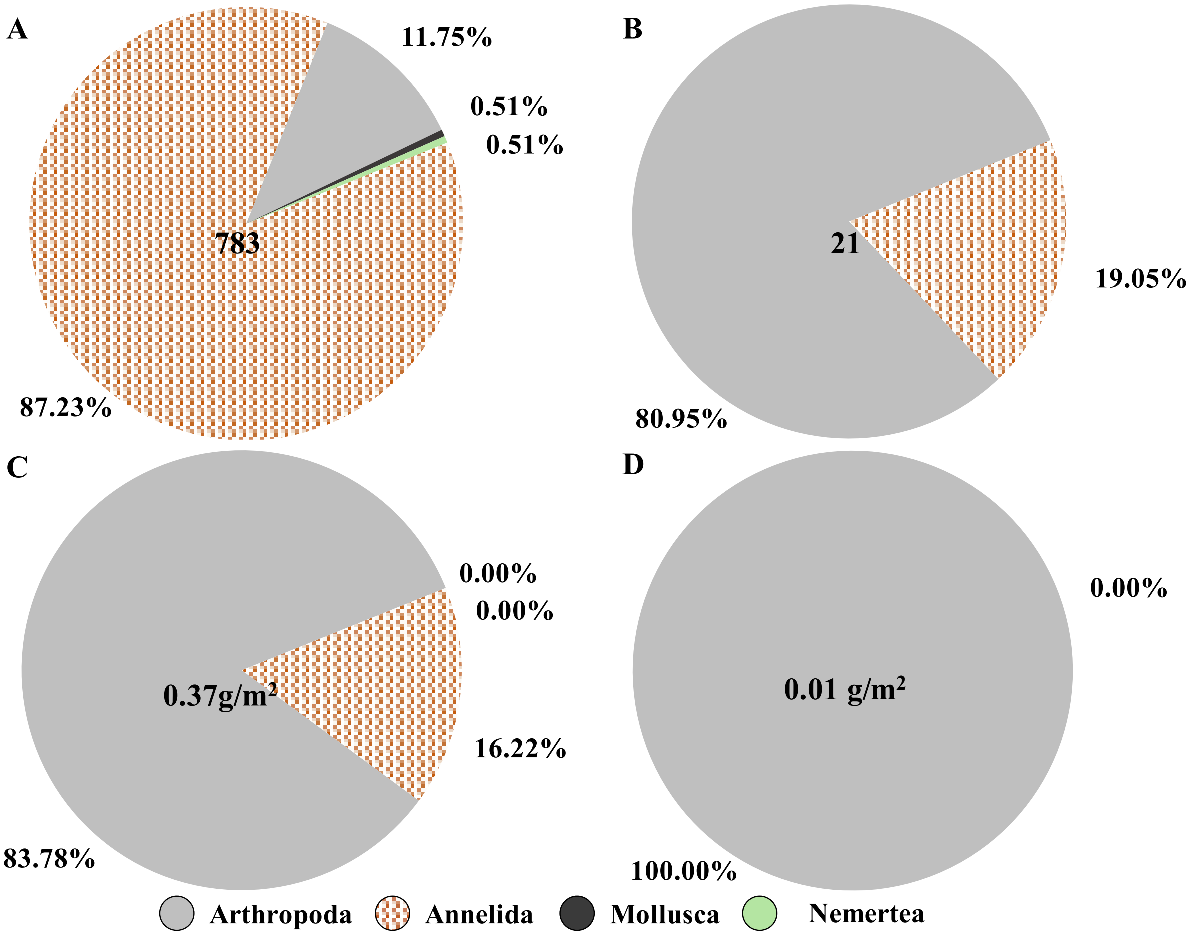

Figure 7: The distribution of abundance and biomass in percentage of the different Phyla found on the plates in both surface water and bottom water from 12.05.23. **A**: Abundance surface, **B**: Abundance bottom, **C**: Biomass surface, **D**: Biomass bottom. The total average individual count and total average biomass are displayed in the centre.

3.2.3. 12. June 2023

In June 2023, a total of 20 species were collected, including 10 arthropods, six annelids, two molluscs, and two hydrozoans. Of these, 19 species were found on the surface plates and 12 on the bottom water plates. Only the surface plate was visually covered by *A. improvisus* (Figure 8).

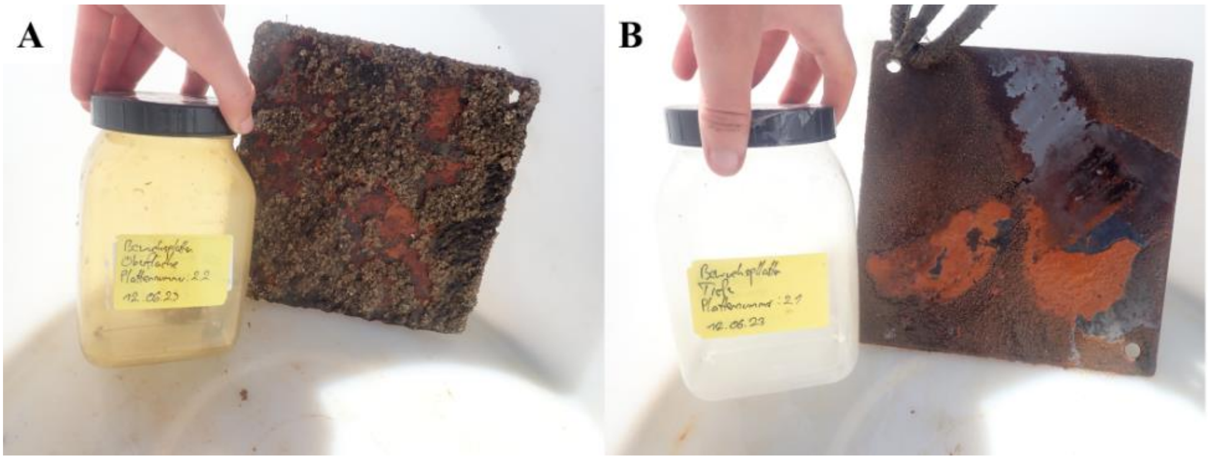

Figure 8: Metal plates of (**A**) surface water and (**B**) bottom water from 12.06.23.

Arthropods were by far the most abundant organisms found on both surface plates (95 %) and bottom plates (99 %) by far (Figure 9). The species with the largest number of individuals was *Amphibalanus improvisus* with 487854 ± 128841 ind./m^2 (99.4 %) on the surface plates and 482850 ± 338287 ind./m^2 (99 %) on the bottom plates. *Nais elinguis* was the next most abundant species, with 26058 ± 13267 ind./m^2 (5 %) in surface waters and 4392 ± 5961 ind./m^2 (0.9 %) in bottom waters (Table 4). *Sinelobus vanhaareni* was the second most abundant arthropod species in surface waters with a count of 2421 ± 1887 ind./m^2. In bottom waters, *Apocorophium lacustre* was the second most abundant arthropod species, with a count of 96 ± 81 ind./m^2. Arthropods comprised 100 % of the biomass in both surface and bottom water, primarily due to *A. improvisus*. However, the average biomass of this Balanidae species varied significantly (t-test: df = 2, p = 0.02). Although the number of individuals for *A. improvisus* was similar at both depths, the biomass of animals colonising the surface plates was 40 times higher than that of the animals on the bottom plates, as shown in Figure 8 and 9. The surface water biomass of *A. improvisus* was 2720.95 ± 713.94 g/m^2, whereas it was only 67.29 ± 86.59 g/m^2 for bottom waters (Table 4). Despite this, *A. improvisus* accounted for over 99 % of the total biomass at both depths. In contrast, annelids represented only 5 % of the individuals on the surface plates and 1 % on the bottom plates (Figure 9). They contributed 0.03 % of the biomass in the surface water and 0.4 % in the bottom water. Although there were 88 ± 111 ind./m^2 (t-test: df = 2, p =

0.31) of *Mya arenaria* in surface waters and 63 ± 108 ind./m^2 (t-test: df = 2, $p = 0.42$) in bottom waters (Table 4), molluscs were insignificant at both depths, contributing 0 % to the total biomass (Figure 9). The cnidarian species *Cordylophora caspia* and *Hartlaubella gelatinosa* were found at both depths. In June, there were still no individuals of *F. enigmaticus* present. The Shannon-Wiener-Index indicates low levels of biodiversity for both depths, with a value of *H'*=0.24 for the surface plates and *H'*=0.06 for the bottom plates. The distribution of individuals was uneven with *E*=0.08 for surface plates, and *E*=0.03 for bottom water plates.

Table 4: List of species found on surface and bottom metal plates with associated mean abundance and mean biomass per m^2 from 12.06.23.

Species	**Mean abundance/m^2**		**Mean biomass (g/m^2)**	
	Surface	Bottom	Surface	Bottom
Amphibalanus improvisus	487854	482850	2720.95	67.29
Apocorophium lacustre	96	96	0.07	0.06
Microdeutopus gryllotalpa	38	8	0.02	0.00
Sinelobus vanhaareni	2421	33	0.64	0.01
Melita nitida	33	4	0.02	0.01
Gammarus sp. (juv)	8	-	0.00	-
Gammarus salinus	92	-	0.04	-
Rhithropanopeus harrisii	29	-	22.36	-
Jaera albifrons	8	-	0.01	-
Chironomidae	79	-	0.02	-
Hediste diversicolor	188	50	0.07	0.10
Polydora cornuta	-	13	-	0.00
Nais elinguis	26058	4392	0.96	0.13
Paranais littoralis	17	13	0.00	0.00
Tubificidae	4	-	0.00	-
Enchytraeidae	21	-	0.00	-
Mya arenaria	88	63	0.01	0.00
Cerastoderma glaucum	4	-	0.00	-
Cordylophora caspia	x	x	-	-
Hartlaubella gelatinosa	x	x	-	-

