Ecology of the invasive species *Ficopomatus enigmaticus* (Fauvel,1923) in an estuary of the southern Baltic Sea

By
Weitzel, Johanna

June, 2021

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1 Abstract

This thesis focuses on the distribution of the recently introduced polychaete *Ficopomatus enigmaticus* (Fauvel, 1923) on the Baltic Sea coast of Mecklenburg-Western Pomerania. Additionally, a review of the current state of research in the literature regarding global distribution, morphology and ecology as well as the influence of the tube-building species is given. Ecologically, both biotic and abiotic factors affecting the establishment are considered. Moreover, a breakdown of the fauna associated with the serpulids is carried out and compared to the literature.

To obtain information on the distribution of the species on the coast of Mecklenburg-Western Pomerania, different sites along the southern Baltic Sea coast and in the Warnow Estuary were investigated for the presence of the tubeworm. Additionally, a quantitative and qualitative study of the fouling on hard substrate in the depth gradient was carried out, which was sampled in a port facility.

The study revealed the presence of *F. enigmaticus* at various sites in the Lower Warnow River with the greatest abundance between three and four meters depth. There it cohabits with species of the taxa Annelida, Bryozoa, Cnidaria, Crustacea, Hexapoda, Mollusca and Platyhelminthes.

The ecological conditions of the estuary fulfill the requirements of the serpulids. The most critical abiotic factor for the species, which originally has a tropical or subtropical distribution, is the water temperature. In late summer, the temperature required for reproduction is reached, but in cold winters a decline in the population is possible. However, it is also likely that a significant increase in abundance may occur if water temperature increases due to climate change. Therefore, even after this inventory, it is important to continue to monitor the spread of the species in the future.

2 Introduction

For many years, *Ficopomatus enigmaticus* (Fauvel, 1923) has been spreading and is therefore found in more and more locations around the world.
The invasive species, also known as the Australian tubeworm, now has a cosmopolitan distribution (Straughan, 1972) and is considered to be a neozoan. This means it has been introduced into areas beyond its native habitat by human influence after 1492 (Nehring, 2000). Most likely, immigration mainly takes place via boats, on whose hulls larvae of *F. enigmaticus* settle (Nelson-Smith, 1967). Until now, it is not conclusively clarified where the true origin of the species is located. The distribution extends from tropical to temperate waters, although there are differences between the populations in various climatic conditions, for example in terms of size (Hill, 1967).
In fall 2020, the first mass occurrence of *F. enigmaticus* was discovered in the Lower Warnow River (Hille et al., 2021), which flows into the Baltic Sea in northern Germany.

Serpulids have a great impact on the ecosystem in which they live (Bastida-Zavala et al., 2017) since they are filter feeders and a substantial part of fouling communities. *F. enigmaticus* also acts as an ecosystem engineer, as the species forms tubes and colonizes, consequently forming reefs (Hartmann-Schröder, 1967). For example, the structure protruding into the water alters the flow and thus the displacement of sediment (Martínez-Taberner et al., 1993). For other species, the reef serves as a substrate and provides shelter (Schwindt & Iribarne, 2000). In addition, the filtering activity of the tubeworm releases nutrients that can be used by associated organisms (Martínez-Taberner et al., 1993). All this leads to a change in the composition of benthic organisms, described, for example, by Bailey-Brock (1976).
The positive effects of the occurrence, such as the reduction of suspended sediment load and eutrophication and thus the increase in oxygen content, are contrasted with negative effects, like the displacement of native species. From a human point of view, fouling caused by *F. enigmaticus*, for example on boat hulls or pipes, is also problematic (Eno et al., 1997).

Despite its high tolerance range for different salinity levels, the polychaete settles mainly in brackish water areas (Eno et al., 1997; Fornós et al., 1997).
In this regard, it is not surprising that individuals of *F. enigmaticus* also colonizes estuaries in the Baltic Sea, the largest brackish water body on earth (Voß & Dippner, 2017). Numerous

rivers flow into the Baltic Sea. One of them is the Warnow River, the lower part of which has a salinity gradient from its mouth to the weir separating it from the Upper Warnow (Seiß & Boehlich, 2019). The presence of different salinities in a small area increases the probability of values suitable for colonization by *F. enigmaticus*.

Due to climate change and other anthropogenic influences, the ecosystem of the Baltic Sea is changing. For example, there is an increase in water temperature (Voß & Dippner, 2017), which encourages the settlement of the Australian tubeworm, since in temperate climates it is mainly limited by temperature, whereas in tropical areas salinity is rather the limiting factor (Hill, 1967). In addition, the fact that more and more banks are built on has a habitat-creating effect, as *F. enigmaticus* only settles on hard substrate (Bianchi et al., 1995).

Since the tubeworm was introduced comparatively recently into the habitat of the Warnow Estuary, hardly any studies could be made in this area until now. Thus, it is important to monitor the status of its distribution regularly to determine the extent and rate at which the species is spreading. This is important to assess potential future impacts on the environment and local population.

Therefore, the present paper aims to investigate selected sites of the coast of Mecklenburg-Western Pomerania regarding the presence of *F. enigmaticus* and its associated fauna. In the context of colonization, different ecological requirements and consequences discussed in the literature are also considered.

3 Materials and Methods

In order to describe the distribution of *Ficopomatus enigmaticus* in the southern Baltic Sea, samples were taken from the coast of Mecklenburg-Western Pomerania. Since the species only settles on hard substrate (Bianchi et al., 1995), examinations were mainly carried out in harbors, on jetties, sheet pile walls and bridge piers. Shores with stockpiled stones were also used as investigation sites (see Tab. 1 & 2).

The first sampling took place within the annual coastal monitoring of the Leibniz Institute for Baltic Sea Research from April 12 to 15, 2021. The monitoring covered stations on the peninsula Fischland-Darß-Zingst, on the islands Usedom, Rügen and Poel as well as in the area of the cities Rostock, Stralsund, Wismar and Greifswald (see Fig. 1A).

The water movement was very different depending on the location. In most harbors there was hardly any wave motion, while at jetties or bridge piers jutting out into the sea there was more wind-induced water flow (e.g. Ahlbeck pier).

In order to be able to discuss other abiotic factors related to the occurrence of *F. enigmaticus*, temperature, salinity and oxygen content of the water were determined at each station by using a portable conductivity measuring instrument (WTW Cond 1970i, Xylem Analytics) and a multimeter (HQ40d, HACH). Water temperature at a depth of approximately one meter ranged from 6.5 °C to 8.3 °C, and oxygen content averaged 11.87 mg/l. While oxygen content and temperature were similar at all stations, significant differences can be seen regarding salinity, which ranged from 1.5 PSU to 14.1 PSU (see Tab. 1). This is due to the fact that some samples were taken in lagoon waters while others were collected in the Baltic Sea. The study sites at Müggenburg, Dierhagen, the Zecherin Bridge and Kamminke are located at a lagoon. In addition, the sampling locations in Greifswald and Rostock are located slightly upstream and not directly on seawater, which also results in a lower salt content.

Through the use of a pile scraper at these study sites, a good overview of the flora and fauna attached to the substrate was obtained. The device consists of a blade fixed to a stick. Under the cutting edge, a water-permeable bag is attached, which serves to collect the scraped biomass (see Fig. 2A). Limited by the stem length, samples could be taken down to 1.5 m water depth.

The scraped material was subsequently checked for the presence of calcareous tubes built by *F. enigmaticus*.

On April 16, 2020, a further investigation took place at different stations of the Lower Warnow River, from its beginning to its mouth into the Baltic Sea. The sampling sites are shown in Figure 1B. In total, this part of the river measures about 13 km in length. The beginning is located at the Mühlendamm, where the upper part of the Warnow River, which contains fresh water, is separated from the brackish lower course by a weir. At this location, there is only little water movement, which rises towards the estuary due to the increasing width of the river and commercial navigation.

At various stations, at which partly already tubes of *F. enigmaticus* were found in the previous year (Hille et al., 2021), samples were also taken by means of a pile scraper. Mainly, the sampled substrates were landing stages of small harbors made of the materials stone, metal or plastic (see Tab. 2).

According to the harbor master of the city harbor east in Rostock, many boats moored there were infested with the polychaetes in 2020. For this reason, organic material was viewed which was found on the hulls of two boats that had been docked in the water since 2020.

On April 28, 2020, additional surveys were conducted at six sites of the Lower Warnow River using a Remotely Operated Vehicle, hereafter referred to as ROV (Blue ROV 2; Blue Robotics). Equipped with a camera, this device (see Fig. 2B) allowed searching for calcareous tubes at depths that could not be reached by the pile scraper. Images were taken every two seconds, which were then evaluated for the presence of the tubes of interest. To have a scale on the photos taken, a frame with the dimensions 20*20 cm was attached in front of the ROV.

As during the previous sampling, water movement was found to be increasing towards the river mouth. With increasing proximity to the Baltic Sea, the salinity also became higher. The salt content measured on the sampling day reached its maximum in Warnemünde with a value of 9.8 PSU. Oxygen content and temperature did not show many differences at these stations either. The temperature ranged between 9.6 °C and 11.8 °C. At the site with the lowest oxygen content, the amount measured was 10.83 mg/l while the highest value reached 13.3 mg/l, as shown in Table 2.

