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From Colonisation Patterns to Habitat Preferences: A Comprehensive Study of the Invasive Tubeworm *Ficopomatus enigmaticus* in a River Estuary and the Baltic Coastal Area

Abstract

Evidence of establishment, as well as one of the most detailed characterisations of the distribution strategies of the invasive tubeworm *Ficopomatus enigmaticus* (FAUVEL, 1923), was provided in this study along the German Baltic Sea coast. Using a novel sampling design consisting of a ROV (Remotely Operated Vehicle), pile scraper, and CTD (Conductivity-Temperature-Depth) probe, colonies in the estuarine Lower Warnow River were monitored over the course of one year (November 2022 to September 2023). Subsequently, the distribution was assessed throughout the river section and along an approximately 60 km stretch of the German Baltic Sea coastline at a total of 36 sites. Colonies in the Lower Warnow River occurred predominantly at water depths between 2 and 14.5 m, with wooden substrates, showing the most homogeneous and dense growth. However, coverage steadily declined downstream towards the distribution limit at the transition to the Baltic Sea. By settling in deeper water layers and exhibiting stronger substrate adhesion, the polychaete could, to some extent, survive under suboptimal ecological conditions. In contrast, the worm appeared unable to expand into the marine waters of the Baltic Sea, likely due to high water movement, scarcity of artificial substrate and increased competition of indigenous species. Ecologically, the invasion fundamentally seems to alter the ecosystem: while the calcareous structures create new microhabitats, they simultaneously prevent the settlement of other invertebrate species. In addition, the so-called *brightening response* in colonies of this tubeworm was described here for the first time. This study provides relevant insights into the species' habitat requirements, highlights the heightened vulnerability of anthropogenically impacted waters to invasive species, and underscores the need for continuous monitoring efforts.

Keywords: *Ficopomatus enigmaticus*, serpulid polychaete, invasive species, bioinvasion, mass colonisation, habitat expansion, estuarine ecology, Baltic Sea

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1 Introduction

The spread of non-indigenous species, which may be invasive, through global shipping poses a significant threat to ecosystems and economic infrastructure worldwide (SEEBENS et al. 2019). One such non-indigenous species is the worldwide distributed Australian tubeworm *Ficopomatus enigmaticus* (FAUVEL, 1923), which was first discovered in 2016 (IfAÖ, 2020) and has been rapidly spreading in the Lower Warnow River at the German Baltic Coast in Mecklenburg-Western Pomerania since 2020 (HILLE et al., 2021).

Ficopomatus enigmaticus belongs to the polychaete family Serpulidae, which comprises around 500 species (TEN HOBE & KUPRIYANOVA 2009). This family is characterised by inhabiting calcareous tubes (Figure 1A). *Ficopomatus enigmaticus* forms its calcareous tube, which can grow up to four times the length of its body (HALL 1954), using a gland that produces calcite and aragonite crystals (BIANCHI et al. 1995). It settles on natural substrates such as stones and wood, artificial surfaces such as metal piles, plastics, or ropes, and on (formerly) living organisms such as seagrass or barnacles (STRAUGHAN 1972; KOPIY et al. 2022). The tube grows predominantly orthogonal to the substrate and only rarely in a horizontal position (Hartmann-Schröder 1967). The substrate type is also decisive for the thickness and stability of the tube wall (KOPIY et al. 2022). In general, *F. enigmaticus* is rarely found as single individuals and, under low-current conditions, forms interwoven, reef-like colonies (HARTMANN-SCHRÖDER 1967). *Ficopomatus enigmaticus* is a filter feeder and feeds mainly on phytoplankton and detritus (HALl 1954). Worldwide records indicate that *F. enigmaticus* occurs at depths ranging from 0.1–15 m (KOPIY et al. 2022; TODOROVA et al. 2008), although settlement depths appear to vary regionally. According to HARTMANN-SCHRÖDER (1967), *F. enigmaticus* generally settles near the water surface. Initial scientific investigations in the Lower Warnow River have shown that *F. enigmaticus* also occurs here at depths of 1–4.5 m (HILLE et al., 2021), with a preference for depths of 3–4 m (WEITZEL 2021).