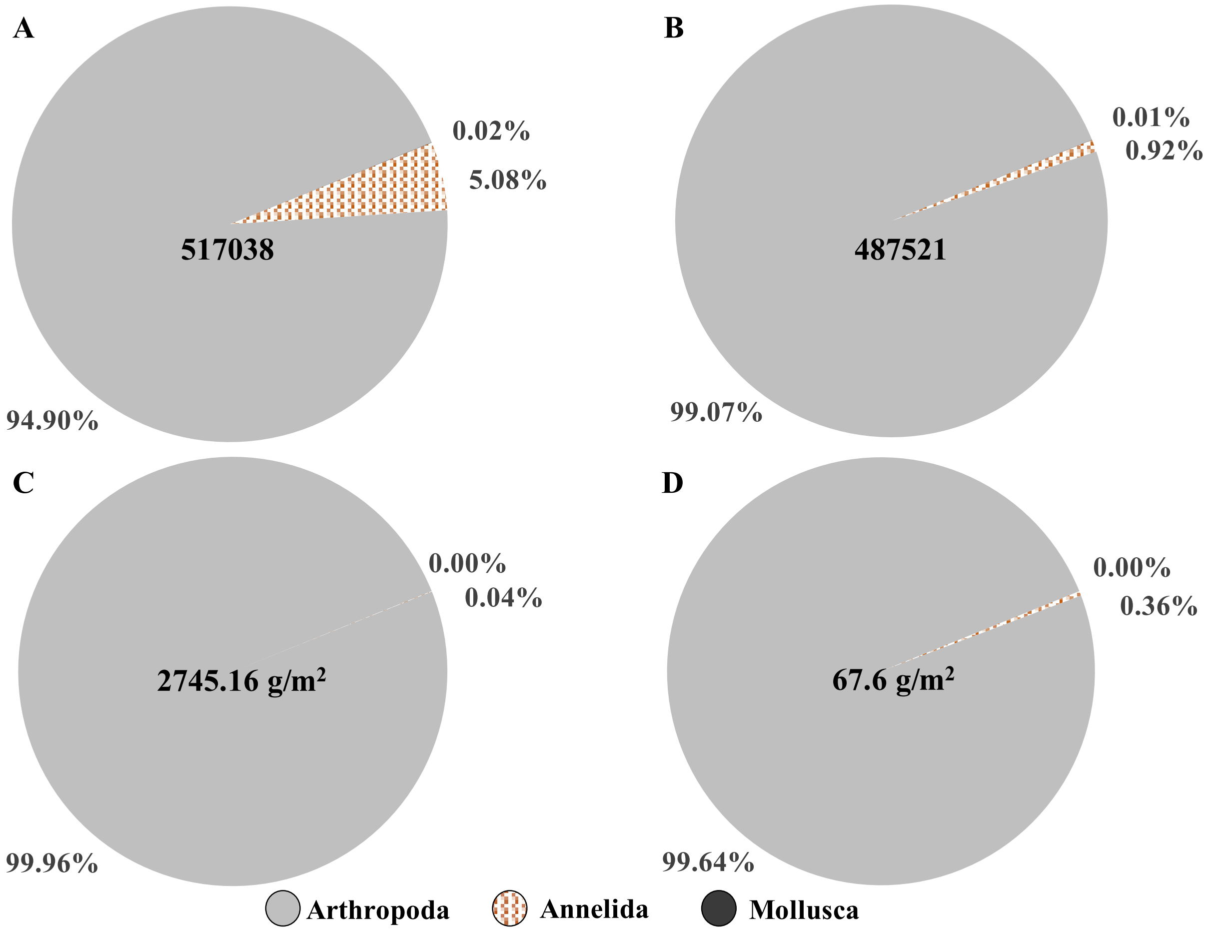

Figure 9: The distribution of abundance and biomass in percentage of the different Phyla found on the plates in both surface water and bottom water from 12.06.23. **A**: Abundance surface, **B**: Abundance bottom, **C**: Biomass surface, **D**: Biomass bottom. The total average individual count and total average biomass are displayed in the centre.

3.2.4. 11. July 2023

In July 2023, a total of 27 species were found, with 15 belonging to the arthropods, five to the annelids, three to the molluscs, one to the hydrozoan, one to the bryozoan, one to the platyhelminths and for the first time *Ficopomatus enigmaticus*. Thereof, 24 were collected from surface plates and 23 from bottom plates. Both plates were covered by *A. improvisus* (Figure 10).

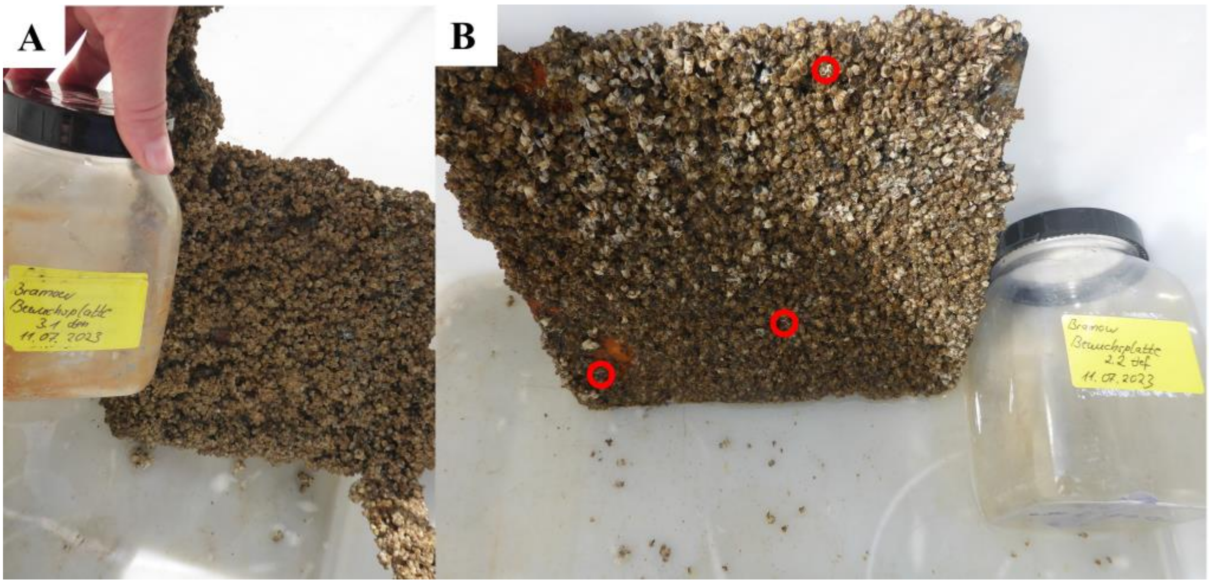

Figure 10: Metal plates of (**A**) surface water and (**B**) bottom water from 11.07.23. Tubes of *F. enigmaticus* are marked with red circles.

The abundance of surface plates was dominated by arthropods (85 %), annelids (14 %), and molluscs (1 %), while the abundance of bottom plates was distributed among arthropods (85 %), annelids (5 %), molluscs (4 %), platyhelminths (4 %) and *F. enigmaticus* (2 %) (Figure 11). *A. improvisus* was the dominant species in both depths (Figure 10 and 11) making up 81.4 % of all individuals in surface waters with 185663 ± 18193 ind./m^2, and 80.4 % in bottom waters with 309383 ± 27598 ind./m^2 (Table 5). *N. elinguis* was the second most abundant species in surface waters with 26571 ± 5140 ind./m^2, representing 11.6 % of the total abundance and 82.6 % of all annelids. On the bottom plates, its population was cut down to 12454 ± 4838 ind./m^2 accounting for 3.2 % of all individuals and 71.7 % of the annelids (Table 5). On the bottom plates, Platyhelminths were the second most abundant population accounting for 4.3 %, with 16338 ± 4019 ind./m^2. *Mya arenaria* was responsible for 99.8 % of the molluscs found on the bottom plates with a count of 14496 ± 2886 ind./m^2 which accounts for 3.8 % of all animals. On the surface plates, the observed population of *F. enigmaticus* was not significant (t-test: df = 2, $p = 0.42$). However, on the bottom plates it accounted for 2 % of the total abundance with a count of 8063 ± 5372 ind./m^2 (Table 5). Figure 11 shows that almost 100 % of the biomass in both depths consisted of arthropods. This was primarily due to *A. improvisus* which made up 99.2 % of the biomass on the surface plates (5674.19 ± 468.55 g/m^2) and 99.3 % of the biomass on the bottom plates (4106.57 ± 1549.43 g/m^2) (Figure 11, Table 5). Despite having almost twice the number of individuals in bottom waters, its mass was lower compared to the surface. On the surface plates, *R. harrisii* had the second largest biomass representing only 0.5 % of the total biomass with 28.07 ± 32.81 g/m^2. In bottom waters, Platyhelminths had the second largest biomass with 10.44 ± 6.67 g/m^2 however only contributed 0.3 % to the total biomass. The biomass of *F. enigmaticus* in bottom waters represented only 0.02 %, with 0.74 ± 0.44 g/m^2 (Table 5). Despite high individual counts among different species, their biomass was comparatively low. As previously mentioned, in both depths *A. improvisus* dominated abundance and biomass (Figure 10, Table 5). The Shannon-Wiener-Index indicates low levels of biodiversity for both depths with a value of H'=0.73 for the surface plates and H'=0.91 for the bottom plates. The distribution of individuals for each depth was uneven with E=0.24 at the surface plates and E=0.29 at the bottom plates.

Table 5: List of species found on surface and bottom metal plates with associated mean abundance and mean biomass per m^2 from 11.07.23.

Species	**Mean abundance/m²**		**Mean biomass (g/m²)**	
	Surface	Bottom	Surface	Bottom
Amphibalanus improvisus	185663	309383	5674.19	4106.57
Apocorophium lacustre	171	4321	0.23	4.46
Microdeutopus gryllotalpa	108	500	0.10	0.24
Sinelobus vanhaareni	5613	9225	0.95	1.84
Melita nitida	633	1733	0.65	1.17
Leptocheirus pilosus	38	3429	0.03	2.18
Gammarus salinus	54	33	0.06	0.03
Gammarus tigrinus	196	-	0.47	-
Gammarus zaddachi	8	4	0.05	0.02
Rhithropanopeus harrisii	54	4	28.07	0.01
Jaera albifrons	33	13	0.01	0.00
Nippoleucon hinumensis	-	4	-	0.00
Lekanesphaera hookeri	4	-	0.00	-
Diastylis rathkei	4	8	0.00	0.00
Chironomidae	13	38	0.01	0.02
Ficopomatus enigmaticus	4	8063	0.00	0.74
Polydora cornuta	-	8	-	0.00
Polydora ciliata	67	2125	0.02	0.40
Hediste diversicolor	1958	1221	11.95	2.21
Nais elinguis	26571	12454	1.16	0.48
Paranais littoralis	3567	1554	0.33	0.11
Mya arenaria	3050	14496	1.35	5.15
Cerastoderma glaucum	21	13	0.07	0.00
Mytilus edulis	-	13	-	0.00
Plathyhelminthes	379	16338	0.19	10.44
Farrella repens	x	-	-	-
Einhornia crustulenta	x	-	-	-

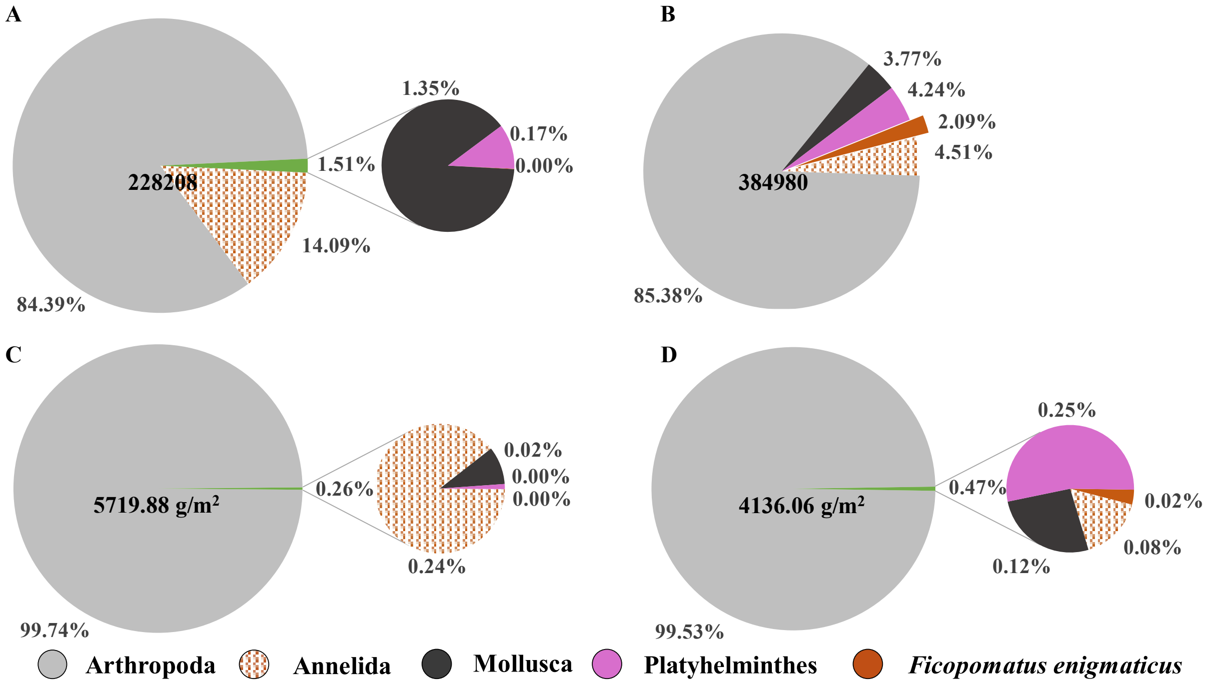

Figure 11: The distribution of abundance and biomass in percentage of the different Phyla found on the plates in both surface water and bottom water from 11.07.23. **A**: Abundance surface, **B**: Abundance bottom, **C**: Biomass surface, **D**: Biomass bottom. The total average individual count and total average biomass are displayed in the centre.