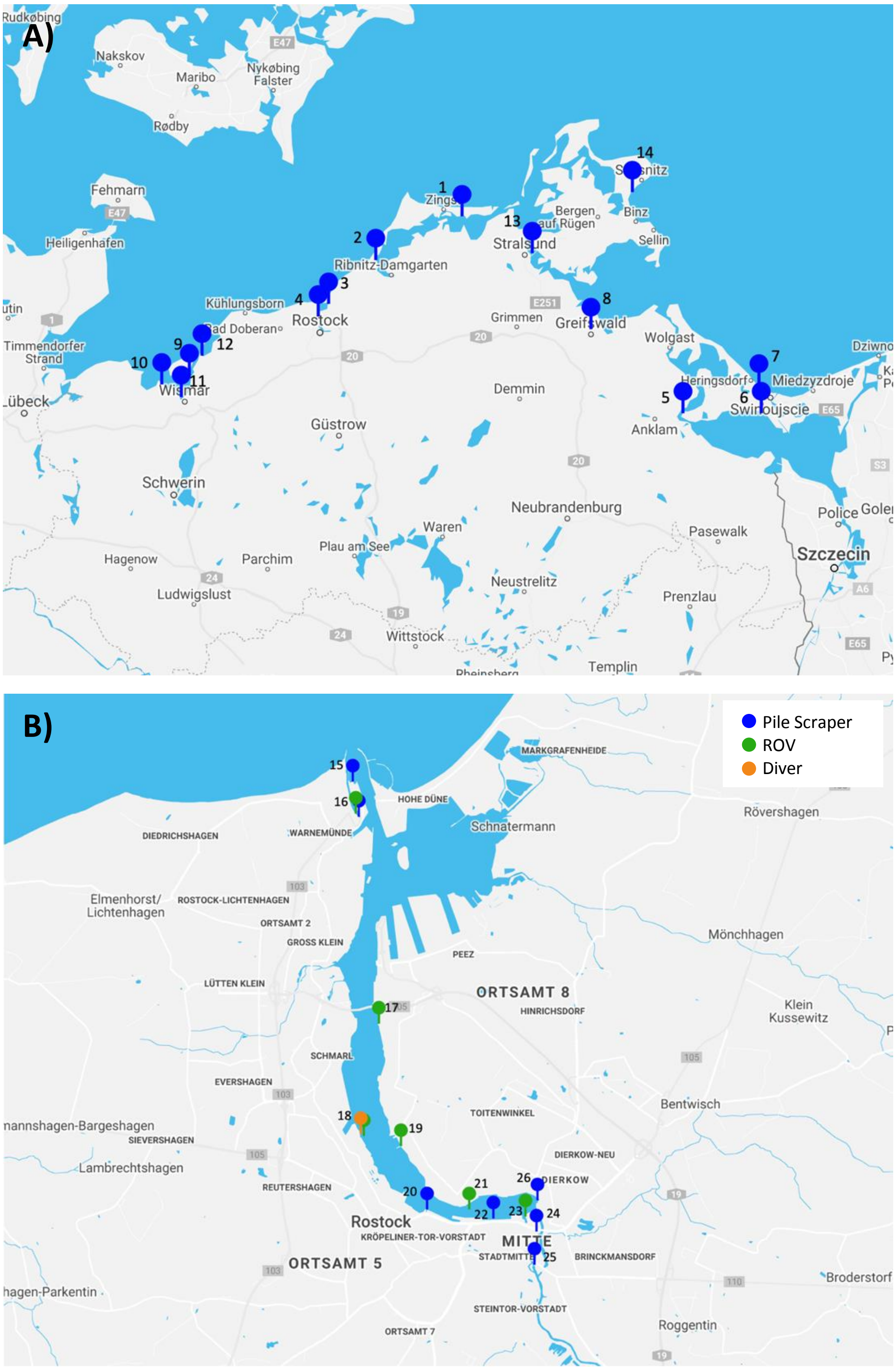

Figure 1: Sampling sites along A) the coast of Mecklenburg-Western Pomerania and B) the Lower Warnow River.

Finally, a last sampling by two divers took place in the Bramow Marina (site 18) on May 4, 2021. Organic material was scraped off a metal pile, previously investigated with the ROV, at intervals of half a meter each. The pier where the sampling took place extends several meters into the river and the pillar faces the current, but the water movement is calmed by another

pier that shields the sampled site from the waves. Water temperature and dissolved oxygen content of the water decreased with increasing water depth, while salinity became higher with increasing depth (see Tab. 3).
The water depth at the site amounts 4.5 m, but since the lowest half meter is covered with mud, the deepest sample was taken at 4 m water depth. The growth was removed from a square area of 400 cm^2 marked out by a frame with the dimensions 20*20 cm and collected in bags. On shore, the samples were rinsed through a sieve with a mesh size of 1 mm and transferred into sample containers with the help of a funnel. Afterwards, the organic material was fixed with 50 ml of 35 % formaldehyde solution. In combination with the water present in the receptacle due to flushing of the sieve, a final concentration of approximately 4 % fixative was obtained. Also, marble chips were added which served as a buffer so that the calcareous tubes did not dissolve.

As described for the first investigation, temperature, salinity and oxygen content were also measured at most subsequent study sites. This does not apply to sampling by the pile scraper along the Lower Warnow River. Dissolved oxygen could only be measured up to a water depth of 2.5 m due to technical limitations.

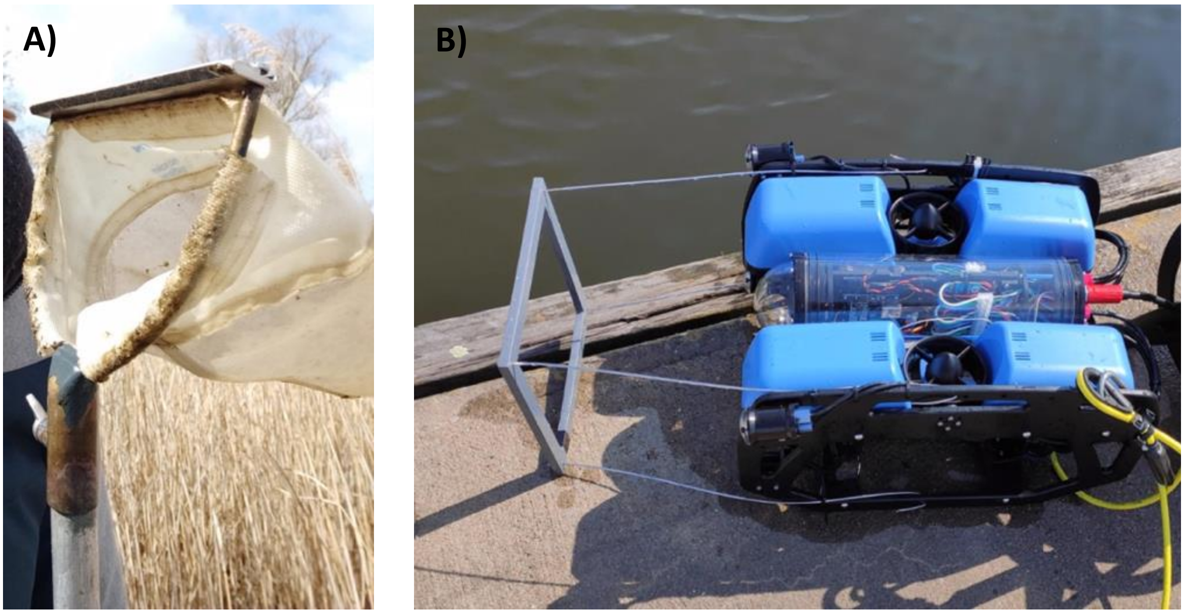

Figure 2: Sampling devices. A) Pile scraper. B) Remotely Operated Vehicle.

The aim of the sample analysis in the laboratory was, first, to investigate whether the tubes found were inhabited by *F. enigmaticus* and, if so, how the species was distributed vertically in the water column. Secondly, the qualitative and quantitative investigation of the associated fauna and the determination of their biomass were of interest. The analysis was limited to macrozoobenthos. This term is generally understood to include all animal individuals that live on or in the soil or on a substrate and are retained by a sieve with a mesh size of 1 mm (Bundesamt für Seeschifffahrt und Hydrographie, 2018).

As the first step the sample was rinsed again. A sieve with a mesh size of 0.5 mm was used for this purpose. Small portions of the oversize material were then covered with water in a separation bowl and studied under the binoculars (SteREO Discovery.V8) with a magnification of 10 to 30 times. Using forceps, all faunal individuals were collected from the bowl and presorted by taxa. Special attention was paid to the species *F. enigmaticus*. To find out whether the scraped tubes were inhabited or empty, they were broken. When a tube worm was found, it was carefully pulled out of the tube by using two forceps. After removal from the tube, completely preserved animals were measured with respect to their length, and in the case of unbroken tubes, the diameter of the opening was determined. The total length of 74 worms and the diameter of 49 tube openings were measured.

Afterwards, the exact morphological identification and counting of the organisms took place. In this process, the heads were counted so that torn animals were not recorded more than once. Since hydrozoans and bryozoans form colonies and the single individuals are difficult to count, only their presence was recorded. As not all organisms could be identified to species level, a higher taxon was sometimes listed. For a more meaningful result, the abundances of *F. enigmaticus* were extrapolated to an area of 1 m^2.

Water from the previous investigations in the separation bowl adhered to the animals. In preparation for the determination of wet weight, this water was removed by placing the animals on absorbent paper. During subsequent weighing, the mass of all animals of a sample belonging to the same taxon was determined at once. If there were significantly more than 100 individuals of a taxon in a sample, only 100 of them were weighed, and afterwards the value was extrapolated to the total number. Mussels were weighed with their shell.

For weight determination, an analytical balance was used (Sartorius Cubis® MSA225S). To obtain an accurate result, the scale was tared to the weighing dish before each measurement. The laboratory analysis of the samples was carried out in accordance with the standard operating procedure of the analytical group macrozoobenthos of the Leibniz Institute for Baltic Sea Research Warnemünde (Zettler, 2018).

Using ZEISS microscope software ZEN, images of the object viewed through the binoculars could be taken and processed.

Within the time available for this work, it was not possible to carry out a larger practical component. For this reason, in addition to the methodology described so far, a literature study covering various topics was carried out (see Fig. 3), the contents of which are taken up in the discussion.

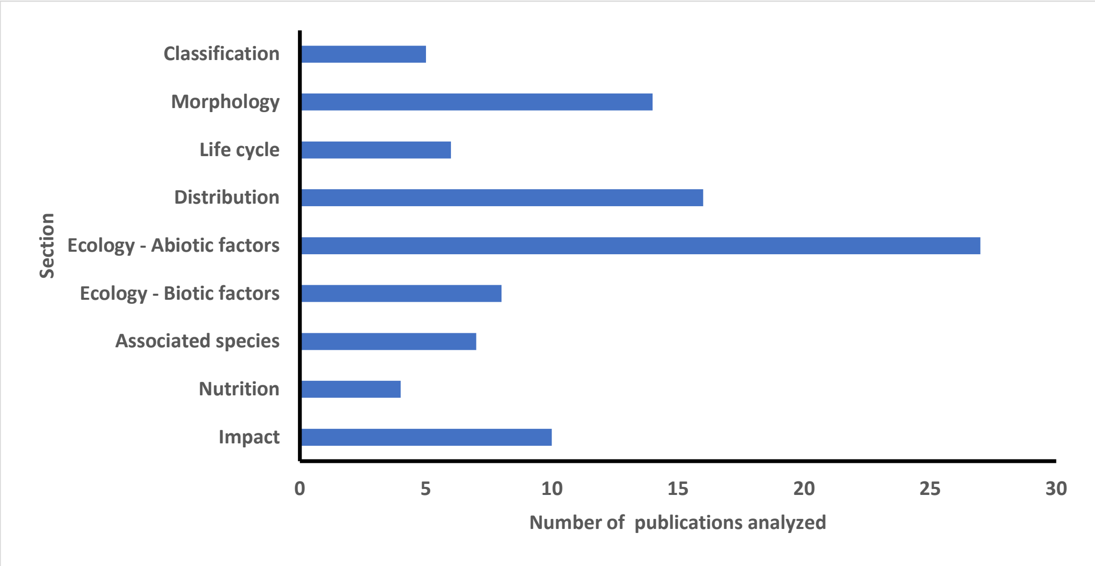

Figure 3: Number of publications analyzed per chapter in the discussion section.