Reported temperature thresholds for the onset of reproductive processes range from 10 °C (THORP 1987) to 18 °C (HARTMANN-SCHRÖDER 1967) in Germany. Appropriately, in the Lower Warnow River juvenile individuals were only found at water temperatures from 18 °C onwards (HILLE et al. 2021). Higher temperatures, in addition, promote increased phytoplankton growth, thereby enhancing both food availability and metabolic rate, which in turn accelerates the growth of the worm and its calcareous tube (THORP, 1987). Conversely, low temperatures not only slow growth and reproduction but can also lead to the complete extinction of a local population (NEHRING & LEUCHS 1999). *Ficopomatus enigmaticus* is able to survive in a salinity range of 1 to 55 (SKAER 1974) and is therefore considered euryhaline. Although it can tolerate both hypersaline marine waters and freshwater, its primary distribution area worldwide is brackish waters, where the largest calcareous tubes have been recorded (HARTMANN-SCHRÖDER 1967). *Ficopomatus enigmaticus* prefers leeward substrates for colony settlement (STRAUGHAN 1972) because its tubes are among the most fragile in the genus and can be easily damaged (BIANCHI & MORRI 2001). Furthermore, strong current velocities hinder the settlement of its almost non-motile larvae or wash them away entirely (KUPRIYANOVA et al. 2001; STRAUGHAN 1968 & 1972). Interspecific competition for substrate space, particularly with barnacles such as *Amphibalanus improvisus* (DARWIN, 1854), and for food may also be relevant for establishing populations (STRAUGHAN 1972). However, once *F. enigmaticus* has successfully established, the significance of interspecific competition appears to be limited (SCHWINDT et al. 2004).

In the Lower Warnow River, *F. enigmaticus* overgrows boat hulls with its colonies in 4–8 weeks according to affected boat owners (Figure 1B, C), which increases hydrodynamic resistance and fuel consumption and, in some cases, can even completely block propulsion systems. The species therefore poses a significant challenge for the local maritime infrastructure. Since previous studies on the distribution and development of *F. enigmaticus* in the Lower Warnow River comprised point-based surveys with partly inconsistent methods and limited time spans (HILLE et al 2021; WEITZEL 2020), the present study aims to close these gaps. At the outset, the question was addressed whether *F. enigmaticus* is capable of overwintering in the Lower Warnow River at all. WEITZEL (2020) suggests that the temperature range in the Lower Warnow River is just sufficient for a restricted establishment. Based on information from NEHRING & LEUCHS (1999) regarding a potential total loss of populations in winter, the occurrence of *F. enigmaticus* may so far also be attributable to annual reintroductions. Subsequently, we investigated how the detailed distribution of *F. enigmaticus* develops along the course of the Lower Warnow River and which environmental factors influence its growth and distribution. Finally, it was examined whether the worm was able to spread to other areas along the Baltic Sea coast. While WEITZEL (2021), in the framework of the annual coastal monitoring programme of the Leibniz Institute for Baltic Sea Research, did not detect any *F. enigmaticus* tubes between the island of Poel and Usedom by scrape samples, HILLE et al. (2020) considered further dispersal, for example up to Stralsund, to be likely due to similar environmental conditions. Previous surveys had shown that scrape samples often reveal only a strongly localised and depth-limited occurrence of *F. enigmaticus* and may therefore be potentially unreliable. To address these limitations, we employed a more comprehensive methodological approach. The following sections describe the sampling sites, outline the methodology, present the results, and discuss their implications before concluding with final remarks.

Fig. 1 Microscopic image of *F. enigmaticus* in its calcareous tube (A) and Extensive colonisation on boat hulls (B, C).