3.2.5. 11. August 2023

In August 2023, a total of 26 species were found, including 11 arthropods, six annelids, five molluscs, one hydrozoan, one bryozoan, platyhelminths and *Ficopomatus enigmaticus*. Thereof, 24 species were collected from surface plates and 20 from bottom plates. The surface plate was completely covered by *A. improvisus*, whereas half of the bottom plate was covered by the tubes of *F. enigamticus* (Figure 12).

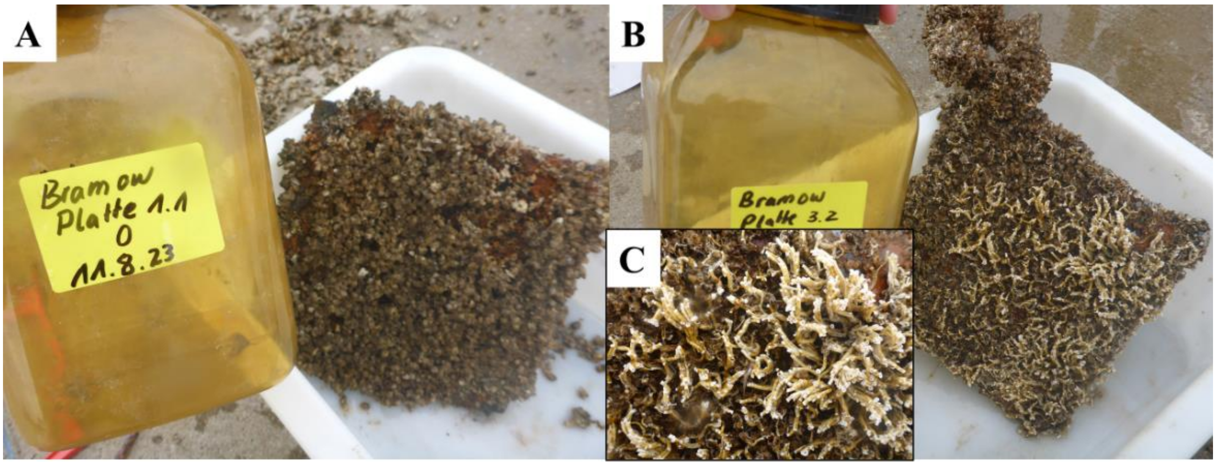

Figure 12: Metal plates of (**A**) surface water and (**B**) bottom water from 11.08.23 with a close-up of (**C**) the tubes of *F. enigmaticus*.

The surface abundance was dominated by arthropods (87 %), annelids (8 %), molluscs (2 %), platyhelminths, (1 %) and *F. enigmaticus* (2 %). The bottom water abundance was more evenly distributed among arthropods (51 %), annelids (3 %), molluscs (4 %), platyhelminths (7 %), and *F. enigmaticus* (35 %) (Figure 13). *A. improvisus* represented 71.8 % of the total individuals, accounting for 140725 ± 19650 ind./m^2, which is the highest number for surface waters. Its population dropped to 79892 ± 33720 ind./m^2 on the bottom plates, representing only 34.4 % of all individuals (Table 6). In surface waters, *S. vanhaareni* was the second most abundant species accounting for 27271 ± 7067 ind./m^2 (13.9 %) however, had only half the population in bottom waters (11450 ± 2162 ind./m^2). On the bottom plates, *F. enigmaticus* was the most abundant species making up 35.5 % of the total individual count with 82300 ± 6746 ind./m^2. In comparison, on the surface plates its population was only 4121 ± 1495 ind./m^2 (2 %) (Table 6, Figure 13). The annelids are dominated by *P. litoralis* in surface waters at 40.5 % (6238 ± 2212 ind./m^2) and *P. cornuta* in bottom waters at 67.2 % (4838 ± 418 ind./m^2) (Table 6). However, the total number of the annelid's individuals decreased by more than half from the surface plates to the bottom plates. In surface waters, *M. arenaria* had the highest abundance of the molluscs with 2113 ± 809 ind./m^2. In bottom waters, *M. leucophaeata* dominated the population of the molluscs with 5267 ± 1382 ind./m^2. The population of platyhelminths had increased by a factor of 11 from the surface to the bottom plates (Table 6). The biomass of the surface plates was primarily composed of arthropods (98%) (Figure 12 and 13). The remaining 2 % was shared between annelids (1 %), and molluscs (1 %). In contrast, the biomass of the bottom water was distributed among arthropods (84 %), annelids (1 %), molluscs (3 %), platyhelminths (6 %), and *F. enigmaticus* (6 %) (Figure 13). In surface waters, *A. improvisus* accounted for 97.4 % of the total biomass, equivalent to 8731.95 ± 1315.69 g/m^2, whereas in bottom waters it accounted for only 1308.93 ± 915.23 g/m^2 yet still representing 82.1 % of the total biomass. These were the highest values among the species at both depths. In surface waters, the second largest biomass was *M. arenaria* accounting for 62.89 ± 30.72 g/m^2 which represented 85.6 % of the mollusc's biomass. In bottom waters, Platyhelminths had the second largest biomass representing 6 % of the total biomass with 98.73 ± 39.65 g/m^2. Despite having the highest individual count in bottom waters, *F. enigmaticus* only contributed 87.19 ± 30.48 g/m^2 to the total biomass. On the surface plates, the biomass was 4.76 ± 2.34 g/m^2 (Table 6). For surface waters, *H. diversicolor* accounted for the largest biomass among the annelids at 86.9 % (54.46 ± 35.46 g/m^2), whereas in bottom waters *A. succinea* contributed the most mass at 70.3 % (10.95 ± 3.16 g/m^2) (Table 6). The biomass of the arthropods, annelids and molluscs decreased overall, while that of *F. enigmaticus* and platyhelminths increased. The cnidarian species *H. gelatinosa* was found in bottom waters, while the bryozoan species was present on the surface plates (Table 6). The Shannon-Wiener-Index indicates that the surface plates had low levels of biodiversity, with H'=1.12, while the bottom plates had a relatively high biodiversity, with H'=1.76. Although the distribution of individuals on the surface plates was uneven with E=0.36; it was more even on the bottom water plates with E=0.6.

Table 6: List of species found on surface and bottom metal plates with associated mean abundance and mean biomass per m^2 from 11.08.23.

Species	**Mean abundance/m^2**		**Mean biomass (g/m^2)**	
	Surface	Bottom	Surface	Bottom
Amphibalanus improvisus	140725	79892	8731.95	1308.93
Apocorophium lacustre	621	12925	0.31	5.26
Microdeutopus gryllotalpa	975	2521	0.66	0.80
Sinelobus vanhaareni	27271	11450	3.68	1.24
Melita nitida	550	1100	0.68	1.14
Leptocheirus pilosus	604	7417	0.23	1.34
Nippoleucon hinumensis	21	4	0.00	0.00
Gammarus salinus	4	-	0.01	-
Gammarus tigrinus	8	-	0.03	-
Lekanesphaera hookeri	8	-	0.01	-
Rhithropanopeus harrisii	858	1896	58.43	26.50
Ficopomatus enigmaticus	4121	82300	4.76	87.19
Polydora cornuta	1113	4838	0.43	1.66
Syllidae	138	-	0.00	-
Hediste diversicolor	2867	671	54.46	2.96
Alitta succinea	267	1304	7.18	10.95
Nais elinguis	4788	196	0.19	0.01
Paranais littoralis	6238	192	0.38	0.00
Mya arenaria	2113	3567	62.89	24.77
Cerastoderma glaucum	8	-	0.07	-
Mytilus edulis	8	621	0.05	9.27
Mytilopsis leucophaeata	1200	5267	10.50	12.77
Potamopyrgus antipodarum	-	4	-	0.00
Plathyhelminthes	1367	15746	30.19	98.73
Hartlaubella gelatinosa	-	x	-	-
Einhornia crustulenta	x	-	-	-

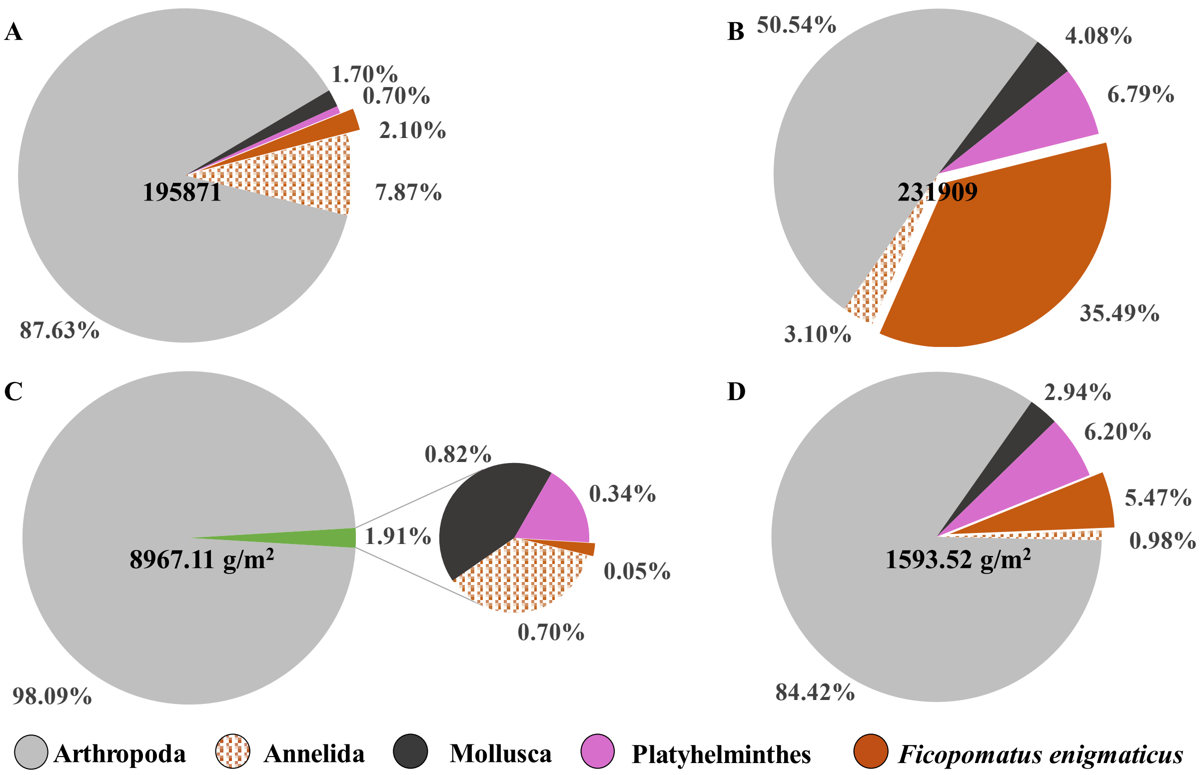

Figure 13: The distribution of abundance and biomass in percentage of the different Phyla found on the plates in both surface water and bottom water, 11.08.23. **A**: Abundance surface, **B**: Abundance bottom, **C**: Biomass surface, **D**: Biomass bottom. The total abundance and biomass are displayed in the centre.