4 Results

No tubes of *Ficopomatus enigmaticus* were found during sampling by means of pile scrapers as part of the coastal monitoring (see Tab. 1). Although some of the substrates were densely covered with other organisms, like barnacles and mussels, there was no evidence for the settlement of the tube worm. Scraping off the substrate at site 12 (Boiensdorf holm) also showed little fouling by other organisms, unlike most of the other stations.
In Stralsund-Dänholm (site 13), according to the harbor master, no tubes were found on the boats that were taken out of the water the previous year (2020) in autumn.
In Hohen Wieschendorf (site 10), in addition to the scratch sample, there was the opportunity to inspect three boats lying on land, which were in the water in 2020 and had not been cleaned up at that time. No evidence of calcareous tubes could be found at this site either.

Similar to the coastal monitoring, the analysis of the Lower Warnow River by scraping off fouling did not show any tubes of *F. enigmaticus* (see Tab. 2).
No evidence of tubeworm presence was found at the harbor near the Vorpommernbrücke (site 24) in Rostock last year either, according to the local harbormaster, so this result was not surprising. However, at other locations, such as site 22 (city harbor east), a finding would have been expected based on previous sightings (Hille et al., 2021).

In contrast to the prior examinations, tubes of *F. enigmaticus* were found during the underwater survey using the ROV. The largest population was recorded at the Bramow Marina (site 18). At the Neptun Marina in Gehlsdorf (site 19), several tubes could also be detected on the photos (see Fig. 4A), while at site 23 (Holzhalbinsel) only single constructs were found on a boat hull. No occurrence was registered at the other stations.

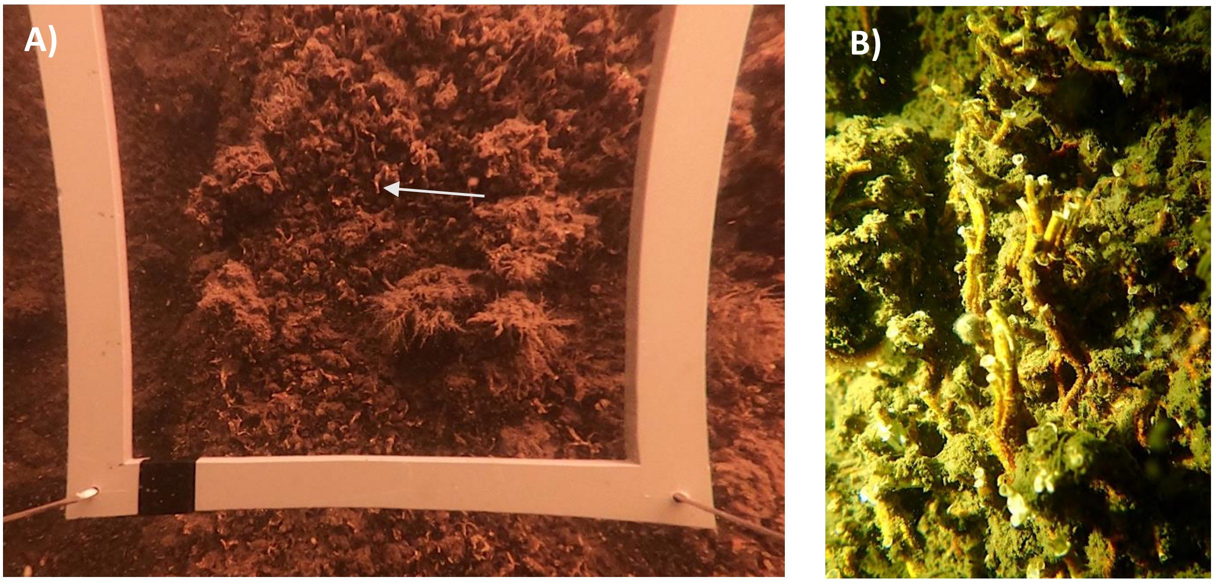

Figure 4: Occurrence of *Ficopomatus enigmaticus.* A) On a metal sheet pile at site 19 (Neptun Marina Gehlsdorf). Photo taken by the ROV at a depth of about 3 m. Frame size: 20*20 cm. Arrow points to a calcareous tube. B) On a metal pile at site 18 (SAB Bramow Marina) at a depth of 4 m. Photo taken by Phillip Hoy.

Because only site 18 (SAB Bramow Marina) in the Warnow River was sampled by divers at various depths, the following results and a part of the discussion are limited to this site.

The analysis of the samples taken by the divers at the Bramow Marina showed a clear result regarding the presence of *F. enigmaticus* in the depth profile.

Very few tubes were found in the first half meter below the water surface, and all of them were empty.

Slightly more tubes could be observed in the samples between 1 m and 2.5 m depth. Some of them were also empty, others contained black tissue fragments, indicating already well-advanced decay of the worms initially inhabiting the tubes. At a depth of 2 m below the water surface, additionally 2 preserved worms were found in the tubes, and the sample taken at 2.5 m depth contained 3 individuals that had not died before sampling.

At depths of 3 m and 3.5 m, significantly more tubes were found on the examined area of 20*20 cm. Although some tubes were also empty, more populated calcareous tubes were found than in shallower depths. Extrapolating the 65 worms counted in the sample taken at 3 m depth, it can be assumed that about 1625 individuals per square meter lived in this area. At a level of 3.5 m, with 51 individuals only a slightly lower number of worms was found. This results in an abundance of approximately 1275 worms in an area of one square meter.

Finally, at the deepest position where sampling took place, at a level of 4 m (see Fig. 4B), both the most tubes and, with a number of 163, the most individuals of *F. enigmaticus* were found. Projected, this results in an occurrence of about 4075 individuals per square meter. Despite this high number, there were still some tubes present that did not contain worms.

With increasing depth, not only the number of tubeworms grew, but also their length. In a depth of 3 m, the average body length of the worms showed 7.53 mm with a standard deviation of 1.63 mm. The longest animal measured 12 mm. 3.5 m beneath the water surface the average length amounted to 9.67 mm (standard deviation: 2.39 mm) with the longest worm showing a body length of 15 mm. Another half meter deeper, the worms measured 9.81 mm on average (standard deviation: 2.58 mm). At this depth, the largest length recorded was 16 mm. The lowest length measured 6 mm at all three depths.

No deviation of the average tube diameter could be detected, which would be caused by the depth. For all samples the diameter averaged 2.04 mm with a standard deviation of 0.29 mm. The operculum with the widest opening had a diameter of 2.8 mm, while the one of the narrowest opening measured only 1.2 mm.

While counting the individuals of *F. enigmaticus*, it was noticed that worms with three different appearances of the operculum occurred in the sample. Of a total of 84 animals, in which the structure of interest was well preserved and had not fallen off during examination, 80.95 % had an operculum with dark colored chitinous spines (see Fig. 5A). Organisms, whose operculum was covered with light, partly yellowish spines (see Fig. 5B), accounted for a proportion of 5.95 %. Unexpectedly, there was an additional form which showed a smooth surface and no chitinous spines at all (see Fig. 5C). This applied to 13.1 % of the animals examined.

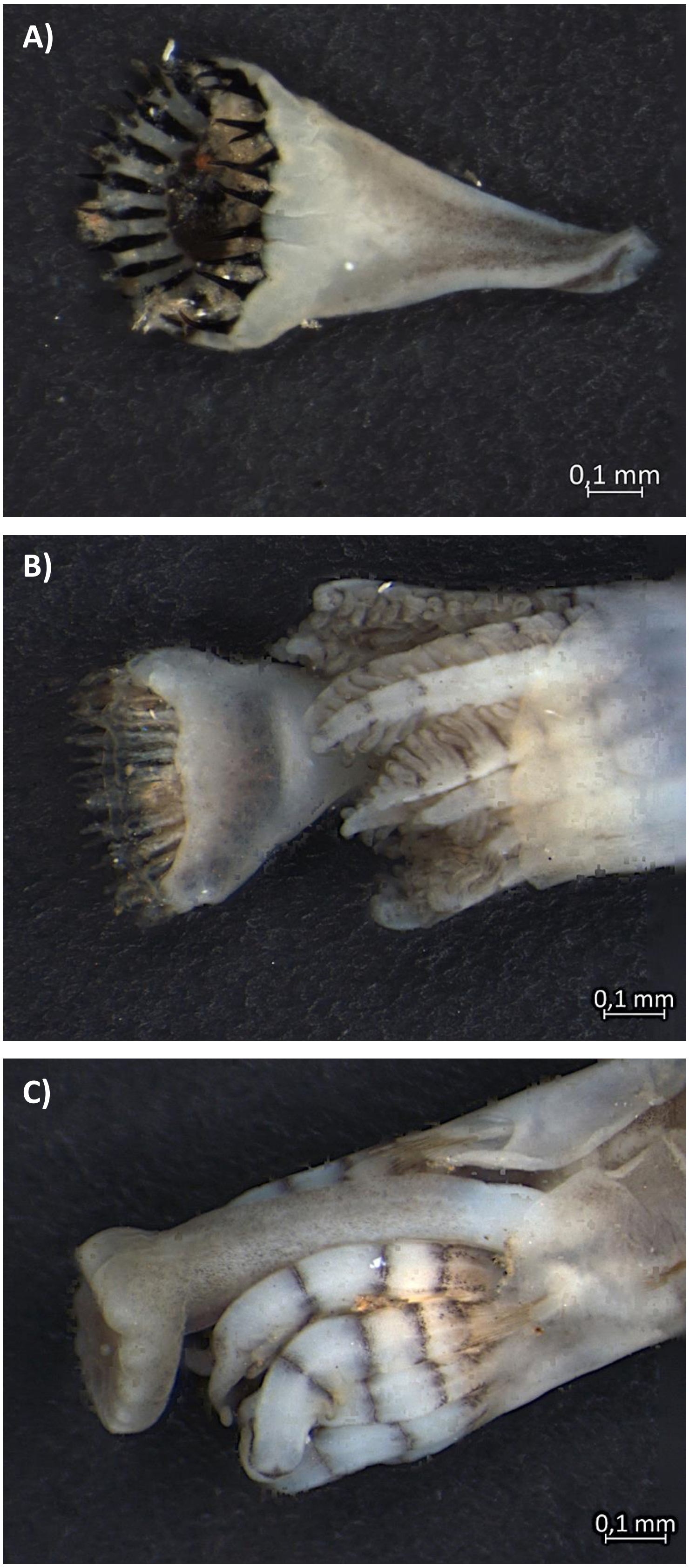

Figure 5: Operculum of *Ficopomatus enigmaticus* A) with dark chitinous spines, B) with light chitinous spines and C) without chitinous spines. Sampled at site 18 (SAB Bramow Marina).