2 Sampling sites, methods, and materials

2.1 Study area

The first part of the investigation focuses on the approximately 12 km long Lower Warnow River, a brackish-influenced estuarine section of the Warnow. From the Mühlendamm, a weir that limits the influence of freshwater, the river flows through the city of Rostock in Mecklenburg-Western Pomerania and discharges into the German Baltic Sea at Warnemünde (Figure 2).

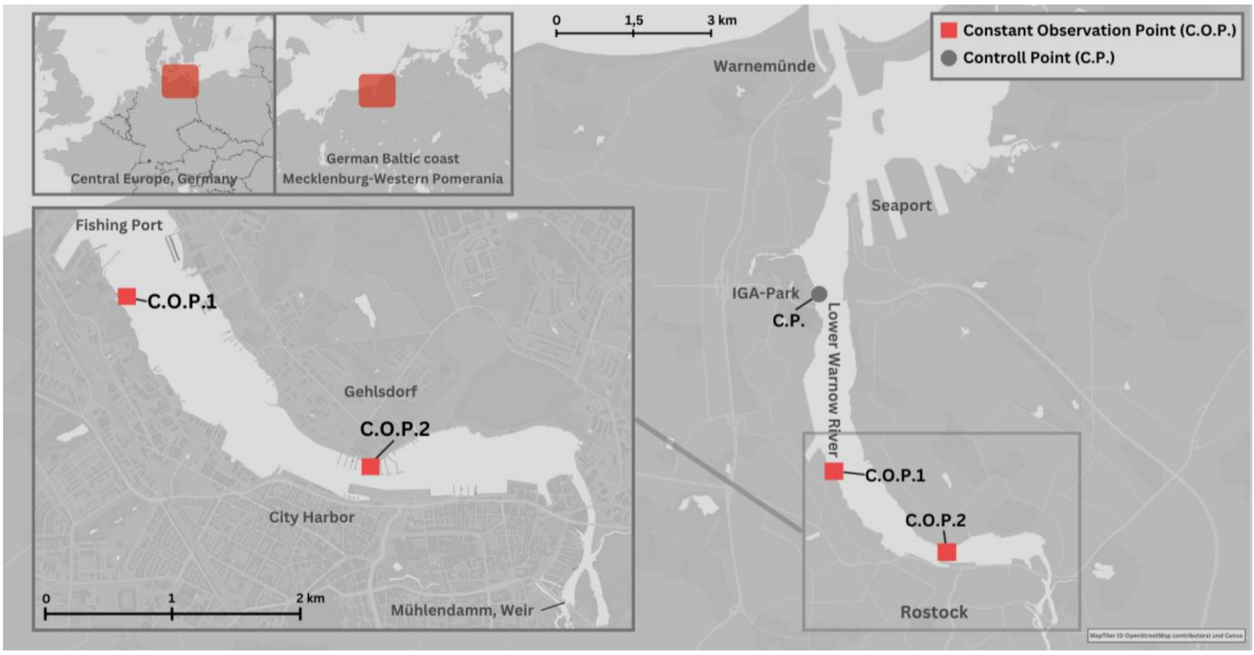

Fig. 2 Map showing the geographical location of the study area and the Constant Observation Points of the one-year investigation. MapTiler (© OpenStreetMap contributors).

To investigate the overwintering behaviour, seasonal development, and environment-dependent distribution of *F. enigmaticus* in the Lower Warnow River, two fixed observation points were selected: C.O.P.1 (Constant Observation Point), a jetty with several metal piles near the fishing harbour, and C.O.P.2, a jetty with wooden piles at the Mecklenburg Yacht Club Rostock in Gehlsdorf (Figure 2, C.O.P.1 & C.O.P.2). Secondarily, fouling on substrates such as old wooden shipwreck structures or surrounding piles at these two sites was examined. These sites were identified as potentially suitable habitats for *F. enigmaticus* based on previous reports and own observations. In addition, due to their different distances from the river mouth, variations in environmental parameters such as temperature, salinity, suspended matter concentration, and water movement were assumed. A site in the IGA Park (Control point) was also tested for suitability through a single sampling, but due to the low occurrence of *F. enigmaticus*, it was not considered further (Figure 2: C.P.). From November 2022 to December 2023 (Table 1), data were collected regularly at the two main study sites (C.O.P.1 and C.O.P.2).