3.2.6. 12. September 2023

In September 2023, a total of 24 species were found, including 11 arthropods, six annelids, three molluscs, one hydrozoan, one bryozoan, platyhelminths and *Ficopomatus enigmaticus*. Thereof, 21 species were collected from surface plates and 20 from bottom plates. The bottom plate was completely covered by the tubes of *F. enigmaticus* (Figure14).

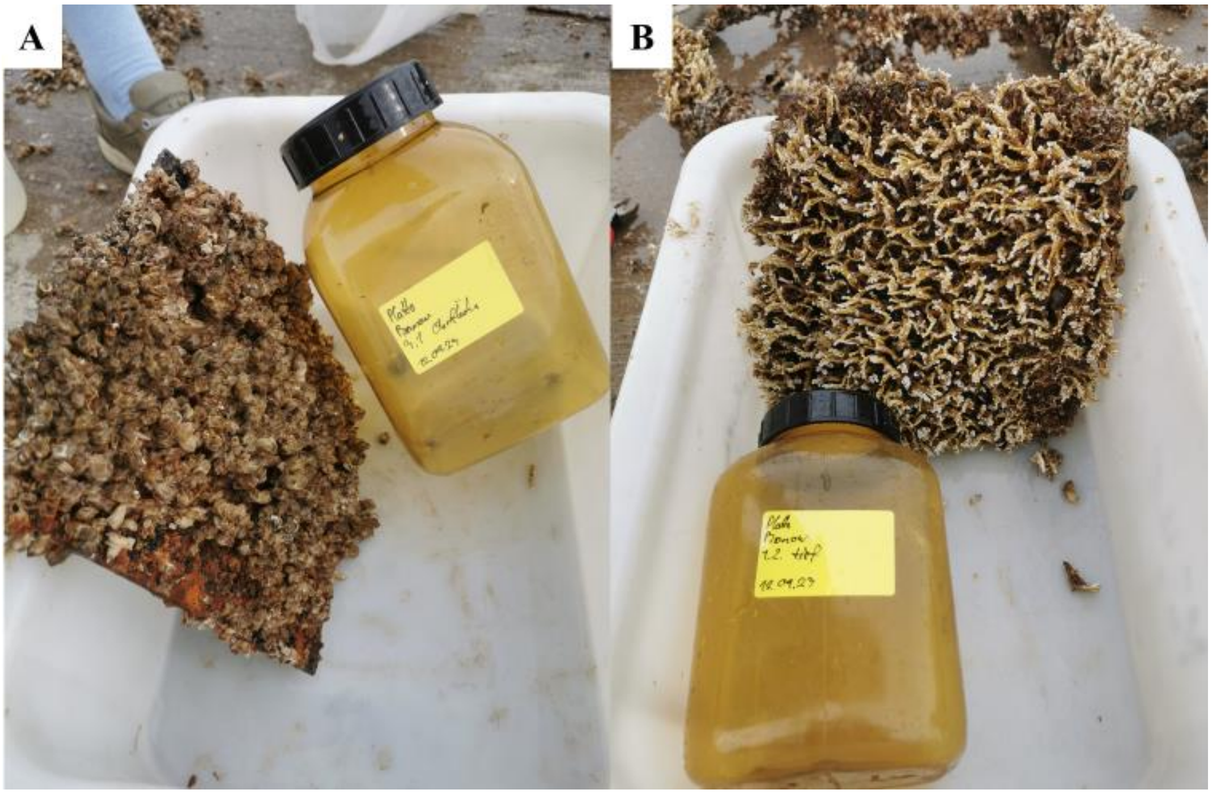

Figure 14: Metal plates of (**A**) surface water and (**B**) bottom water from 12.09.23.

The surface abundance was primarily composed of arthropods (91 %), annelids (6 %), molluscs (1 %) and *F. enigmaticus* (2 %). The bottom water abundance was distributed among arthropods (29 %), annelids (4 %), molluscs (3 %), platyhelminths (2 %), and *F. enigmaticus* (62 %) (Figure 15). *A. improvisus* represented 73.4 % of the arthropods and 66.4 % of all individuals with 73950 ± 3994 ind./m^2 on the surface plates. On the bottom plates, *A. improvisus* represented only 70.6 % of the arthropods and 20.4 % of all individuals which was a decline of 40.4 % (Table 7). In contrast*, F. enigmaticus* dominated the bottom water plates with 61.6 % (132663 ± 13728 ind./m^2) of the total individuals, while it only reached 2 % (1996 ± 871 ind./m^2) in surface waters (Table 7, Figure 15). In surface waters, *S. vanhaareni* was the second most abundant species representing 21.1 % (23521 ± 817 ind./m^2) of the total individuals. However, its population in bottom waters was low with 3483 ± 680 ind./m^2. On the surface plates, *P. cornuta* had the highest individual count among the annelids, with 3738 ± 909 ind./m^2 (57.3 %), and twice as much in bottom waters (6708 ± 1147 ind./m^2) (Table 7). While most of the species' population increased from surface to bottom plates, the population of most annelids' species decreased. However, the total number of individuals increased due to the previously mentioned increase of *P. cornuta* and *A. succinea*. *Mytilopsis leucophaeata* was the dominant mollusc species in both surface and bottom waters with 1171 ± 213 ind./m^2 and 5333 ± 660 ind./m^2 respectively. The population of platyhelminths also increased significantly from 421 ± 64 ind./m^2 in surface waters to 4808 ± 318 ind./m^2 in bottom waters (Table 7). The biomass of the surface plates was primarily composed of arthropods (99 %). In contrast, the biomass of the bottom plates was distributed among arthropods (61 %), annelids (1 %), molluscs (6 %), platyhelminths (1 %), and *F. enigmaticus* (31 %) (Figure 14 and 15). On the surface plates, *A. improvisus* represented 97.6 % of the total biomass with 7060.65 ± 573.63 g/m^2 followed by *M. leucophaeata* with the second highest biomass, accounting for 60.86 ± 16.15 g/m^2 (Table 7, Figure 15). A. *succinea* represented 71.8 % of the annelid's biomass with 15.24 ± 2.99 g/m^2. On the bottom plates, *A. improvisus* remained the dominant species accounting for 58.4 % of the total biomass with 1382.68 ± 1312.61 g/m^2. *F. enigmaticus* made up for the second largest biomass in bottom waters accounting for 31 %, with 735.38 ± 62.07 g/m^2. In contrast, its biomass on the surface plates was only 9.67 ± 5.19 g/m^2 (Table 7). The annelids biomass was again dominated by *A. succinea*, which accounts for 89 % with 19.11 ± 3.49 g/m^2. Despite twice the number of *P. cornuta* in bottom waters, its biomass decreased. The same applied to the biomass of *M. arenaria* which decreased from 19.16 ± 6.75 g/m^2 in surface waters to 15.48 ± 3.84 g/m^2 in bottom waters. Additionally, *M. edulis* and *M. leucophaeata* contributed the most mollusc biomass on the bottom plates, with 48.95 ± 24.67 g/m^2 and 67.31 ± 11.55 g/m^2 respectively. In bottom waters, the biomass of the platyhelminths increased to 28.52 ± 4.4 g/m^2 (Table 7). *H. gelatinosa* and *E. crustulenta* were only found in bottom waters (Table 7). The Shannon-Wiener-Index indicates low levels of biodiversity for both depths with a value of H'=1.14 for the surface plates and H'=1.34 for the bottom plates. The distribution of individuals at both depths was uneven with E=0.37 for surface waters and E=0.46 for the bottom plates.

Table 7: List of species found on surface and bottom metal plates with associated mean abundance and mean biomass per m^2 on 12.09.23.

Species	**Mean abundance/m^2**		**Mean biomass (g/m^2)**	
	Surface	Bottom	Surface	Bottom
Amphibalanus improvisus	73950	44038	7060.65	1382.68
Apocorophium lacustre	167	5904	0.09	1.67
Microdeutopus gryllotalpa	1971	2579	1.30	1.13
Sinelobus vanhaareni	23521	3483	3.34	0.37
Melita nitida	379	879	0.50	0.89
Leptocheirus pilosus	96	3963	0.03	0.92
Nippoleucon hinumensis	8	-	0.00	-
Idotea chelipes	-	4	-	0.03
Lekanesphaera rugicauda	4	-	0.03	-
Rhithropanopeus harrisii	642	1513	48.68	64.30
Chironomidae	4	-	0.00	-
Ficopomatus enigmaticus	1996	132663	9.67	735.38
Polydora cornuta	3738	6708	2.62	2.34
Syllidae	17	-	0.00	-
Hediste diversicolor	400	4	3.25	0.01
Alitta succinea	354	1292	15.24	19.11
Nais elinguis	846	121	0.05	0.01
Paranais littoralis	1175	13	0.09	0.00
Mya arenaria	429	1713	19.16	15.48
Mytilus edulis	4	408	0.11	48.95
Mytilopsis leucophaeata	1171	5333	60.86	67.31
Plathyhelminthes	421	4808	6.16	28.52
Hartlaubella gelatinosa	-	x	-	-
Einhornia crustulenta	-	x	-	-

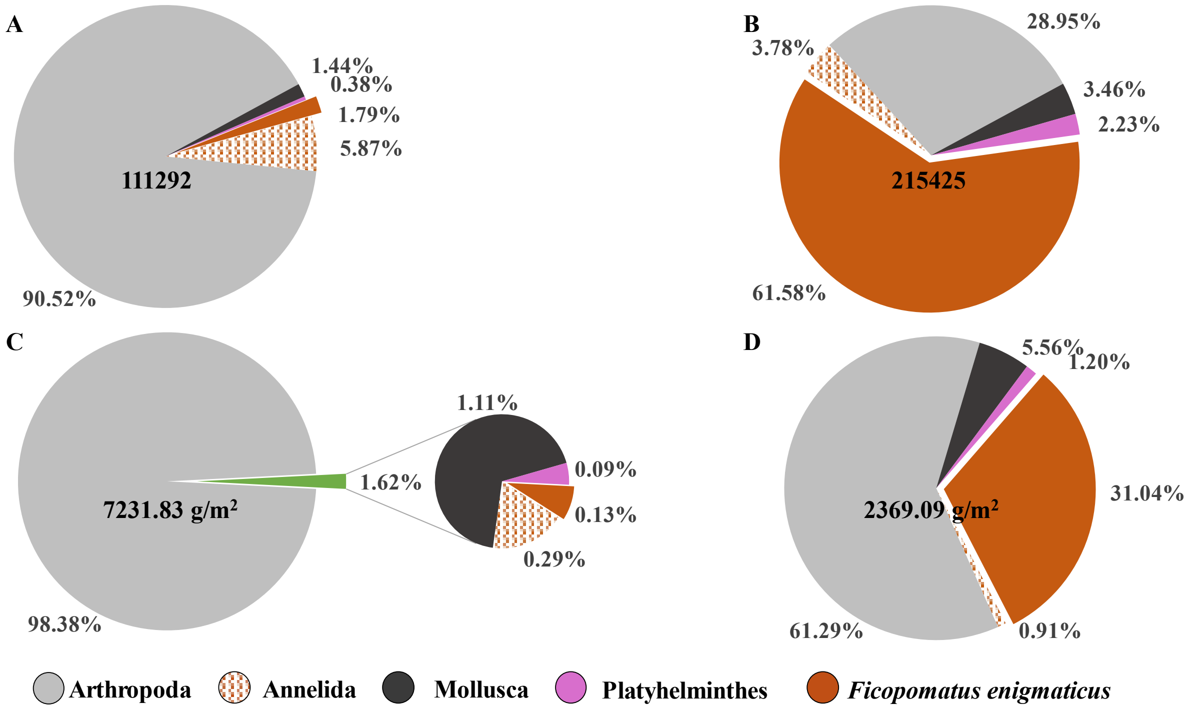

Figure 15: The distribution of abundance and biomass in percentage of the different Phyla found on the plates in both surface water and bottom water from 12.09.23. **A**: Abundance surface, **B**: Abundance bottom, **C**: Biomass surface, **D**: Biomass bottom. The total average abundance and average biomass are displayed in the centre.