Especially in the samples taken at depths of 3 m and 4 m, it was noticed that some calcareous tubes were overgrown by the bryozoan *Einhornia crustulenta* (Pallas, 1766). In some cases, even the openings of the tubes were overgrown (see Fig. 6), which probably led to the death of the worms, since only fragments of tissue and no preserved animals were found inside these tubes.

Figure 6: Tube of *Ficopomatus enigmaticus* overgrown with the bryozoan *Einhornia crustulenta* found at depth of 3 m at site 18 (SAB Bramow Marina).

A listing of all taxa found at the different depths, the number of individuals and their wet mass is shown in Table 4 to Table 11.

It was found that the abundance and the biomass of the fauna increased from the water surface to a depth of 2 m. While the number of species reached its maximum of 24 at 2 m depth (see Fig. 7), the maximum wet weight of the fauna, mainly due to *Amphibalanus improvisus* (Darwin, 1854) and *Mytilus edulis* Linnaeus, 1758, was found at a depth of 3.5 m (see Fig. 9).

The taxa containing the most species of all samples taken were Crustacea Brünnich, 1772, Annelida Lamarck, 1802 and Mollusca, as shown in Figure 7. Figure 8 illustrates that the largest number of individuals also belonged to these taxa. In terms of wet weight, crustaceans made up the largest proportion as well. However, mollusks accounted for the second largest biomass, followed by annelids (see Fig. 9). In addition to the size of the animals, this is because the mussels found were weighed with their shells.

Below a depth of 3 m, *F. enigmaticus* accounted for the second largest number of individuals behind *Fabricia stellaris* (Müller, 1774) within the Annelida (see Tab. 9-11). At the same depth, the tubeworm was a clearly perceptible component of the macrozoobenthos, in terms of abundance (see Fig. 8). With respect to biomass, the proportion of *F. enigmaticus* was significantly lower (see Fig. 9).

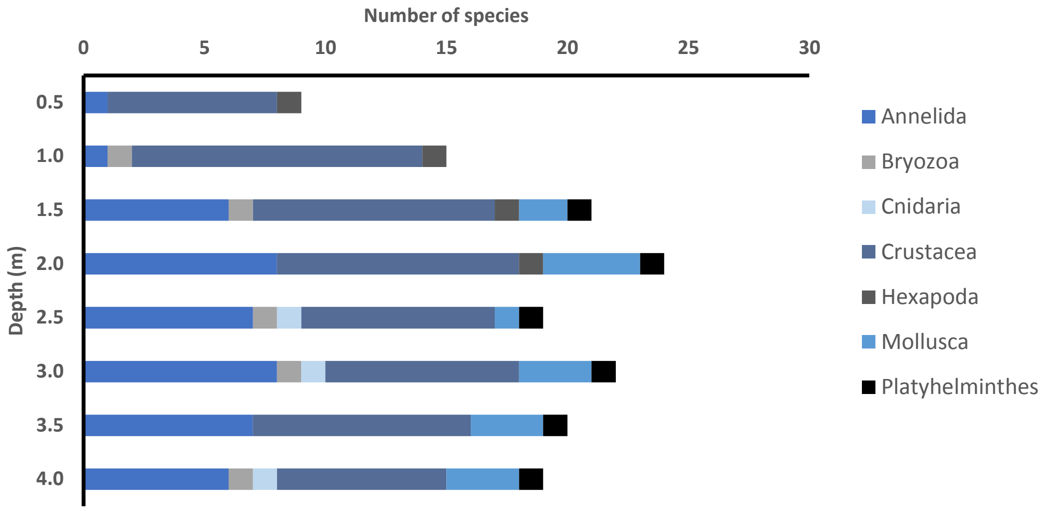

Figure 7: Proportion of taxa within the total macrozoobenthos community in the depth profile. Sampled from a metal pile at site 18 (SAB Bramow Marina). Some individuals could not be determined to species level. Platyhelminthes were not further identified and are treated as one species.

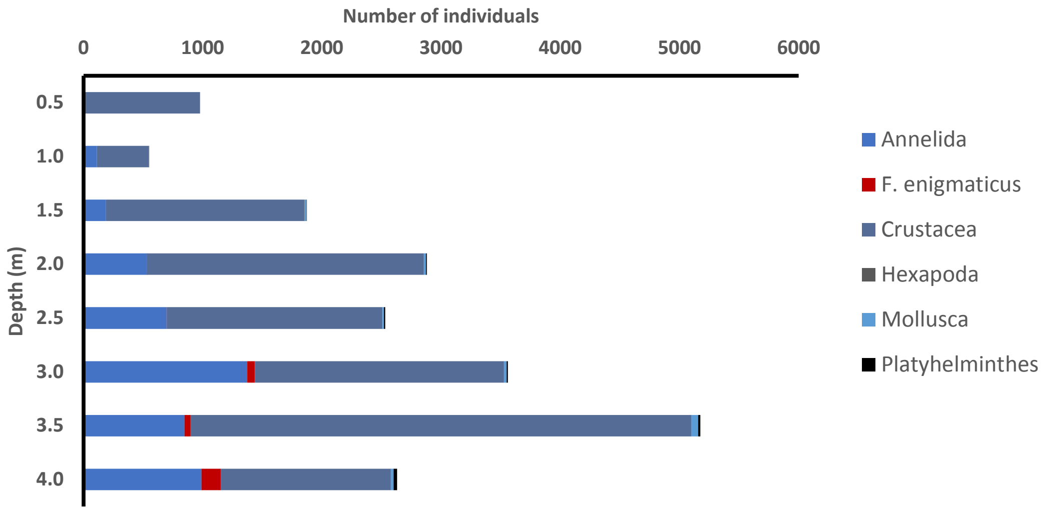

Figure 8: Number of individuals in the large taxonomic groups within the depth profile. Sampled from a metal pile at site 18 (SAB Bramow Marina). The proportion of *Ficopomatus enigmaticus* is highlighted. Bryozoans and hydrozoans (cnidarians) are not listed as their abundance was not recorded.

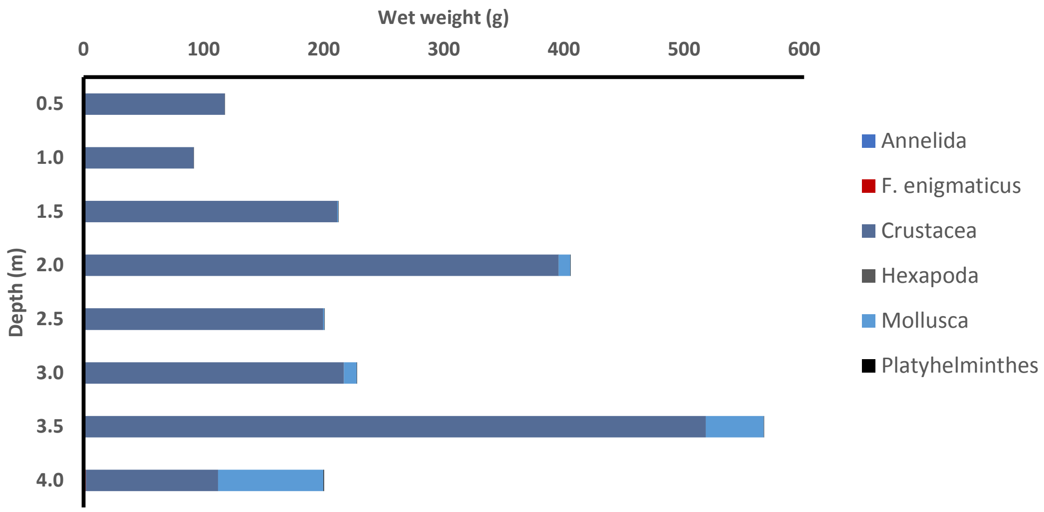

Figure 9: Wet weight of the large taxonomic groups within the depth profile. Sampled from a metal pile at site 18 (SAB Bramow Marina). The proportion of *Ficopomatus enigmaticus* is highlighted. Bryozoans and hydrozoans (cnidarians) are not listed as their weight was not recorded.

5 Discussion

5.1 Classification

Kingdom: Animalia
Phylum: Annelida Lamarck, 1802
Class: “Polychaeta” Grube, 1850
Subclass: Sedentaria Lamarck, 1818
Order: Sabellida Levinsen, 1883
Family: Serpulidae Rafinesque, 1815
Genus: *Ficopomatus* Southern, 1921
Species: *Ficopomatus enigmaticus* (Fauvel, 1923)

Figure 10: Systematics of *Ficopomatus enigmaticus* according to the World Register of Marine Species (WoRMS, 2021).

As already mentioned in the beginning, the annelid first named *Mercierella enigmatica* was subordinated to the genus *Ficopomatus* several years after its first description, in 1978 (ten Hove & Weerdenburg, 1978).
Within the order Sabellida Levinsen, 1883, the species belongs to the family Serpulidae (see Fig. 10), which contains over 500 species in 70 genera that live sedentarily in calcareous tubes (ten Hove & Kupriyanova, 2009).

According to Bick (2021, personal communication), *Ficopomatus enigmaticus* represents a species complex. Styan et al. (2017) examined mitochondrial DNA sequences, more precisely cytochrome B haplotypes, from individuals of *F. enigmaticus* collected in southern Australia. They discovered three distinct genetic groups, each of which they suspected to represent a single species. No morphological differences were apparent between two haplotype clades, while the third was more similar to the closely related species *Ficopomatus uschakovi* (Pillai, 1960).

5.2 Morphology

Depending on the region in which they occur and the environmental conditions, the adult tubeworms can show different lengths. In this study, an average worm length of 9 mm was found, with length increasing slightly with depth. Since a similar increase was found in the number of settled worms, it can be assumed that both were due to better ecological conditions in the deeper zones. However, it is also possible that the different lengths are partly due to the age of the animals. The longest worms found measured 16 mm. For the English Channel coast Hartmann-Schröder (1967) described the longest animals with 27 mm. Hill (1967) concordantly discovered worms with a maximum length of 30 mm in Nigeria.

The coloration ranges from green to brown and varies in intensity (Hartmann-Schröder, 1967).

Ficopomatus enigmaticus is divided into prostomium, thorax and abdomen, which is typical for serpulids, but the prostomium is reduced. While the thorax constantly consists of 7 segments, the number of segments of the abdomen is variable (Hall, 1954). More than 120 segments can occur (Hartmann-Schröder, 1967).

The appendages of the peristome are transformed into a branchial crown. It consists of two extensions around the mouth. Both are usually divided into eight to ten radioles, each carrying double rows of ciliated pinnules (see Fig. 11A & 11C; Hall, 1954).