Tab. 1 Overview of sampling events, applied methodology and a result summary for the one-year sampling in the Lower Warnow River (November 2022 to December 2023).

Date	Site	Sampling material	Results
2 Nov 2022	C.O.P.1	ROV	first detection and investigation of colony stage 3
7 Nov 2022	C.P.	ROV	unsuitable for research objective, colony stage 1
14 Nov 2022	C.O.P.2	ROV	first documentation of the *brightening response*, colony stage 4
22 Dec 2022	C.O.P.1	ROV	absence of *brightening response*
16 Jan 2023	C.O.P.1	CTD	temp. (surface, bottom): 5.2 °C, 6.1 °C sal. (surface, bottom): 10.65, 10.30
16 Jan 2023	C.O.P.2	CTD	temp. (surface, bottom): 5.8 °C, 6.2 °C sal. (surface, bottom): 2.27, 15.62
6 Feb 2023	C.O.P.1	ROV	beginning algal growth
27 Feb 2023	C.O.P.2	ROV, CTD, pile scraper	temp. (surface, bottom): 4.2 °C, 4.8 °C sal. (surface, bottom): 2.00, 10.34 fixing of scrape sample in ethanol
6 Mar 2023	C.O.P.1	ROV, pile scraper	fixing of scrape sample in ethanol
8 May 2023	C.O.P.1	ROV	strong algal growth and high water turbidity
8 May 2023	C.O.P.2	ROV	strong algal growth and high water turbidity
22 Jun 2023	C.O.P.1	ROV, pile scraper	juvenile individuals of *Amphibalanus improvisus* overgrowing *F. enigmaticus*
11 Jul 2023	C.O.P.2	ROV	/
4 Sep 2024	C.O.P.1	pile scraper	Scrape sample of juvenile individual of *F. enigmaticus*
11 Sep 2023	C.O.P.1	ROV	observation of active colonies
17 Sep 2023	C.O.P.2	pile scraper	colonies with this year's individuals
19 Dec 2023	C.O.P.1	pile scraper	analysis of live specimen in the laboratory

Based on the results of the one-year monitoring, the distribution pattern and ecological aspects of *F. enigmaticus* in the entire river section were then studied in two phases (Table 2). Unlike the one-year monitoring, sampling sites were not accessed from land but from the water using an inflatable boat. Built upon the experiences of the one-year monitoring sampling campaigns, a standardised sampling design using ROV, CTD probe, and scrape samples was applied at all sites whenever possible. Site selection was carried out through adaptive on-site assessment, considering criteria such as distance to shore, substrate composition, and influence of currents. In Phase I of the sampling on 2 October 2023, a total of 11 sites (I.1 to I.11) along the entire Lower Warnow River (Table 2) were investigated. Based on the results of Phase I, the hypothesis of a mass distribution limit emerged, which was to be tested in Pre-Phase II. For this purpose, on 30 October 2023, only the pole scraper was used to gradually sample different substrates at a site in the IGA Park (Table 2). With the permission of Rostock Port GmbH, Phase II finally closed the last gap on the map and investigated in greater detail the influence of water depth as well as constant human impact through shipping. For this purpose, on 15 December 2023, 9 sites in the seaport (II.1 to II.9) and 1 site in Warnemünde (II.10) were examined with ROV and CTD probe (Table 2). Due to the overgrowth of the harbour wall edge and the beginning of colonisation below 5 m depth, no scrape samples could be taken.

Tab. 2 Overview and site details about the Small-Scale Distribution Analysis in the Lower Warnow River (02 October, 30 October & 15 December 2023).