3.2.7. 11. October 2023

In October 2023, a total of 23 species were found, including nine arthropods, six annelids, four molluscs, one hydrozoan, one bryozoan, platyhelminths and *Ficopomatus enigmaticus*. Thereof, 20 species were collected from surface plates and 21 from bottom plates. On the bottom plates, the tubes of *F. enigmaticus* had grown to such an extent that they created a bulge-like protrusion in the overall structure (Figure 16).

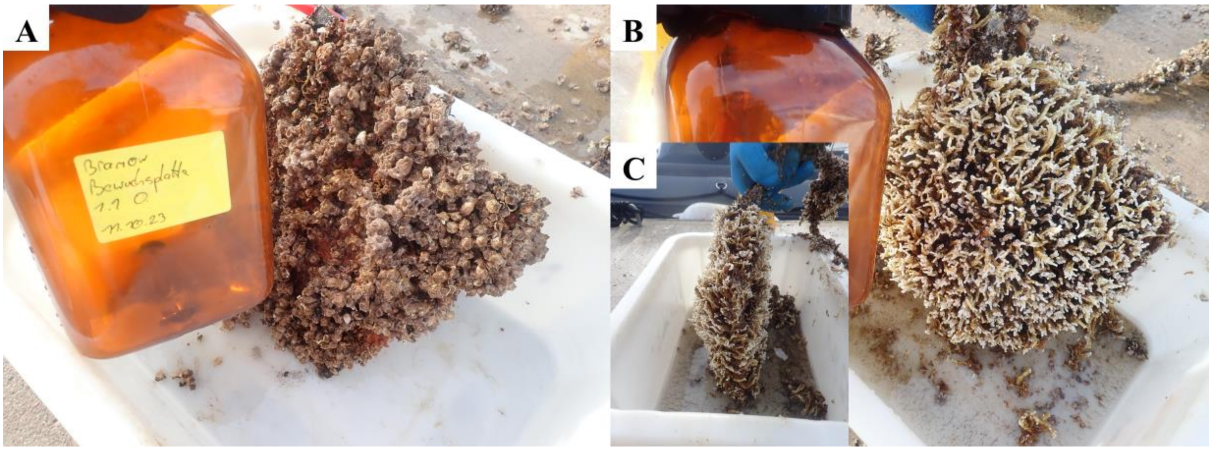

Figure 16: Metal plates of (**A**) surface waters and (**B**) bottom waters from 11.10.23 with (**C**) a side view of the bottom water plate.

The surface abundance was distributed among arthropods (80 %), annelids (14 %), molluscs (1 %), platyhelminths (1 %) and *F. enigmaticus* (4 %). The bottom water abundance was shared among arthropods (20 %), annelids (7 %), molluscs (3 %), platyhelminths (2 %) and *F. enigmaticus* (68 %) (Figure 17). On the surface plates, *A. improvisus* accounted for 50 % of the total individual count and 62.7 % of the arthropods with 48575 ± 10719 ind./m^2. On the bottom plates, *A. improvisus* represented only 15 % of all animals with 26575 ± 10582 ind./m^2, whereas *F. enigmaticus* dominated at 68.3 % with 121133 ± 32893 ind./m^2 (Table 8). In surface waters, *S. vanhaareni* was the second most abundant species with 22771 ± 3688 ind./m^2 however, provided a small population in bottom waters (988 ± 472 ind./m^2). The population of *P. cornuta* represented 87 % of the annelids with an individual count of 11617 ± 4408 ind./m^2 for surface plates and 85.3 % with 10208 ± 4287 ind./m^2 for bottom plates (Table 8). However, the total individual count of annelids decreased from surface to bottom. In contrast, all three mollusc species increased their individual count from surface to bottom water, with *Mytilopsis leucophaeta* being the most abundant at both depths. In addition, the population of platyhelminths doubled from 1425 ± 229 ind./m^2 in surface waters to 2671 ± 462 ind./m^2 in bottom waters. The population of *A. lacustre*, *M. nitida*, *L. pilosus* and *R. harrisii*, as well as *A. succinea*, increased from surface water to bottom water, whereas the population of *M. gryllotalpa*, *N. elinguis* and *P. litoralis* decreased (Table 8). Arthropods accounted for 99 % of the surface biomass, while molluscs accounted for the remaining 1 %. In contrast, the bottom water biomass was more evenly distributed among the different Phyla, with arthropods accounting for 39 %, annelids for 1 %, molluscs for 12 %, platyhelminths for 1 % and *F. enigmaticus* for 47 % (Figure 17). Overall, biomasses were either increasing or decreasing depending on the count of each individual species. Although, *A. improvisus* biomass accounted for 98.1 % of the total biomass with 7882.92 ± 722.64 g/m^2 on the surface plates, it was only 34.3 % with 773.89 ± 183.25 g/m^2 for bottom water plates. Here, *F. enigmaticus* accounted for the largest biomass at 46.7 % with 1054.62 ± 248.63 g/m^2 (Table 8, Figure 17) For bottom waters, the annelids biomass was primarily composed of *Alitta succinea* accounting for 91.4 % with 31.72 ± 14.81 g/m^2. On the surface plates, *Mytilopsis leucophaeta* had the second largest biomass at 59.79 ± 18.16 g/m^2 and was, thus, main contributor to the mollusc biomass accounting for 87.7 %. On the bottom plates, *Mytilus edulis* had the largest mollusc biomass at 129.97 ± 96.86 g/m^2. *H. gelatinosa* and *E. crustulenta* were found at both depths (Table 8). The Shannon-Wiener-Index indicates that the surface plates had high levels of biodiversity with *H'*=1.51, while the bottom plates had a low biodiversity with *H'*=1.2. The distribution of individuals at both depths was relatively uneven with *E*=0.52 for surface plates and *E*=0.41 for bottom plates.

Table 8: List of species found on surface and bottom metal plates with associated mean abundance and mean biomass per m^2 on 11.10.23.

Species	**Mean abundance/m^2**		**Mean biomass (g/m^2)**	
	Surface	Bottom	Surface	Bottom
Amphibalanus improvisus	48575	26575	7882.92	773.89
Apocorophium lacustre	513	1842	0.21	0.57
Microdeutopus gryllotalpa	4400	3183	2.20	0.89
Sinelobus vanhaareni	22771	988	2.76	0.09
Melita nitida	196	446	0.26	0.53
Leptocheirus pilosus	554	1521	0.21	0.53
Nippoleucon hinumensis	-	8	-	0.00
Jaera albifrons	4	-	0.00	-
Rhithropanopeus harrisii	492	1596	28.32	96.69
Ficopomatus enigmaticus	4033	121133	21.95	1054.62
Polydora cornuta	11617	10208	7.33	2.99
Syllidae	42	17	0.00	0.00
Hediste diversicolor	129	-	0.95	-
Alitta succinea	546	1633	18.75	31.72
Nais elinguis	617	108	0.04	0.01
Paranais littoralis	408	4	0.03	0.00
Mya arenaria	133	1083	8.35	23.07
Mytilus edulis	-	296	-	129.97
Mytilopsis leucophaeata	646	4050	59.79	122.36
Potamopyrgus antipodarum	-	4	-	0.02
Plathyhelminthes	1425	2671	4.91	20.06
Hartlaubella gelatinosa	x	x	-	-
Einhornia crustulenta	x	x	-	-

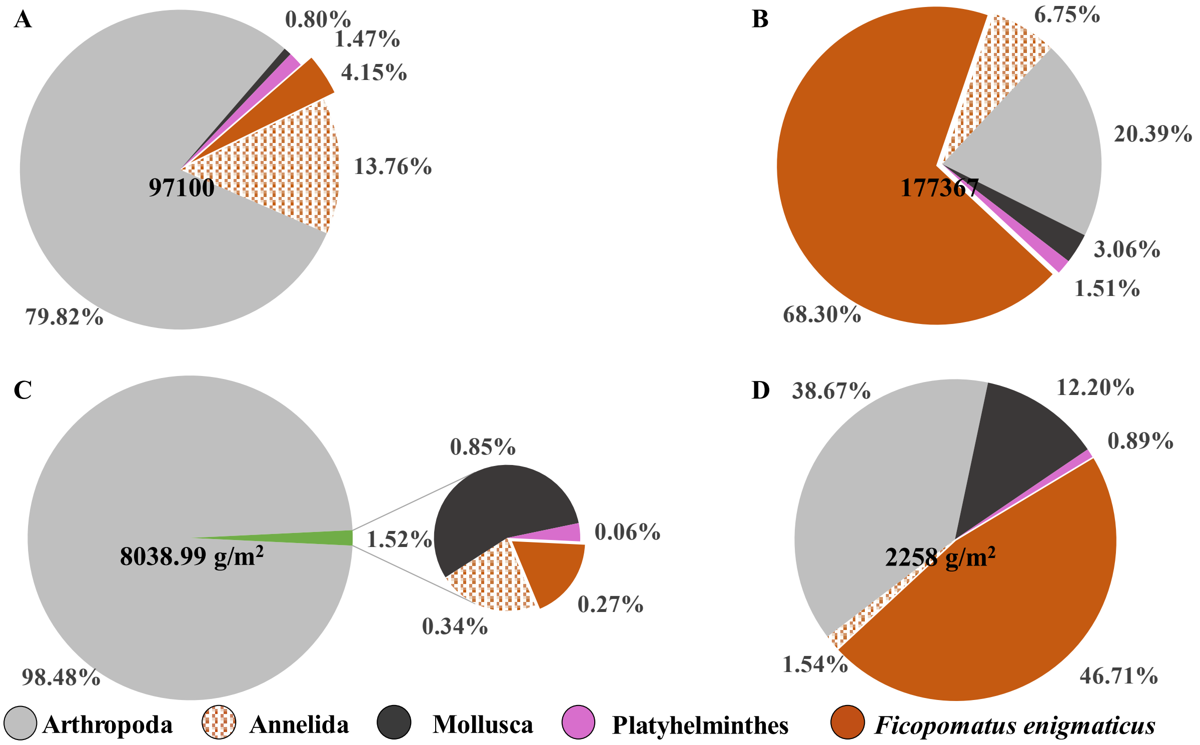

Figure 17: The distribution of abundance and biomass in percentage of the different Phyla found on the plates in both surface water and bottom water from 11.10.23. **A**: Abundance surface, **B**: Abundance bottom, **C**: Biomass surface, **D**: Biomass bottom. The total abundance and biomass are displayed in the centre.