A special forming of the tentacle crown is the operculum, which is located on a shaft with a dorsal longitudinal furrow (see Fig. 11A & 11D). Since it is not calcified, it is soft and serves to close the tube (Hartmann-Schröder, 1967). Distally the operculum is covered with slender chitinous spikes bent inward (Sun et al., 2012). The coloration of the spines, which are arranged in one to seven concentric rows, can vary from yellowish to black (Hartmann-Schröder, 1967). In line with most authors describing the spines as black (e.g. Pernet et al., 2016; Styan et al., 2017), also in this work mostly dark chitinous spines were found. The fact that also a light cover of the operculum was found and partly the spines were even missing completely, can be due to different reasons. One possible explanation is that the individuals found belong to more than one species. But even though *F. enigmaticus* is considered a species complex, it is unlikely that more than one species has migrated into the Baltic Sea (Bick 2021, personal communication). Bick (2012) further stated that operculum variability in serpulids is not uncommon and occurs in many species. Sun et al. (2012) described an absence of chitinous spines as an exception. Pernet et al. (2016) discovered that the animals with lighter spines or uncovered operculum in his samples were juvenile animals, and for some individuals Gabilondo et al. (2013) also observed that the operculum does not develop spines until several weeks after its formation. Thus, it is also possible that these variations were due to different developmental stages.

The base of the crown is surrounded by the collar, which is a thin muscular lobe that folds back over the beginning of the thorax (Hall, 1954). The thoracic membrane is only fused ventrally and therefore protrudes laterally (see Fig. 11B). This lobe-like structure has wavy and entire margins (Hartmann-Schröder, 1967). Through the surfaces of the latter two structures, respiration occurs (Straughan, 1968).

To ensure that all vital processes can take place, virtually the entire body surface of the animal is covered with cilia (Hall, 1954). In addition, slightly curved, coarsely or finely toothed setae are found, especially on the thorax but also on the abdomen (Hartmann-Schröder, 1967).

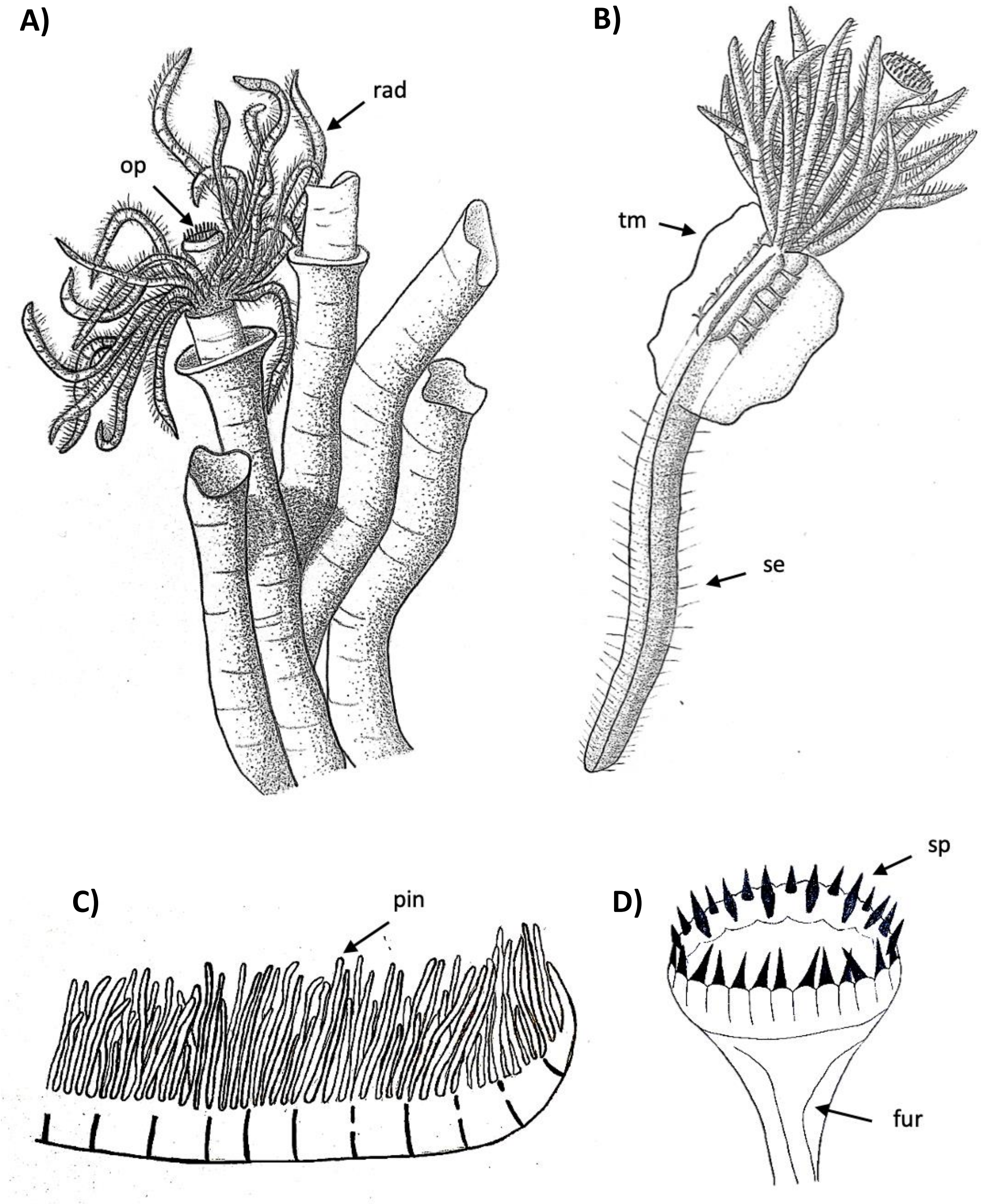

Figure 11: Morphology of *Ficopomatus enigmaticus*. A) Tentacle crown protruding out of the tube. B) Worm removed from the tube. C) Radiole. D) Operculum. Abbreviations: *fur* longitudinal furrow, *op* operculum, *pin* pinnule, *rad* radiole, *se* seta**,** *sp* chitinous spine, *tm* thoracic membrane.

F. enigmaticus secretes calcareous tubes, consisting of aragonite and calcite, at the collar region (Bianchi et al., 1995). Their length can be up to 200 mm, and they can reach a diameter of

1.6 mm (Martínez-Taberner et al., 1993). Hartmann-Schröder (1967) found a lower maximum length of 100 mm in England. According to Straughan (1972), the ratio between the length of the tube and the length of the worm ranges from 1.7 to 3.0, depending on the salinity and the concentration of calcium ions present in the habitat. The tube length could not be determined in this study because scraping off the growth during sampling did not result in fully preserved tubes.

At their base, the brownish tubes are very narrow, but the width increases up to the free end of the tube with a trumpet-like widened opening (Hall, 1954), whose diameter averaged 2.04 mm in the tubes found during this investigation.

The juvenile tube is initially membranous and calcifies only during growth. For this reason, it lies on the substrate and thus forms a half cylinder. Sometimes a longitudinal keel is found, and the tube shows ringlets (Hartmann-Schröder, 1967). On the tubes found in this work, no keel could be observed.

The likewise ringed adult tube is rarely recumbent, but usually orthogonal to the substrate (Hartmann-Schröder, 1967). The tubes consist of a thin inner layer and a thicker outer layer. They are formed from dense calcite lamellae (Fornós et al., 1997). If good conditions prevail, broad calcareous bands are added to the preexisting ones and the tube grows rapidly. Equally, slower growth occurs with less accumulation (Hartmann-Schröder, 1967). This results in irregular growth rings along the tube, which are very characteristic (Hall, 1954).

The tubes of *F. enigmaticus* are rarely isolated but form a colony that can vary in size depending on the prevalent circumstances. For example, in Australia Dittmann et al. (2009) discovered reefs ranging in size from 0.12 m^2 to 12.56 m^2 during a survey on Hindmarsh Island, and reefs measuring 0.049 m^2 on average during sampling in Clayton.

In terms of shape, three forms of growth can be distinguished. First, there is the upright form, in which the tubes are perpendicular to the substrate. The bundles that form grow parallel to each other or around each other. The second possibility is the crawling form. In this case, the tubes also grow parallel but are resting on the substrate and are partly completely fused with it. Finally, the reef may also occur in an undirected form. It is characterized by tubes growing in different directions and forming a clew. The shape a reef assumes depends on the density of larvae during initial settlement (Hartmann-Schröder, 1967).

Since the tubes did not rest on the substrate and the openings were mainly oriented in one direction (see Fig. 4B), the colony examined in this study represents the first form described, which grows upright. As particularly the undirected form indicates a high larval density, it can be assumed that there was no mass occurrence of larvae during the first settlement in the Warnow River.

5.3 Life cycle

In order to understand some aspects concerning the ecology of *Ficopomatus enigmaticus*, it is important to briefly consider its ontogenesis. Since these aspects could not be investigated in the present work, solely findings of other authors presented in previous studies are summarized.

The period of breeding lasts about six to seven months (Martínez-Taberner et al., 1993).

Tubeworms four to five millimeters in length are sexually mature (Straughan, 1972). After maturation, eggs and sperm are released into the water during neap tide (see 5.5.6), where fertilization finally occurs. The blastulae, which develop after the first cell divisions, subsequently evolve into free-swimming trochophores. Afterwards, the larvae grow and develop for approximately three weeks before settling (Straughan, 1968). The trochophores, mature for metamorphosis, attach themselves to a substrate using fine secretion threads and begin to form an initial membranous tube, into which calcareous material is subsequently deposited. With the construction of the tube, the development to the adult polychaetes takes place (Hartmann-Schröder, 1967).

In the Thames Estuary for example, in 1975 spawning took place from August to September. After fertilization, fission began at 20 °C after about two hours. Settlement finally started in October. The time during which the larvae lived free-swimming in the plankton thus totaled one to three and a half months in this area (Dixon, 1981). This period is significantly longer than Straughan (1968) described. Poor conditions, such as salinity or temperature that are too high or too low, may prevent larvae from maturing (Hill, 1967).

Depending on the location and its ecological conditions, one or more generations may occur per year (Dixon, 1981; Martínez-Taberner et al., 1993)

5.4 Distribution

As mentioned in the introduction, the exact origin of the species is unknown, but it is known that *Ficopomatus enigmaticus* is native to the southern hemisphere. More precisely, the origin is presumed to be somewhere along the coasts of Australia or the Indian Ocean (Nelson-Smith, 1967).
Meanwhile, the tubeworm is found in temperate and warmer areas in both the northern and southern hemispheres. There it inhabits waters of various salinities, but mostly brackish coastal areas (Eno et al., 1997).
The distribution takes place mainly via ships (Nelson-Smith, 1967), but the species is also partly introduced with other taxa imported for aquaculture, for example with oysters (Bailey-Brock, 1976). Therefore, the polychaete is now widespread throughout Europe (see Fig. 12A) and the world (see Fig. 12B). While present on all continents except Antarctica, *F. enigmaticus* is considered to be introduced in some places and even to be invasive in others, meaning it has a negative impact on the native ecosystem (CABI, 2021). As shown in Figure 12B, the species is mainly present in the Atlantic Ocean, the Indian Ocean, the Black Sea, the Mediterranean and the Pacific Ocean.