Site	Material and sampling method	Temperature [°C] surface & bottom	Salinity surface & bottom	Substrate
I.1	ROV, CTD, scrape sample	17.3, 17.6	6.52, 14.30	concrete sheet pile wall
I.2	ROV, CTD, scrape sample	17.5, 17.5	5.74, 8.40	wooden pile
I.3	ROV, CTD, scrape sample	17.7, 17,7	4.60, 11.66	wooden pile
I.4	ROV, CTD, scrape sample	17.6, 17.6	5.20, 11.96	wooden pile
I.5	ROV, CTD, scrape sample	17.5, 17.7	4.69, 11.93	wooden pile
I.6	ROV, CTD, scrape sample	17.5, 17.8	4.71, 12.99	metal sheet pile wall
I.7	ROV, CTD	17.5, 17.5	7.30, 13.30	metal sheet pile wall
I.8	ROV, CTD, scrape sample	17.6, 17.2	10.29, 11.94	metal pile
I.9	ROV, CTD, scrape sample	17.8, 16.7	12.24, 18.00	metal pile
I.10	ROV, CTD, scrape sample	17.2, 16.7	10.90, 9.45	metal pile
I.11	(ROV), CTD	16.7, 16.8	10.30, 11.57	metal sheet pile wall
II.0	scrape sample	/	/	wooden pile
II.1	ROV, CTD	4.08, 7.20	5.20, 15.63	metal sheet pile wall
II.2	ROV, CTD	4.37, 7.21	5.67, 14.44	metal sheet pile wall
II.3	ROV, CTD	5.63, 6.79	11.20, 14.27	metal sheet pile wall
II.4	ROV, CTD	6.42, 7.12	12.85, 10.54	metal sheet pile wall
II.5	ROV, CTD	6.30, 7.09	10.13, 10.42	metal sheet pile wall
II.6	ROV, CTD	5.44, 6.71	9.43, 10.12	metal sheet pile wall
II.7	ROV, CTD	5.50, 7.60	9.02, 10.30	metal sheet pile wall
II.8	ROV, CTD	5.34, 7.43	9.27, 10.14	metal sheet pile wall
II.9	ROV, CTD	5.34, 6.90	9.58, 10.05	metal sheet pile wall
II.10	ROV, CTD	5.36, 7.63	9.54, 8.87	metal sheet pile wall

The second part of the investigations focused on testing the spread of *F. enigmaticus* into coastal areas of the Baltic Sea. Within the framework of the German Ocean Foundation's marine competition on the research vessel *Aldebaran*, a total of 14 sites (S.1 to S.14) along the Baltic Sea coast between the Wiek river near Greifswald and the Lower Warnow River near Rostock were sampled from 22 to 26 July 2024 (Table 3). Site selection was carried out, as in the distribution investigations in the Lower Warnow River, by adaptive on-site assessment considering the same criteria.

Tab. 3 Water depths, bottom salinity, and colony forms according to the scale for the sites of the survey along the Baltic Sea coastline (22 to 26 July 2024).

Site	Water depth [m]	Temperature [°C] surface & bottom	Salinity surface & bottom	Colony form	Site	Water depth [m]	Temperature [°C] surface & bottom	Salinity Surface & bottom	Colony form
S.1	2.9	21.1, 21.2	1.18, 4.91	-	S,8	3.9	19.4, 19.4	8.23, 8.24	-
S.2	3.7	22.2, 21.9	5.02, 6.50	-	S.9	2.9	19.4, 20.0	8.46, 8.34	-
S.3	4.0	21.5, 21.4	6.32, 6.32	-	S.10	3.5	18.6, 18.6	7.94, 7.20	-
S.4	3.4	21.4, 21.3	6.46, 6.48	-	S.11	3.9	19.1, 19.1	8.97, 8.97	-
S.5	3.7	22.9, 22.8	6.36, 6.36	-	S.12	4.0	19.1, 19.1	9.61, 9.53	Stage 1
S.6	2.0	20.7, 20.7	6.65, 6.64	-	S.13	3.9	19.2, 19.2	9.31, 9.30	Stage 1
S.7	4.9	22.7, 22.4	6.42, 6.41	-	S.14	2.5	19.8, 20.0	7.99, 9.87	Stage 3