3.2.8. Distribution ratio

In May 2023, annelids were the most present Phylum on the surface plates (Figure 7) with approximately 85 % but were considerably replaced by arthropods (primarily balanids) in the following month. From June onwards, arthropods dominated the species composition accounting for 80-90 % of the total individual count, while annelids made up approximately 10 % (Figures 9, 11, 13, 15, 17). Molluscs and platyhelminths were present throughout the investigation period but accounted for only approximately 1 %, respectively. In July 2023, *Ficopomatus enigmaticus* appeared for the first time in both depths. However, it only accounted for 0-4 % of the total abundance on the surface plates each month. Conversely, arthropods dominated the abundance on the bottom water plates for the first 3 month reaching up to 100 % of the total individual count in June yet were quickly displaced by *Ficopomatus enigmaticus* in the following month with up to 65 % abundance in October. Arthropods only accounted for 20 % of the individuals around this time (Figure 18). In May 2023, annelids reached a maximum of 19 % of the total individual count, yet their abundance decreased over time to a minimum of 1 % in June. Although individual molluscs and platyhelminths were already observed in May, they did not significantly constitute the total abundance. Their population increased over time starting in July 2023 and fluctuated between 3-4 % (molluscs) and 2-7 % (platyhelminths) (Figure 18). Throughout the investigation period, arthropods completely dominated the biomass of the surface plates. Even though annelids, molluscs, platyhelminths, or *Ficopomatus enigmaticus* were present in high individual counts, the biomass was primarily composed of arthropods, especially *Amphibalanus improvisus* (refer to Figure 7, 9, 11, 13, 15, 17 and Table 3-8). The only exceptions were the annelids in May 2023, which made up 16 % of the biomass (Figure 7), and molluscs, which accounted for 1 % of the biomass from August 2023 to October 2023 (Figure 18). From May 2023 to July 2023, the bottom water biomass was as well primarily composed of arthropods. However, from August 2023, the mass was more evenly distributed. In August, the biomass of *Ficopomatus enigmaticus* was at 6 % but it increased to 47 % in October, while the biomass of arthropods decreased from 84 % to 39 % (Figure 18). The increase in the individual count corresponded to an increase in biomass and vice versa. Molluscs constituted an exception to this trend as they exhibited a 12 % increase in biomass during October, while their abundance remained constant at around 3 % throughout the investigation period. Although annelids contributed to the total abundance, they accounted for only 1 % or less of the total biomass (Figure 18).

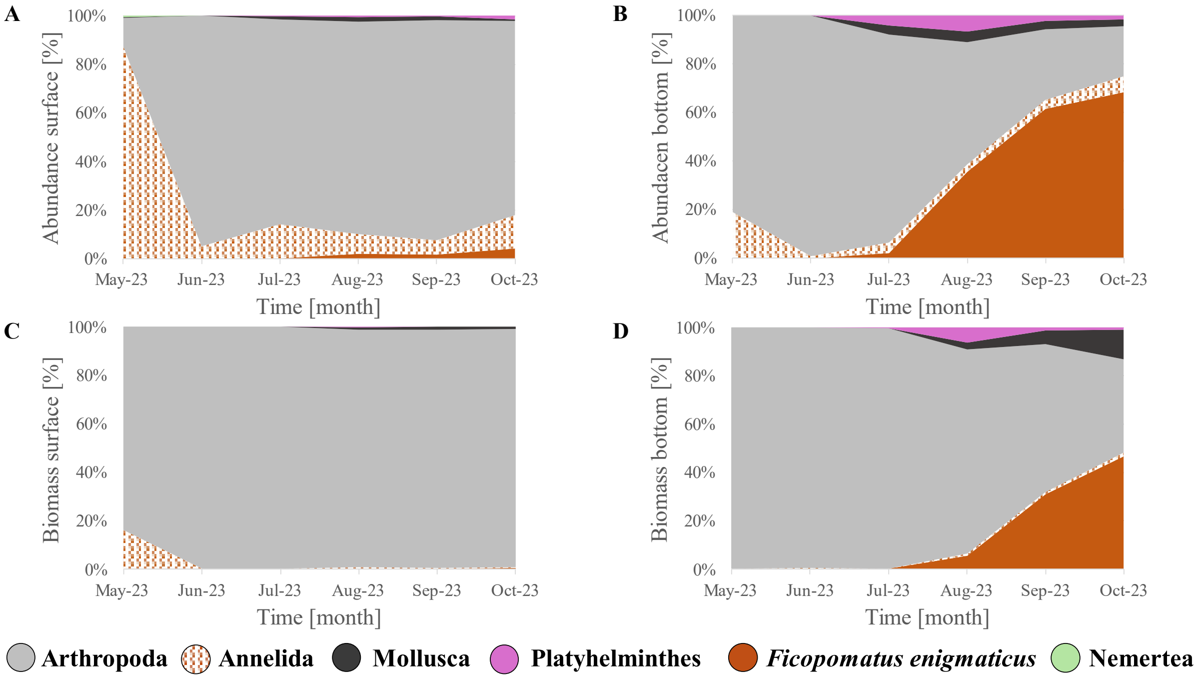

Figure 18: The dominance ratio of the abundance and biomass of each phylum compared between surface and bottom water plates in percentage from May 2023 to October 2023. **A**: Abundance surface, **B**: Abundance bottom, **C**: Biomass surface, **D**: Biomass bottom.

3.2.9. *Ficopomatus enigmaticus*

Ficopomatus enigmaticus was first observed in both depths in July 2023 with 4 ± 7 ind./m^2 in surface waters and 8063 ± 5372 ind./m^2 in bottom waters (Table 3). The population on the surface plates fluctuated (Figure 19) with a peak of 4121 ± 1495 ind./m^2 in August (Table 4), while the population on the bottom plates continuously increased with a maximum of 132663 ± 13728 ind./m^2 in September (Table 5). The increase in abundance on the bottom plates corresponded to the observed increase in biomass. The biomass in July was 0.74 ± 0.44 g/m^2 and peaked in October at 1054.62 ± 248.63 g/m^2 (Table 5 and 8). A production rate of 86.45 g/m^2 could be observed between July and August, while the production rate between August and September was 648.19 g/m^2. Consequently, a succession rate of 2.7 g/m^2 per day was determined between July and August and a rate of 20.9 g/m^2 per day between August and September. The biomass grew seven times faster between August and September than between July and August. However, the production rate decreased to 319.24 g/m^2 with a succession rate of 10.6 g/m^2 per day between September and October. Furthermore, the average biomass of a single *Ficopomatus enigmaticus* increased from 0,09 mg in July over 1 mg in August and 6 mg in September to 9 mg in October. Therefore, the biomass of one *F. enigmaticus* increased by a factor of 11.7 between July and August and by 1.6 between September and October, which indicates that not only the number of individuals but also the weight of each individual polychaete had increased. Particularly, since the abundance decreased in October, yet the biomass kept increasing. There was a significant decrease in the number of individuals settling per day over the investigation period. While 2395 individuals settled per day from July to August, their number dropped to 1625 individuals per day from August to September. From September to October, there was no increase observed, yet a decrease of -384 individuals per day. This is another indication for the increasing growth of each individual polychaete by the fact that a decrease in settlement and total individual count was observed yet the biomass increased. In opposition, the weight of a single animal on the surface plates remained constant between September and October (5 mg for both months) which indicates that the increase in biomass was a result of an increase in the number of individuals. Despite fluctuations in surface water abundance, the biomass steadily increased from month to month (Figure 20). In August, the biomass was at 4.76 ± 2.34 g/m^2 with 4121 ± 1495 ind./m^2 (Table 6). In September, the biomass doubled to 9.67 ± 5.19 g/m^2 with half the number of individuals (1996 ± 871 ind./m^2) and doubled again with 21.95 ± 18.84 g/m^2 in October (Table 7). The growth rate peaked between September and October with 12.28 g/m^2. Succession rates ranged from 0.2 g/m^2 and 0.4 g/m^2 per day throughout the months. Overall, a larger population and consequently a greater biomass were observed on the bottom water plates (Figure 19 and 20).

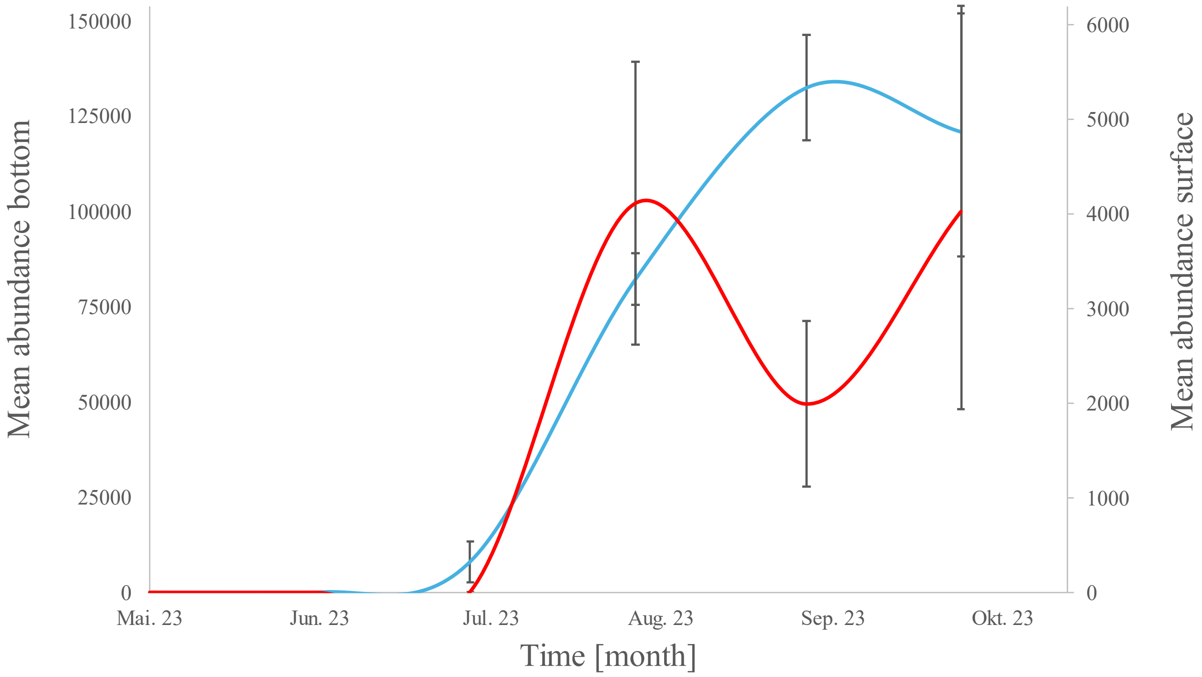

Figure 19: Mean abundance of *Ficopomatus enigmaticus* for surface plates (red line) and bottom plates (blue line) over the time span of 6 months. Standard deviations are highlighted in black.