F. enigmaticus is broadly distributed in Europe as well. After the first description in France (Fauvel, 1923), discoveries followed for instance in southern England (including London), Wales, Ireland, Spain, Belgium, the Netherlands and Denmark (Friedrich, 1938; Vaas, 1975; Kühl, 1977; Zibrowius & Thorp, 1989; Eno et al., 1997).
In the western Baltic Sea, the first finding of the tubeworm occurred early after the initial description. For example, it was found on the Danish island Ærø in 1939 (Wesenberg-Lund, 1941, cited from Jensen & Knudsen, 2005) and in the Kattegat and the Belt Sea in 1953 (Streftaris et al., 2005).
The first time the species was described for Germany was in 1977 by Kühl. It was assumed that the settlement in Embden was possible due to thermal emission of a nearby power plant. Nehring and Leuchs (1999) stated that the tubeworm can only settle in temperate latitudes in the vicinity of anthropogenic heat input. Due to climate change and the associated warming of water bodies, this can probably no longer be assumed. This assumption is also supported by the occurrence of *F. enigmaticus* in the Trave Estuary in 2015 without exposure to additional heat. The occurrence in this area was the first time the species was recorded in the southern Baltic Sea (Bock & Lieberum, 2016).

The first major appearance in the Warnow River was found in fall 2020, primarily on ship hulls and other metal or wooden substrates. Thereby the tubes were mainly not found directly at the river mouth but slightly further upstream. The highest occurrence was located in the Bramow Marina (Hille et al., 2021). The same applies to this study. The first river level where *F. enigmaticus* was detected (site 18, SAB Bramow Marina) is located approximately 7 km away from the mouth. At site 17, the old ferry terminal, which is situated 2 km further downstream, the species was not found.

Before 2020, *F. enigmaticus* only occurred in low abundance in 2016 and 2019 and temporarily disappeared in between (Institut für Angewandte Ökosystemforschung, 2020).

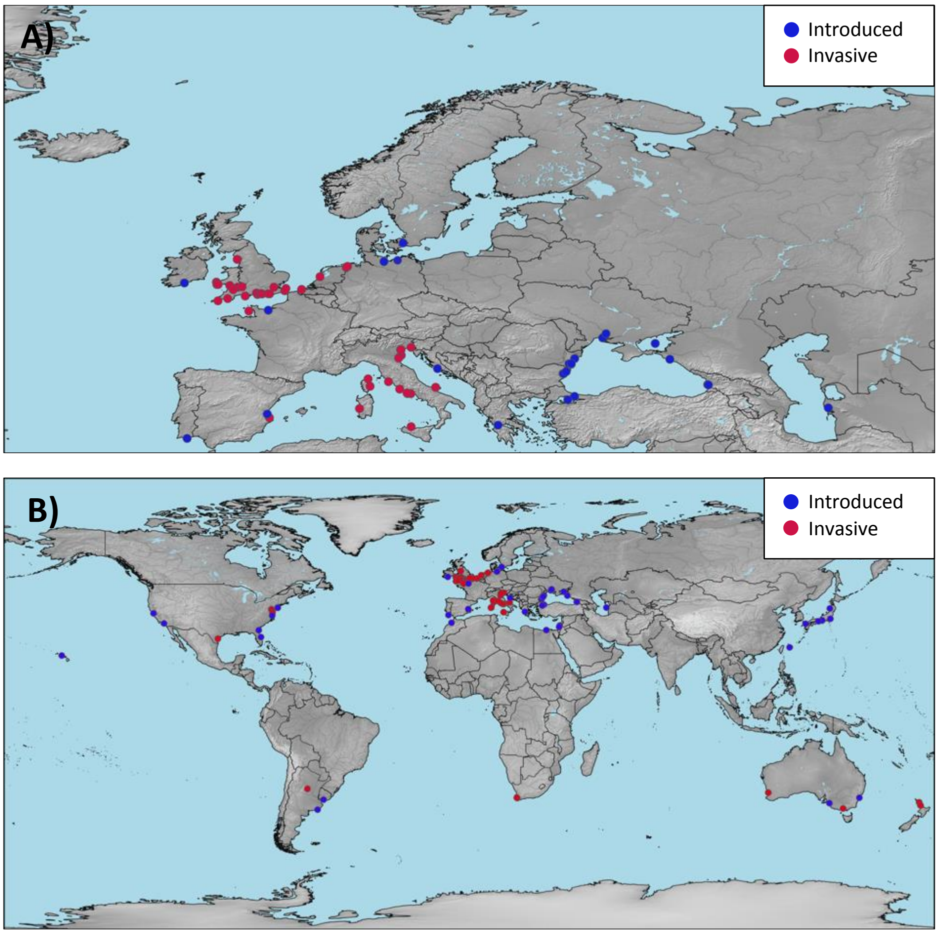

Figure 12: Distribution of *Ficopomatus enigmaticus* A) in Europe and B) globally. Markings do not show exact locations but regions where the abundance is recorded. Tagging in Ukraine is exemplary for numerous sites on the coast as well as in inland marine waters. Since the assumed origin of the species from the Australasian area is not confirmed, the distribution in this area is described as invasive. Created according to Bastida-Zavala et al., 2017; Zettler & Zettler, 2017 and CABI, 2021.

5.5 Ecology - Abiotic factors

5.5.1 Temperature

In waters of temperate climates, the distribution of *Ficopomatus enigmaticus* is limited mainly by the present temperature (Hill, 1967). Actually, the species prefers tropical to subtropical climate (Hartmann-Schröder, 1967). There the period of reproduction is significantly longer than in colder areas (Dixon, 1981).

According to Hartmann-Schröder (1967), the temperature mainly influences two processes, first the maturation of the gonads, which requires at least 18 °C to 20 °C, and second the development and attachment of the trochophore, which also needs a minimum temperature of 18 °C. This is also supported by Straughan's (1972) observation that the first settlement in the Brisbane River begun at the earliest three weeks after temperatures have risen to 18 °C to 19 °C. In addition, he discovered that the growth rate also increased significantly with a rising temperature. Equally, Schwindt et al. (2004) described stronger reef growth during the summer months than in the cold seasons as well.

Thorp (1987), on the other hand, described larval settlement for Emsworth starting at 10 °C to 12 °C. In addition, he drew a connection to the presence of phytoplankton. He concluded that with increasing temperature and solar radiation algal blooms accompany and provide food for *F. enigmaticus*. One week after the proliferation of phytoplankton he could observe settlement of larvae.

However, the maturation of gametes, which takes about half a year, is triggered during a period of lower temperatures and short days. In the Thames Estuary in 1975, temperatures were around 9 °C when maturation began (Dixon, 1981).

Excessively cold temperatures in winter can lead to total population loss (Nehring & Leuchs, 1999).

As in summer the cold water of the Baltic Sea is layered under the warm water from the Warnow, stratification occurs. According to Thäns (2012), in 2011 temperature rose to values of 17 °C to 19 °C in June and July, with the surface water showing the highest temperatures. Before, temperatures prevailed that would not be sufficient for the reproduction of *F. enigmaticus*. In August, 18 °C to 20 °C were measured in the entire river course of the Lower Warnow.

In winter, strong stratification is avoided by convection. In December 2016, water temperatures ranged from 4 °C to 8 °C between Warnemünde and Gehlsdorf and from 2 °C to

6 °C from Gehlsdorf to Mühlendamm. The surface water up to the Seaport was recorded to reach temperatures of 2 °C to 4 °C (Seiß & Boehlich, 2019).
These temperatures are just sufficient for the establishment of *F. enigmaticus*, which could be the reason why the species does not seem to be so widely distributed in the Warnow River yet. However, as water temperatures rise due to climate change, it is expected that conditions for the species will continue to improve in terms of temperature in the future.
Since between 1 m and 2.5 m water depth only worms were found in which the decomposition process was already advanced, it is assumed that they already died some time before sampling. The previous winter was quite cold, and the water surface partially froze over, so it is suspected that this was the cause of the death. Because the temperature was probably even warmer in deeper water layers, as described by Seiß and Boehlich (2019) for winter 2016, the individuals settled there were able to survive.
This situation seems to occur at other locations as well. Styan et al. (2017) observed recolonization of shallower water depths in Australia after cold winter temperatures. The larvae originated from reproduction of the deeper settled worms which survived the cold.

5.5.2 Salinity

Although *Ficopomatus enigmaticus* is an euryhaline organism, salinity is an important factor determining its distribution. The species can occur in hypersaline marine water as well as in freshwater, but a medium salinity is preferred. It was observed that the largest tubes of the species are found in brackish water (Hartmann-Schröder, 1967).

In his study 1967, Hill pointed out that each physiological process has its own optimum, so that compromises must be made, also regarding the salt content. Only in this way all important processes in the animal can run to the extent necessary.
Overall, *F. enigmaticus* as an osmoconformer can survive in a salinity range of 1 ‰ to 55 ‰ (Skaer, 1974), but this does not imply that it can establish itself under these conditions. For example, sperm is not active in fresh water. However, while fertilization is possible at comparatively low salinities, fertilized eggs need even higher salinities to develop into trochophores. This occurs at salinities of 6 ‰ and above. In marine waters, development to larvae proceeds without problems, but adults that are permanently exposed to such high salinities are unlikely to reproduce (Straughan, 1972).

According to Straughan (1968), larval settlement occurred in the Brisbane River in Queensland at salinities of 10 ‰ to 30 ‰. Bailey-Brock (1976) described the strongest settlement on Hawaiian Islands in a range between 9 ‰ and 23 ‰.
Negative effects of salinity levels outside the optimum of *F. enigmaticus* occur only in case of lasting poor conditions. The tubeworms are tolerant of diurnal fluctuations (Hill, 1967).