2.2 Sampling methods and laboratory analyses

To observe *F. enigmaticus* colonies in their natural habitat, substrates were visually examined underwater with a remotely operated vehicle (ROV). The videos recorded by the ROV (Blue-ROV 2; Bluerobotics) in combination with depth data served as the primary basis for analysis (Figure 3A). To measure temperature and salinity (salinity determined as practical salinity according to the Practical Salinity Scale 1978), a conductivity-temperature-depth probe (CTD probe) (CTD48, Sea & Sun Technology) was additionally deployed (Figure 3B). For field sampling of *F. enigmaticus*, a pole scraper (Leybold) with a reach of 4 m was used (Figure 3C). All samples were photographed and either released back into the water or transferred into a container for further analysis. By photographing on graph paper, colonisation densities could be determined. For each colony form (Stage 1 to Stage 4), colonisation density was exemplarily determined with an associated scrape sample.

During the one-year monitoring, targeted scrape samples were taken on 27 February 2023 (C.O.P.2), and March 6, 2023 (C.O.P.1) and fixed in 70 % denatured ethanol. These samples were specifically used to study the overwintering strategies of *F. enigmaticus by investigating abundances and age structure of the population*. In quantitative laboratory analyses, the proportion of inhabited tubes was calculated by determining the number of calcareous tubes and the number of individuals.

Additionally, in December 2023, live specimens of *F. enigmaticus* were transferred to the laboratory in river water to analyse the *brightening response* and the life cycle under a stereomicroscope. At room temperature, the warming of the samples was monitored with a thermometer. For detailed analysis, individual worms were carefully removed from their tubes and examined microscopically. After 24 hours, the water temperature had stabilised at 21 °C. From the multitude of calcareous tubes of the approximately 5 cm × 5 cm colonies, the tentacle crowns of active worms protruded. Thus, the colony behaviour of the animals under the influence of an adjustable lamp (light intensity) and mechanical disturbance could be documented. All investigations were recorded by camera.

Fig. 3 Sampling devices: Remotely operated vehicle (ROV) (A), CTD probe (B), and pile scraper (C).

2.3 Assessment based on standardised scales

Based on the ROV video data collected in this study, a standardised scale was developed that efficiently, differentially, and semi-quantitatively characterises the spatial colonisation of *F. enigmaticus* colonies (Figure 4). It is divided into four stages, each representing a clearly distinguishable and central state of *F. enigmaticus* occurrence and allowing conclusions on ecologically determined population densities and growth forms. Stage 1 characterises colonies with a colonisation density of 0–0.5 individuals per cm² (up to 5,000 per m²), where the correspondingly small calcareous tubes (1–3 cm) adhere to the substrate with more than half of their length and grow at clear distances from one another. In Stage 2, the calcareous tubes form initial spaghetti-like groupings and occur at a density of 0.5–3 individuals per cm² (up to 30,000 per m²). While parts of the tubes still show horizontal attachment to the substrate, growth of up to 3 cm vertically away from the surface already occurs. From Stage 3 onward, calcareous tubes up to 7 cm long form cohesive colonies that grow almost exclusively vertically from the substrate. However, the tubes often do not grow evenly and tend to grow independently of each other, reaching a density of 3–7 individuals per cm² (up to 70,000 per m²). Finally, Stage 4 marks another increase in density, with more than 7 individuals per cm² (≥ 70,000 per m²), forming a homogeneous surface of calcareous tubes of similar length (up to 8 cm). This scale serves as a central evaluation tool in the analysis of the ROV data.