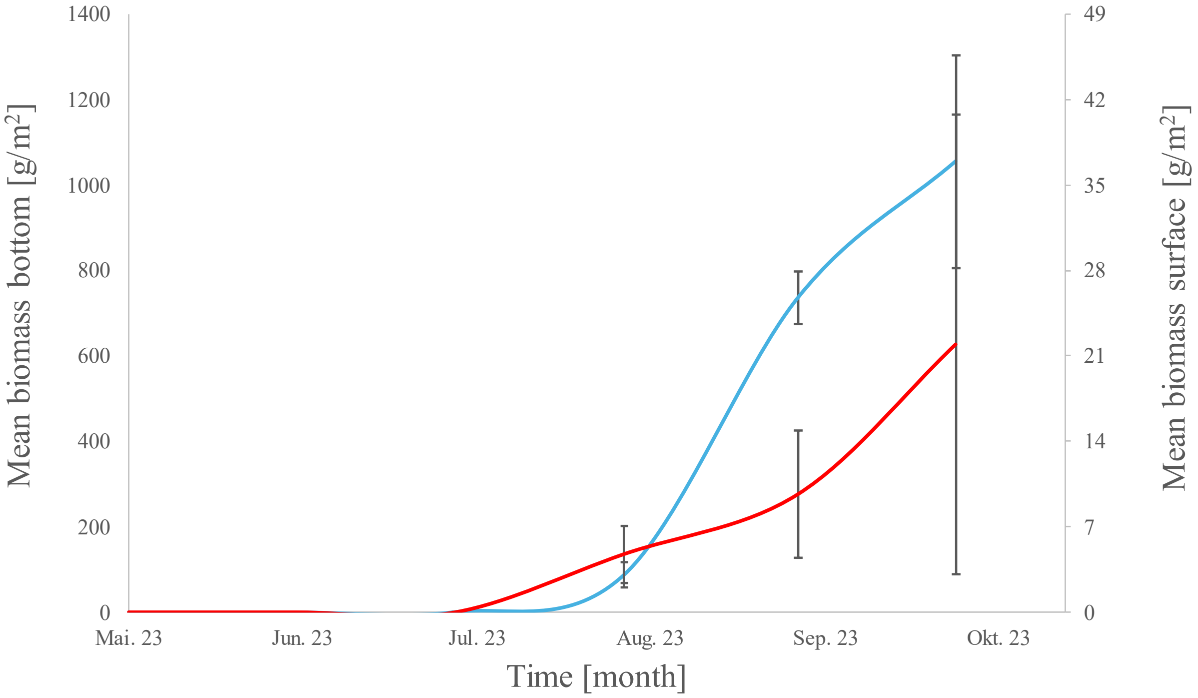

Figure 20: Mean biomass of *Ficopomatus enigmaticus* for surface plates (red line) and bottom plates (blue line) over the time span of 6 month. Standard deviations are highlighted in black.

4. Discussion

Aim of this study was to get insights into ecological aspects of production and growth, succession, the possible shift in biodiversity and species composition and the impact of *F. enigmaticus* onto the system regarding its function as an ecosystem engineer. In order to achieve appropriate results, metal plates attached to a string were placed at two different depths in the water of the Lower Warnow, an estuary of the Baltic Sea. It has been observed that population sizes varied significantly between either depth resulting in a strong relevance for the bottom plates.

The exposure of the plates began in April and the first appearance of *F. enigmaticus* on the plates was in July 2023 (Table 5, Figure 11). Straughan (1972) estimated approximately three weeks for Larvae development. Hence, Larvae presence since mid-June 2023 is to be anticipated. However, a laboratory study by Gabilondo et al. (2013) revealed a much shorter development time. After fertilisation the trochophore larvae stage developed within 18 hours, succeeded by Metatrochophores after four days. Settlement then started on the fifth day. Similar development times were observed in studies by Oliva et al. (2019, 2020). The new and altering data might lead to the conclusion that reproduction and larvae development of *F. enigmaticus* only started 1-2 weeks prior to its first observation, in late June. Both statements would agree with observations made by Dixon (1981) who stated spawning times from June to October. Furthermore, the measured abiotic values provided optimal conditions for *F. enigmaticus* with a salinity of above 9 PSU and a temperature of 20 °C in surface waters (Table 1) (Straughan, 1972; Bianchi and Morri, 1996). Increasing salinity and temperatures of above 10 °C in bottom waters can trigger spawning (Straughan, 1972; Dittmann *et al.*, 2009). Both values increased between June 2023 and July 2023 (Table 1). Finally, exact spawning times, larvae development, and the abiotic parameters which favour or trigger these processes are controversially discussed and may depend on geographics (Hill, 1967; Straughan, 1972; Dixon, 1981; Thorp, 1994). Initially, monitoring the larvae of *F. enigmaticus* in the Lower Warnow was part of the study though (human) errors during the sampling led to unsuitable or even no data. A methodological approach better organized would have been required to monitor spawning, larvae development, and settlement in detail.

In-between the investigation period of six month, biomasses of *F. enigmaticus* for both surface plates and bottom plates increased despite fluctuations in the number of individuals. The biomass peaked in October with 21.95 ± 18.84 g/m^2 for surface plates and 1054.62 ± 248.63 g/m^2 for bottom plates (Table 8). This considerable difference is also recorded in density, with a peak of 4121 ± 1495 ind./m^2 (August) on the surface plates and a peak of 132663 ±13728 ind./m^2 (September) on the bottom plates (Table 6 and 7). The population size of the bottom plates corresponds to observations made at e.g. the Italian Po River, the South African Marina da Gama or Zandvlei Estuary, or at the Danube Estuary (Table 9) (Bianchi and Morri, 1996; Micu and Micu, 2004; McQuaid, 2013; Bezuidenhout and Robinson, 2020). Only two years prior, Hille et al. (2021) reported lower numbers for the Warnow Estuary but at the same time predicted a rapid increase and dispersal of individuals and even the reefs. The surface plates population, however, seems rather small in biomass and abundance. The population difference between the depths may be attributed to the position of the plates in the water column (Figure 4). Despite abiotic parameters such as salinity and temperature ranging in favourable conditions (Table 1) for growth and reproduction (Straughan, 1972; Bailey-Brock, 1976; Bianchi and Morri, 1996), an approximated population on the surface plates to that of the bottom plates was not achieved. An explanation might be the mechanical stress in surface waters caused by turbulences or waves (Table 1) (Wołowicz et al., 2007) which might as well be supported by own data that animals on the surface plates were shorter with thicker and harder tubes. However, tube thickness might also depend on higher CO_2 concentrations and therefore a higher uptake of calcium hydroxide. Kopiy et al. (2022) revealed varying tube thickness due to different substrates. Nonetheless, there is no data on varying tube thickness depending on water depth. Moreover, a lower average weight of individuals on the surface plates was observed. *F. enigmaticus* on the surface plates appears to allocate more resources into tube construction than animals on the bottom plates. However, since it is a biofouling organism and is primarily distributed by ships (Allen, 1953; Hewitt *et al.*, 2004), it definitely has the ability to settle in lower depths and withstand high mechanical stress. Consequently, the depth in which *F. enigmaticus* appears is again controversially discussed. Hille et al. (2021) demonstrated that no animals were found in the area of 2 m below the water surface with a maximum of 4.5 m in the Lower Warnow, whereas Bianchi & Morri (1996) and Kopiy et al. (2022) reported findings in that very area. Nonetheless, the results of the present study show that *F. enigmaticus* was found 0.5 m below the water surface indicating that it can settle from the surface down to a depth of 4.5 m. Another possible explanation for the low numbers on the surface plates could be the competition for space with the balanid species *Amphibalanus improvisus*. *A. improvisus* is a cosmopolitan, brackish, shallow-water species with high salinity tolerance (Foster, 1970; Furman and Yule, 1990) that was dominant in the early successional stages in both depths but was quickly overgrown on the bottom plates after the arrival of *F. enigmaticus*. However, on the surface plates the species had remained dominant since colonisation and had not been replaced. Temperatures were similar at both depths and therefore probably did not limit the distribution. Salinity, however, might have limited the settlement rate of *F. enigmaticus* in shallow water. The measured values for bottom water between July and October were all above 13 PSU, surface waters salinity ranged between 9.1 PSU and 11.4 from July to September (Table 1) instead. As stated by Straughan (1972) and others, optimal salinity conditions for *F. enigmaticus* start at 10 PSU. Nevertheless, it is to be argued whether such a minor deviation of less than 1 PSU from a norm condition stated in literature ought to be considered as a significant impact for surface distribution. Most likely, a combination of abiotic factors (salinity) and biotic factors (*A. improvisus*) limited its distribution in shallow waters although Schwindt et al. (2004a) claimed that once a reef is established competition and predation does not limit its distribution. Food availability might have played a role in settlement success of the surface plates. Due to high filtration and ingestion rates and the much larger population of *F. enigmaticus* on the bottom plates in July 2023 (Table 5) (Davies *et al.*, 1989), resources for the establishment of a large population on the surface plates might have been exhausted. Anyway, this is rather not the case. The Lower Warnow is a eutrophic water body with a high nutrient inflow (nitrogen and phosphor) that favours particle and plankton concentrations (Justić *et al.*, 1995; Wasmund *et al.*, 1998; Cloern, 2001; Pastuszak *et al.*, 2018). Additionally, the seasonal spring and summer phytoplankton bloom should provide a high enough food concentration (Wasmund *et al.*, 1998; Kahru *et al.*, 2007). It remains open to question whether *F. enigmaticus* would as well have overgrown the surface plates if abiotic conditions had remained constant and larvae had been present throughout the year.