Salinity influences both the area of the estuary and the height of the water column at which trochophores settle. The latter is mainly dependent on the stratification of the water body, while freshwater inflow and precipitation determine the proximity of settlement to the mouth of a river or the opening of a lagoon to the sea (Straughan, 1972; Thorp, 1987).
The salinity in the Warnow River is mainly dependent on the freshwater inflow coming from the upper part. At higher water levels and strong onshore winds, more water enters from the Baltic Sea, but this is mainly absorbed by the Breitling, which is an extension of the river near its mouth. In December 2016, the salinity at the mouth of the Warnow River averaged 16 ‰ and decreased continuously up to the Mühlendamm. There, the average salinity was only 1 ‰. At the same time, near site 18 (SAB Bramow Marina), a clear depth gradient was present, ranging from 8 ‰ in surface water to 11 ‰ near the soil. This gradient occured throughout the Lower Warnow River as cold saline Baltic water was stratified underneath the freshwater of the river (Seiß & Boehlich, 2019). The largest abundances of *F. enigmaticus* found during the present study were in a range of salinities between 12.1 ‰ and 12.6 ‰ at Bramow Marina (see Tab. 3). Thus, the salinity at this location was higher than measured in 2016. The lower salinities in higher areas of the water column (see Tab. 3) could be another reason for *F. enigmaticus* preferring deeper levels, besides the winter temperatures (see 5.5.1).

5.5.3 Dissolved oxygen content

Since *Ficopomatus enigmaticus* has a high tolerance towards a broad range of dissolved oxygen (Fornós et al., 1997), this factor has only a minor influence on the distribution of the species. It can occur in a range of 1 mg/l to 14 mg/l, with the optimum being between 6 mg/l and 8 mg/l (CABI, 2021).
As the concentration of dissolved oxygen decreases with depth and thus becomes increasingly distant from the optimal range, hardly any reefs are found in the zone near the bottom of

waters which are low in oxygen. There, anoxic conditions may occur periodically, under which the tubeworms cannot survive (Martínez-Taberner et al., 1993).
From the surface water down to a depth of 2.5 m, the oxygen content of station 18 (SAB Bramow Marina) decreased by 1.61 mg/l and amounted 8.85 mg/l at this depth. Therefore, it can be assumed that even up to 4 m depth there is a dissolved oxygen content that can be well tolerated by the species.

5.5.4 pH value

According to Bianchi and Morri (2001), *Ficopomatus enigmaticus* tolerates low pH values. The scope in which the animals can live ranges from 4 to 9 (Oliva et al., 2019). Because the species' calcareous tubes are formed from calcium carbonate, they would dissolve if the pH value dropped even further (Dittmann et al., 2009).

In three measurements near the bottom in 2017, the pH value in proximity to the weir averaged 7.6 and slightly upstream of the Breitling it had an average of 7.7. At the level of the Bramow Marina (site 18), the mean pH measured 8.0 with a minimum of 7.6 and a maximum of 8.6 (Institut für Fisch und Umwelt, 2017). Thus, the values are within the range tolerated by
F. enigmaticus.

5.5.5 Substrate

The larvae of *Ficopomatus enigmaticus* can only attach themselves to hard substrate. Due to its introduction by boats, the species is mainly found on their hulls and harbor structures (Nelson-Smith, 1967). In general, organic and inorganic substrates are used as basis for tube construction. In addition to debris, rocks, ropes and stakes consisting of metal, stone or wood, tubes are also found on dead barnacles and bryozoans (Straughan, 1972). During this survey along the Lower Warnow River, tubeworms were mainly found on metal substrates in harbor facilities. There, however, the tubes could also be discovered on shells of *Amphibalanus improvisus* and *Mytilus edulis*. Additionally, a rope was used as substrate (see Tab. 2). Mud,

on the other hand, does not have the necessary stability to serve as a substrate (Straughan, 1972).
Near the shore, parts of trees and macrophytes protruding into the water can be colonized (Martínez-Taberner et al., 1993). Trochophores can also attach to pre-existing tubes of their own species, creating large aggregations (Bianchi et al., 1995). Even human waste, such as bottles, can serve as substrate for the tubeworm, according to Schwindt (2001, cited from Schwindt et al., 2004).
Depending on the kind of substrate, the shape of the reef may vary (Martínez-Taberner et al., 1993).

The larvae prefer surfaces with a thin film of microorganisms for colonization. Microbial growth should have begun at least one week prior to colonization but should not exceed one month. After this time, the biofilm is excessively pronounced. The time after which the optimum growth is achieved depends, among other things, on the roughness of the surface (Straughan, 1972).
In addition to the cover with microorganisms and the hardness, also texture and orientation of the substrate is important. Thus, colonization tends to occur on a dark and opaque substrate, and rough textures are preferred over smooth ones (Straughan, 1968). Furthermore, substrates that are only exposed to low currents are suitable, for example those oriented towards the shore (see 5.5.6; Straughan, 1972).

The level in the water column at which settlement on the substrate occurs seems to vary regionally. For the Magra Estuary in the Po River, for example, a depth from the water surface to 2 m was described (Bianchi & Morri, 1996). This agrees with the statement of Hartmann-Schröder (1967), *F. enigmaticus* prefers to settle near the water surface. As a result, animals exposed to the air die when water levels temporarily fall (Martínez-Taberner et al., 1993).
In contrast to the previously mentioned authors, Martínez-Taberner et al. (1993) described reefs in the Albufera of Menorca in the Balearic Islands up to a depth of 3 m, and in the German Warnow River tubes were found even up to 4.5 m and occurred no higher than 1 m below the water surface (Hille et al., 2021).
The results of the present investigation agree with the observations mentioned last. Tubeworms were mainly found at a depth of 3 m to 4 m. However, tubes with decayed

remains of worms suggest that previously individuals of *F. enigmaticus* also lived up to one meter water depth.

5.5.6 Current

Ficopomatus enigmaticus only occurs in areas where at most gentle, steady water movement occurs. Non-constant wind and tidal disturbances are more frequent at settlement sites (Hartmann-Schröder, 1967). Schwindt et al. (2004) described a lagoon in the Atlantic Ocean where the tubeworms grew faster and larger in the calm water inside the lagoon than in the outer area. Likewise, in the Po River Delta, reefs showed greater development when they were not under the direct influence of flowing marine or fresh water (Bianchi & Morri, 1996). In order not to be directly exposed to the current of a water body, reefs are often located on substrates that do not face the flow and point towards the shore. In these locations, where the flow is less, settlement is possible higher in the water column (Straughan, 1972).

Apart from a possible destruction of the tubes, which can only occur through strong water movement, current is an obstacle to fertilization of the released eggs. It is assumed that for this reason the gametes are predominantly released during the neap tide in areas with pronounced tides. The low water movement increases the probability that sperm and egg can fuse (Straughan, 1972). The timing of such a precise moment of gamete release seems to be less important in the Baltic Sea, where hardly any tides occur.

Currents also influence the settlement of larvae. If the freshwater flow from an estuary is very low, salinity in the river increases and settlement occurs further upstream (Straughan, 1968 & 1972). In case the current speed exceeds 0.29 m/s, the trochophores are flushed away and cannot settle (Straughan, 1972).

According to the Federal Waterways Engineering and Research Institute (Seiß & Boehlich, 2019), the current in the Lower Warnow River is created by the river discharge, water level changes in the Baltic Sea and, most importantly, the density gradient that results from the stratification of dense Baltic Sea water over the freshwater of the Warnow, which is less dense.

Depth-averaged current velocities typically range from 0.1 m/s to 0.2 m/s and are exceeded only in the estuary area. There, in exceptional cases, velocities can reach 0.5 m/s. Accordingly, flow does not appear to be an obstacle to the establishment of *F. enigmaticus* in the Warnow River, except within close proximity of the mouth.

5.5.7 Pollution

Ficopomatus enigmaticus also appears to be tolerant of various types of pollution.

For example, for years the species was found in the Lake of Tunis. The water body was very polluted because large amounts of wastewater were injected into it (Keene, 1980). However, after attempts were made to remedy the pollution by changing hydrological conditions, temperature, salinity and amount of organic material also changed. This seemed to adversely affect the tubeworm more than the previous pollution, and consequently it disappeared from the lagoon (Diawara et al., 2008).

Also, in the Spanish Estuary of Bilbao, the polychaetes live under the influence of both domestic and industrial pollution. Even the heavy metals present in the water do not impede the distribution of *F. enigmaticus* in this area (Bustamante et al., 2007).

Johnston and Keough (2003) described the response of the tubeworms to the introduction of copper into surrounding waters. The chemical element is a common ingredient in waste ending up in the environment and is also contained in antifoulants. The animals were exposed to 1.6 g to 3.1 g copper II sulphate anhydrous at four-week intervals. The settlement plates were located directly next to the copper source. Ultimately, the species was found to be insensitive to this amount and frequency of copper input.

In the Brisbane River, Straughan (1972) found that, in line with previous findings, the influence of sewage and fat waste from a neighboring butcher had no effects on *F. enigmaticus* populations. However, contamination of the water with oil caused a decrease in the population.

5.6 Ecology - Biotic factors

5.6.1 Competition

Because *Ficopomatus enigmaticus* can tolerate a wide range of salinities, there is little competition from other serpulids, which can hardly tolerate fluctuations. Tolerance towards pollution and low dissolved oxygen levels also results in low competition in several areas (Eno et al., 1997).

Straughan (1972) observed *Balanus* Costa, 1778, encrusting bryozoans and common mussels, belonging to the genus *Xenostrobus* B. R. Wilson, 1967, competing for space with *F. enigmaticus* in the Australian Brisbane River. The species *Mytilus edulis*, belonging to the same family as *Xenostrobus*, was found between the calcareous tubes in the present study. However, Straughan (1972) suspected that competition for food and material for tube building is much more important than competition for space since tubes can be built on top of each other and perpendicular to the substrate (see 5.2). Consequently, he described barnacles as the only competitor found in Brisbane River that can limit the growth of the tubeworm. One of them is the species *Amphibalanus improvisus*, found during this investigation.

Nevertheless, competition seems not to restrict *F. enigmaticus* in a serious way, once it is established (Schwindt et al., 2004).

Intraspecific competition must also be considered. Trochophores prefer to settle where tubes of their species have already been constructed. Thereby, the settlement takes place preferentially close to the tubes which contain living worms. It could be observed that worm growth decreases with increasing population density. This correlation is attributable to competition for food. For the reasons mentioned above, rivalry for space is not likely in this case either (Straughan, 1972).

5.6.2 Predation

Similar to the influence of competition, predators do not appear to pose a major threat to the survival of *Ficopomatus enigmaticus* populations (Schwindt et al., 2004).

In the case of sudden shade, the worms retreat into their tube. This fact led Straughan (1972) to suggest that fish are among the predators of the polychaetes. In fact, some species such as *Gobius niger* Linnaeus, 1758 and *Anguilla anguilla* (Linnaeus, 1758) feed on the tubeworm

(Bianchi & Morri, 1996), with the latter seen rather near deeper reefs (Fornós et al., 1997). Although *Liza saliens* (Risso, 1810) does not predate on *F. enigmaticus*, the species grazes its tubes and breaks them in this process (Bianchi & Morri, 1996). While this mullet species does not occur in the Baltic Sea, another of the same family, *Chelon labrosus* (Risso, 1827), does. Since it also grazes on organic bottom sediments (Muus & Nielsen, 2013), a similar effect can be expected.