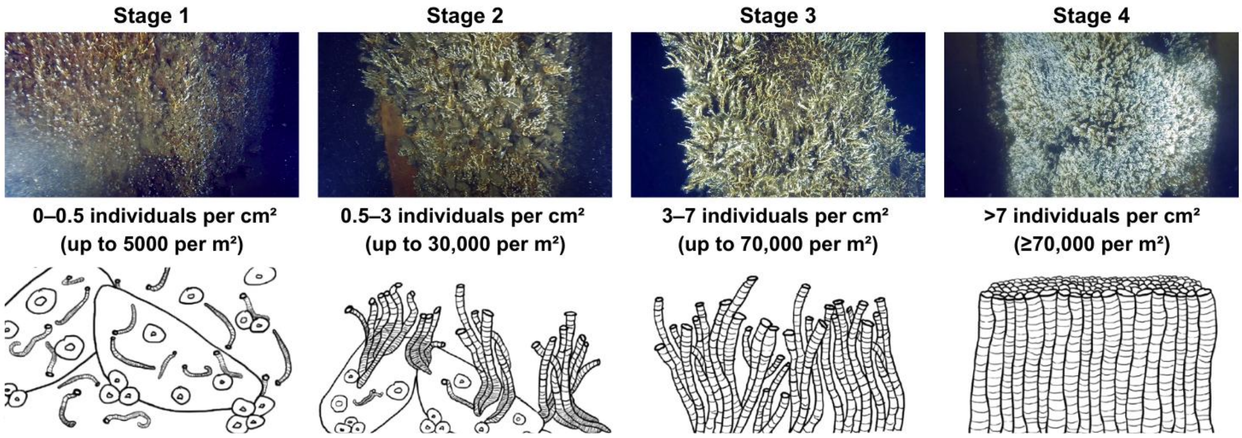

Fig. 4 Scale of colony forms based on ROV images and schematic colonisation sketches of Stage 1–4.

3 Results

3.1 One-Year Sampling in the Lower Warnow River

During the first sampling at C.O.P.1 on 2 November 2022, the ROV detected initial tubes of *F. enigmaticus* between the surface and a water depth of 2 m on the pile. Between 2 and 4 m depth, extensive, substrate-covering colonies corresponding to Stage 3 were observed. In addition, smaller structures were present on the bottom in close proximity to the pile. *Ficopomatus enigmaticus* was also found on surrounding substrates in the water at similar depths and with comparable structures. During investigations at the IGA Park on 7 November 2022, *Amphibalanus improvisus* and the blue mussel *Mytilus edulis* (LINNAEUS, 1758) predominated, and individuals of *F. enigmaticus* could only be found sporadically (colony form Stage 1). With regard to the question of overwintering and seasonal development, the site appeared unsuitable for further investigations due to the low settlement density of *F. enigmaticus.*

During the first investigations at C.O.P.2 in Gehlsdorf, *F. enigmaticus* could be clearly detected. Below 1 m water depth, colonies of stage 4 projecting from the pile were observed by ROV. The colonies appeared as cauliflower-like round or oval structures, which in some places hung from the wooden piles without covering them entirely. Around vertically stretched steel cables in the water, sectional colony structures with a diameter of 30 cm formed. In addition, for the first time, something was observed that is here summarised under the term *brightening response* (Figure 5). As the ROV approached the fouling on the pile, the colonies, which appeared dark from a distance, suddenly became bright and clearly visible. In the course of this brightening spreading across the fouling, suspended particles were stirred up from the calcareous structures. Considering the anatomy of *F. enigmaticus,* it is assumed that the observation corresponds to the sudden retraction of the tentacle crowns, which normally protrude from the tube in feeding position. Possibly triggered by the hydrodynamic and light influence of the ROV, this may result in the calcite-white tube opening becoming visible instead of the dark-coloured tentacles. Due to the large-scale fouling by a high number of worms, the phenomenon may indeed appear as an illumination or brightening effect on the predominantly dark underwater surfaces. Upon closer inspection after the *brightening response*, dark spots were visible in the white tube openings, presumably showing the retracted worms. Consequently, in this study the observation was used as an indicator of active and living individuals of *F. enigmaticus*. The hypothesis could be confirmed later with *in vivo* investigations. Upon re-analysis of the video data from 2 November 2022 at C.O.P.1, the *brightening response* was also discernible there, although markedly weaker due to the lower colony density.