In order to gain insights into the growth of *F. enigmaticus* and elaborate on the increasing biomass (despite the decline in the number of individuals and settlement rate), the production rate and succession rate were analysed. The settlement rate on the bottom plates decreased from 2395 individuals per day between July and August to a state of recession of -384 individuals per day between September and October. In opposition, the production rate remained positive at both depths. Between July and August, the production rate was at 86.45 g/m^2 and increased to 648.19 g/m^2 between August and September in bottom waters. Succession rates were at 2.7 g/m^2 per day for July and August and 20.9 g/m^2 per day for August and September (Table 9). Biomass doubled monthly on the surface plates, whereas on the bottom plates the biomass initially increased by a factor of eight between August and September but only by a factor of 1.4 between September and October. The production rate first increased by a factor of seven between August and September, but then declined again to 319.24 g/m^2 in October (Table 9). Then in October, the continuous increase of both biomass – despite the before mentioned recession in abundance – and of the rates of settlement, production, and succession is likely to be referred to the increase in individual biomass. Throughout the investigation period, the weight of each *F. enigmaticus* on the bottom plates increased from 0.009 mg in July to 9 mg in October. Bianchi & Morri (1996) reported worms that weight 1.1 ± 0.006 mg (Table 9). It is to be assumed that each worm on the plates could have become even heavier. This might indicate an increasing biomass beyond October 2023 despite an ongoing density recession or an increasing mortality rate. However, the decline of the different biotic values and a lack of space on the plates indicate that the climax stage is surpassed. Furthermore, the decline in larvae abundance (Dixon, 1981) and the onset of mortality might be additional reasons. The high production rate in the early months after settling might have been enabled due to space for expansion. *A. improvisus* is easily displaced and overgrown. Each worm has space to expand their mass and tube mass. Furthermore, the rate of clearance was presumably the major factor for the high production rates in August and September. Davies et al. (1989) measured the clearance rate of *F. enigmaticus* in a study in the Marina da Gama near Cape Town. They revealed that an estimated population of 2.88 ± 2.24 t biomass (excluding tubes) cleared the entire water body in approximately one day with a clearance rate of 8.59 ml per milligram of worm per hour (Table 9). This resulted in an uptake of 130 kg of wet mass of suspended material. Bruschetti et al. (2008) also observed high filtration rates of *F. enigmaticus* for the Mar Chiquita Lagoon in Argentina. They showed that the particle concentration was reduced by 50 % during summer and 20 % during spring which even impacted water turbidity and light penetration enhancing microphytobenthic production. Similar clearance rates were as well observed in other sabellids or nereids (Riisgård *et al.*, 1996; Jordana *et al.*, 2001) which confirms the important role of filter feeding polychaetes for maintaining water quality and their impact on phytoplankton and food concentrations. Such an effect can therefore be also expected for *F. enigmaticus* in the Warnow Estuary. In addition the inflicted changes in light penetration or water turbidity affecting benthic communities (Davies *et al.*, 1989; Bruschetti *et al.*, 2008) needs to be investigated. In conclusion, a high clearance rate might explain the high production rate of *F. enigmaticus* in the early months of investigation. Due to the earlier mentioned eutrophic nature of the Baltic Sea and its seasonal events a food depletion is not likely. Space and the recession in larval abundance seem to limit productivity(Kahru *et al.*, 2007). Nonetheless, there was still enough space and resources for the growth of each individual. During this study no data was obtained regarding clearance rates, filtration rates, ingestion rates, and food concentrations of the worms in the Lower Warnow. This is certainly necessary and is to be further investigated.

Table 9: Biotic parameters of *F. enigmaticus* in estuaries, recorded by studies at different geographical locations. **Abu.**: Abundance, **Bio.**: Biomass, **Prod./m.**: Production rate per month, **Prod./d.**: Producion rate per day, **Ind. w.**: Individual weight, **G. rate**: Growth rate, **Set. r./d.**: Settlement rate per day, **Clear. rate**: Clearance rate. **DW**: Dry weight, **WW**: Wet weight.

Parameters/ Location	**Abu.**	**Bio**	**Prod./ m.**	**Prod. /d.**	**Ind. w.**	**G. rate**	**Set. r./d**	**Clear. rate**	**Reference**
Baltic Sea Warnow Estuary	132663 ind./m^2	1055 g/m^2 WW	648 g/m^2	20.9 g/m^2	9 mg	5 mg	2395 ind./m^2	-	Hille et al. (2021), Weitzel (2021), Martin (2023)
Atlantic Marina da Gama	-	8050 g/m^2 DW	-	-	-	-	-	8.59 ml/mg worm/ h	Davies et al. (1996), McQuaid (2013), Bezuidenhout & Robinson (2020)
Zandvlei Estuary	-	2240 g/m^2 WW	-	-	-	-	-	-	Davies et al. (1996), McQuaid (2013), Bezuidenhout & Robinson (2020)
Mar Chiquita Lagoon	-	47 g/m^2 DW	10 mm	-	4-7 mg	-	-	-	Obenat & Pezzani (1994), Schwindt et al. (2004a), Bruschetti et al. (2008)
English Channel	-	4.450 g/m^2 DW	-	-	-	-	-	-	Charles et al. (2018)
Black Sea Danube Estuary	145250 ind./m^2	-	-	-	-	-	-	-	Micu & Micu (2004)
Mediterranean Sea Po River Estuary	145000 ind./m^2	2000 g/m^2 DW	10 - 12 mm	0.3 - 0.4 mm	1.1 mg		100 - 500 ind./m^2		Bianchi & Morri (1996)
Lagoon of Orbetello	150000 ind./m^2	-	-	-	-	-	-	-	Bianchi & Morri (2001)
Magra Estuary	180000 ind./m^2	-	-	-	-	-	-	-	Aliani et al. (1995)
Pacific Goolwa Estuary	-	-	4 - 10 mm	-	-	-	-	-	Dittmann et al. (2009)

In accordance to the function of *F. enigmaticus* as an ecosystem engineer and a reef builder, monitoring the species which thrived in these ecosystems enables valuable insight into possible shifts in diversity and species composition. The Shannon-Wiener-Index indicates low levels of biodiversity for almost every month which is partly due to early succession stages (May and June). Nonetheless, determining biodiversity remains difficult whatsoever (Romoth *et al.*, 2023). Thus, the Shannon-Wiener-Index provides an approximate calculation but is very much biased in terms of logarithmic arrangements. Succession stages and mobile fauna can be considered as two possible factors that influenced biodiversity and species composition. However, it is to be expected that heterogeneous structures such as the reef of *F. enigmaticus* as well as any other habitat-creating structure do benefit diversity level and population sizes (Obenat *et al.*, 2006a). The reefs were habitat to different bivalves, polychaetes, clitellates, malacostracan, and thecostracan. Especially juvenile crustaceans were observed which leads to the assumption that the reefs might function as nurseries with enough space and food for development. Accordingly, this was also observed by Schwindt & Iribarne (2000) who recorded different arthropod families, nematodes, and juveniles in their study in the Mar Chiquita Lagoon. A same species composition was observed by McQuaid (2013) in the Zandvlei Estuary in South Africa. Furthermore, many of the species found on the plates were introduced as alien species in the last decades (Ojaveer *et al.*, 2017; Zettler and Zettler, 2017). The reef structures of *F. enigmaticus* provide shelter and habitat for a variety of species and can sustain larger populations. This was also observed during this study. Almost all species, including *F. enigmaticus*, produced a higher population on the bottom water plates than on the surface plates. Total biomass, however, is higher on the surface plates. This is quickly explained due to the mass of *A. improvisus*. There are few exceptions for smaller populations on the bottom plates. First, *A. improvisus* who got overgrown by *F. enigmaticus* and therefore had smaller populations on the bottom plates starting in August. Previously, *A. improvisus* populations were similar or larger on the bottom plates. Second, the population of most annelid species is much smaller on the bottom plates (Table 3-8). This is most likely due to abiotic factors, particularly due to water depth. A high predation rate on smaller annelids might also be likely. Before *F. enigmaticus* occurs on the plates (May and June), the difference in annelids population sizes can already be observed between the depths (Table 3 and 4). Consequently, an impact of *F. enigmaticus* which might have competed with other annelids for space and food on the bottom plates is rather unlikely (Table 7 and 8). Furthermore, species of the early succession stages (Tubificidae, gammarids,) are displaced or outcompeted which led to a constant species composition. However, individual species sporadically found their way onto the plates (Table 2). Overall, total individual numbers are observed to decline after the initial settlement in May and June (Figure 7, 9, 11, 13, 15 and 17). The highest count of individuals was observed in June with juvenile *A. improvisus* (Table 4). Initially increasing in size, this species seems to displace itself to a certain degree. On the bottom plates *F. enigmaticus* tend to force the suppression of *A. improvisus*. However, in both depth a recession of the total individual count is observed which might be explained with a decreased settlement rate in correspondence with an increasing mortality rate. Mortality rate is increasing due to natural death, decreasing abiotic parameters, oxygen and food depletion, or possible predation.

Finally, the reef structures might influence water turbidity, light penetration, food and phytoplankton concentrations as reported by several other studies (Davies *et al.*, 1989; Bianchi and Morri, 1996; Bruschetti *et al.*, 2008). This might affect diversity and productivity of local benthic systems and is to be further investigated.

Conclusion

To conclude, *Ficopomatus enigmatiucs* shows high development rates and a rapid spread from larval stage to the adult animal. Production and succession rates are favoured by its high clearance rate. This appears to enable it to successfully colonise estuaries worldwide. Moreover, being able to build up a high biomass in a short period of time might explain its distribution on ship hulls and its resilience to mechanical stress. However, it still seems limited by certain abiotic and biotic parameters. Water depth might limit its population size whereas adaptations in tube aggregation and body size might enable colonisation of peripheral abiotic areas. Salinity and temperature had but minor impacts on its distribution and growth though further investigation is required. The impact on the benthic community remains inconclusive. Other sessile filter feeders might compete with *F. enigmaticus* for settlement space and food. On the same time the reef structure enables living space for larger populations of bivalves, crustacean, and annelids and creates resources by itself. Conversely, the reported impact on phytoplankton and particle concentration in South African and Argentinean waters in terms of food concentration is likely to be also valid for the Warnow waters. Finally, the impact on artificial structures and therefore human life is undeniable, and the knowledge received about the rapid production rates and biomass growth is indeed worrying. Anyway, further inquiries with a focus on optimising the experimental set-up as well as including additional abiotic and biotic parameters are required.

Prospect

Since the originally intended aim of the study – to monitor the annual course of growth rate, succession rate, larval abundance, biodiversity, and species composition – has not been feasible within the schedule of a master's thesis, it still remains a desideratum for further investigations. Accordingly, further research is recommended to particularly focus on different parameters like seasonal aspects, mortality, changes in species composition, clearance-, filtration-, and ingestion rates as well as reproduction. Especially, data on clearance rates might explain its rapid growth not only within a local ecosystem but all over the world. Furthermore, it is important to emphasize the error rate of such investigations which makes methodological competence key. In order to monitor the zooplankton, nets with different mesh sizes (63 µm, 150 µm) are to be used. Additionally, monthly sampling might be even too scarce considering the stated larval development time of *F. enigmaticus*. Certainly, these two considerations should optimise the monitoring of reproduction times and larval development. A revision of the experimental set-up could also be useful. In fact, it would have been sufficient to apply smaller plates instead of the ones used as the amount of epibenthos makes processing of individual plates considerably more difficult as well as time consuming. An alternative would be to hang the surface plates a little deeper – for example at a water depth of 1 m – and possibly add a third depth level. There is also potential for improvement in the measurement of abiotic values. Oxygen saturation should also be measured at the bottom water to be able to observe possible depletion. Phytoplankton and particle concentrations should be monitored as well. Moreover, similar to the set-up used in this investigation, a second or third location for the attachment of plates would scale up and therefore validate the data. A set-up near the river mouth and one near the weir in the south could be options to provide an insight in *F. enigmaticus'* distribution in the Warnow system. Furthermore, relocating the experimental set-up to other nearby river systems is also necessary. Finally, an exchange with the shipping industry might be favourable to develop methods to restrict or prevent the spread of *F. enigmaticus*.

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6. Abbreviations

°C	Degree centigrade
µm	Micrometre
B	Bottom
cm	Centimetre
clear. rate	clearance rate
d	day
DW	Dry weight
g	Gram
g/m^2	Gramm per square metre
ind.	Individuals
Ind. w.	Individual weight
Ind./m^2	Individuals per square metre
l	Litre
m	Metre
m^2	Square metre
m^3	Cubic metre
mg	Milligram
ml	Millilitre
mm	Millimetre
PSU	Practical Salinity Unit
prod./d	production rate per day
prod./m	production rate per month
S	Surface
SD	Standard deviation
set. rate	settlement rate
t	Ton
WW	Wet weight

7. Literature

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8. Declaration of independence

I declare that I have written this thesis independently and without the assistance of any third parties. Any direct or indirect references to other publications are clearly marked as such.

I understand that making a false declaration may result in failure of the examination.

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