According to Thomas and Thorp (1994), in addition to fish, the crab *Carcinus maenas* (Linnaeus, 1758) is known to be a predator of these polychaetes. However, some crabs are not able to break the thick older tubes, so they only eat juvenile worms (Straughan, 1972).

Additionally, a study on the closely related species *Ficopomatus uschakovi* in South Australia suggested that some mollusks may also feed on *F. enigmaticus* in the euhaline zone (Dittmann et al., 2009).

Hydroids and algae, that sometimes overgrow reefs, can protect against high feeding pressure. However, they also collect mud around themselves, which can cause the tubeworms to suffocate (Straughan, 1972).

5.7 Associated fauna

Due to their structure and texture, there are some species that settle in or on *Ficopomatus enigmaticus* reefs.

For example, for the Sacca del Canarin in the Po River Delta, Bianchi and Morri (1996) described that the reefs built by the serpulid form the most important hard substrate and therefore greatly increase biodiversity. They provide shelter and nutrients but also benefit from coexistence. Some tubes, for instance, are stabilized by the growth of the bryozoan *Conopeum seurati* (Canu, 1928). Although this species also lives in the southern Baltic Sea and has been found, for example, on the island Poel (Nikulina & Schäfer, 2006), it was not sampled in the present study. Instead, some tubes of *F. enigmaticus* were covered with the bryozoan *Einhornia crustulenta*.

According to Matricardi and Bianchi (1982), barnacles were associated in reefs found in the Sacca del Canarin, including *Amphibalanus improvisus*, which was also discovered in the German Warnow River along with *F. enigmaticus* both in 2020 (Hille et al., 2021) and during the investigations for this study.

According to Bianchi and Morri (1996), in areas of low salinity, Morri (1980) found the tubes covered with *Cordylophora caspia* (Pallas, 1771), a hydrozoan. *Hartlaubella gelatinosa* (Pallas, 1766) which also belongs to the class Hydrozoa Owen, 1843 was found together with the tubeworm in the samples collected during the present work.

Also sampled in the Warnow River were species of amphipods belonging to the genera *Leptocheirus* Zaddach, 1844, *Gammarus* Fabricius, 1775 and *Apocorophium* Bousfield & Hoover, 1997, among others (e.g. see Tab. 10). Similarly, Diviacco and Bianchi (1987) discovered the genera *Leptocheirus*, *Gammarus*, and *Corophium* Latreille, 1806, which is closely related to *Apocorophium*, within reefs in the Po River Delta.

In a Californian estuary, Heiman et al. (2008) determined that five of the associated species only co-occured with *F. enigmaticus* and did not inhabit native oyster reefs. These included the invasive polychaete *Polydora cornuta* Bosc, 1802, which was also found during this study along with *F. enigmaticus*, and *Sphaeroma quoianum* H. Milne Edwards, 1840, an isopod that is also invasive but was not found in the present work. The other three species found by Heiman et al. (2008) were representatives of the taxa Polychaeta Grube, 1850 and Malacostraca Latreille, 1802, all of which are native to the area. Species that also co-occurred with native oysters were nevertheless more common in tubeworm reefs, where the highest density of associated organisms was found in the marginal area.

In Mar Chiquita lagoon, the reefs formed by *F. enigmaticus* have fundamentally changed the species community. By creating a hard substrate and thus reducing the area of soft bottom, besides amphipods, gastropods, polychaetes, ostracods and further taxa, particularly the crab *Cyrtograpsus angulatus* Dana, 1851 was strongly favored in its occurrence. The abundance of the crabs was significantly higher than in the surrounding muddy area (Schwindt & Iribarne, 2000). Schwindt et al. (2001) counted 42 adult individuals of this species per reef at a density of 99 reefs per hectare. During this study, the crab *Rhithropanopeus harrisii* (Gould, 1841) was found in association with *F. enigmaticus*. Investigating whether the species is favored by the tubeworm was not subject of this work.

5.8 Nutrition

Ficopomatus enigmaticus is a filter feeder subsisting on phytoplankton and suspended organic matter (Bastida-Zavala et al., 2017). For filtering, they possess a branchial crown and numerous cilia (see 5.2). The latero-frontal cilia generate currents, that transport the food particles towards the tentacular crown. Subsequently, the particles are transferred to the mouth in food channels with the contained mucus. Particles that are too large are reflexively sorted out by pinnules. For this mechanism to work, the polychaetes must be in the feeding position, where the collar is folded back, and the brachial crown protrudes from the tube. Once the worms are removed out of the tube, they are unable to feed (Hall, 1954).

According to Davies et al. (1989), the optimal size of the food particles ranges from 2 μm to 12 μm; if they are larger, filtration is less efficient. The efficiency increases with rising particle concentration. It was found to be 8.59 ml/mg dry mass of worms per hour at a concentration of 5.27 mg/l in an estuary near Cape Town.

Although temperature is the main determinant of larval settlement (see 5.5.1), it does not occur unless sufficient food is available (Thorp, 1987).

5.9 Impact

Ficopomatus enigmaticus impacts the habitat in which it lives from both an ecological and economic perspective.

As a primary frame builder, it forms aggregates that have an influence on the surrounding flora and fauna (Bianchi et al., 1995). The formation of hard substrate providing habitat and protection usually results in an increase in biodiversity and, in some cases, abundance of other animals and plants. However, for organisms that require a soft substrate, this results in a reduction of habitat (Schwindt & Iribarne, 2000). In addition, reefs have an indirect negative impact on organisms that are fed by reef dwelling animals. In some cases, the tubeworm is also spreading to such an extent that native species are displaced by it. For example, more than

80 % of Mar Chiquita lagoon was covered with *F. enigmaticus* reefs in 2000 (Schwindt et al., 2001).

As structures protruding into the water column, tubeworm reefs alter the water flow and influence both transport and deposition of sediment. For example, dissolved sediment concentrations were 3.5 times lower in the presence of reefs in a survey conducted on the Argentine coast (Schwindt et al., 2004). In the same area, studies by Schwindt and Iribarne (1998) found that the aggregations prevented sediment from being flushed out of the lagoon. This finally led to an accumulation and thus to a reduced water depth. In addition, degraded fragments of the calcareous tubes are an essential source of sediment (Martínez-Taberner et al., 1993).

Being a filter feeder, *F. enigmaticus* can reduce the eutrophication of a water body and increase the concentration of dissolved oxygen (Keene, 1980). During a study conducted by Bruschetti et al. (2008), a reduction of turbidity and thus of dissolved particles as well as of chlorophyll a by more than 50 % was observed. Differences between the seasons could be noted.

In ecosystems with lower levels of dissolved organic matter, the filtering activity of the polychaetes can lead to competition for food with other filter feeders (Thomas & Thorp, 1994).

From an economic point of view, *F. enigmaticus* is an essential component of fouling on various structures and substrates (Streftaris & Zenetos, 2006). Especially at harbors, quay walls, jetties and buoys are affected and need regular cleaning. On ship hulls, the fouling causes slower speed. Sometimes, water pipe systems are also overgrown, which reduces their functionality (Dittmann et al., 2009).

5.10 Summary and Conclusion

The aim of this study was to obtain an overview of the current distribution of the invasive species *Ficopomatus enigmaticus* in the area along the Baltic Sea coast of Mecklenburg-Western Pomerania and to provide an outline of its ecological requirements as well as of the accompanying fauna. This information is important to assess the potential future spread of the tubeworm and to prevent possible negative impacts.

The findings of this study show that the globally distributed species complex grouped under *F. enigmaticus* now appears to establish itself in the Warnow Estuary. It is assumed that only one species has migrated to the southern Baltic Sea.

Since the investigated area is located in temperate latitudes, temperature is the main limiting factor for the further establishment and spread of the species. In case it is not warm enough in summer, neither reproduction nor settlement of larvae can take place, and if temperatures are too low in winter, there is a risk of the whole population dying. With increasing proximity to the open coast, the current speed has an additional limiting effect. Due to a high tolerance of the polychaetes towards a broad range of values concerning salinity, dissolved oxygen content, pH value and pollution, these factors are not expected to cause any further restrictions in the Lower Warnow River. The present values correspond to the requirements of the species. In addition, there is little competition, mainly limited to food competition with barnacles, and predation also usually has little or no limiting effect on the population.

Due to aggregation of the calcareous tubes into reefs, *F. enigmaticus* provides shelter and habitat for many taxa and can change the dynamics of the water body. However, a mass occurrence of the species can also cause displacement of native fauna. As an important component of fouling, a high abundance is also problematic from an anthropogenic perspective.

Despite this work has provided important results, a few errors were made. First, the pile scraper has proven to be a less suitable device to determine where calcareous tubes can be found.

F. enigmaticus, possibly due to a previous cold winter, was only found in greater abundances beneath a depth of 3 m. Since the scraper only has a limited range of about 1.5 m, there is the possibility that the species was not found at some sampling sites, even though they were present at greater depths.

Regarding the determination of abiotic factors at the sampling sites, it must be mentioned that the values only represent a snapshot. To obtain more meaningful values, temperature, salinity and oxygen content would have had to be determined over the course of the year at various depths of all stations. However, this exceeds the scope of this work.
Unfortunately, comparison with other values has shown that the measured salinities listed in Table 2 are very low. In addition, for one station, which is located close to the weir, a higher salinity has been measured than at sites further downstream. These values are probably caused by a measurement error.

The identification of *F. enigmaticus* in this study was based solely on morphological characteristics. Further work needs to be done to find out more about the genetic variability. It is important that comparable DNA sequences are studied globally to be able to describe all species behind *F. enigmaticus* separately in the long term.
Additionally, the operculum is an interesting issue for future research. A more detailed examination could clarify the question what the variability of the chitinous spines is finally due to.
Lastly, it is important to monitor the distribution of *F. enigmaticus* in the southern Baltic Sea continuously to be able to follow the development in its distribution. To obtain a more complete picture than this study could provide, more sites should be investigated using the ROV. The diving robot represents a well-suited device to examine substrates for growth in the entire depth of water bodies, with the main advantage being its large operating range.

6 References

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7 Appendix

7.1 List of abbreviations

CABI	Commonwealth Agricultural Bureaux International
DNA	deoxyribonucleic acid
fur	longitudinal furrow
op	operculum
pin	pinnule
rad	radiole
ROV	Remotely Operated Vehicle
se	seta
sp	chitinous spine
tm	thoracic membrane
WoRMS	World Register of Marine Species

7.2 Original data

Given in the Bachelor Thesis manuscript