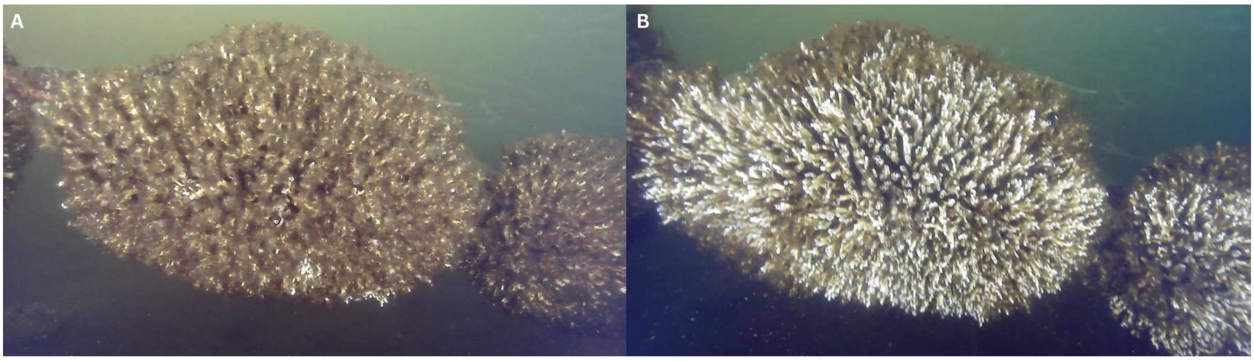

Fig. 5 Changes in *F. enigmaticus* colonies before and after the *brightening response* based on ROV images.

After a cold snap of up to −10 °C (air temperature) in December 2022, the *brightening response* could no longer be observed at C.O.P.1 on 22 December. In the permanently and clearly visible white calcareous tubes (openings), individuals of *F. enigmaticus* could be seen as a dark closure set back from the opening. Furthermore, at a previously unexamined metal pole 100 m from the shore, it was observed that the colony structures grew not only on the 4 m deep pole but also knoll-shaped on the bottom within a 5 m radius around the pole (Figure 6A).

CTD probe measurements from 16 January 2023 show that at C.O.P.1 the bottom water temperature reached a minimum of 6.2 °C, with a salinity of 10.3. At C.O.P.2, the water temperature in January was at a similar level, at 6.2 °C. By the end of February, the bottom temperature had dropped to 4.8 °C at C.O.P.2, which was not measured but also assumed for C.O.P.1. At C.O.P.1, surveys in February and March revealed almost no changes in fouling, apart from the onset of algal growth on the substrate. Dark spots in the white tube openings continued to indicate that the worms had likely retreated permanently into their calcareous tubes during winter. The absence of the *brightening response* further supports the assumption that, in winter, the animals do not actively move into a feeding position or take in food. At C.O.P.2, *F. enigmaticus* structures were barely identifiable due to heavy turbidity, and were also covered with algae, suspended particles, and unknown organic material. Quantitative laboratory analyses of scrape samples from the winter months showed that, at C.O.P.1 (06 March 2023), 77 % of tubes were inhabited (mean number of tubes: 567; number of individuals: 438), whereas tubes in the sample from C.O.P.2 (27 February 2023) were 50 % inhabited (mean number of tubes: 422; number of individuals: 211).

By the next site survey in May, algal fouling had intensified further. Visually observed water turbidity at both sites was higher than before, and *F. enigmaticus* structures were heavily overgrown with a thick layer of suspended matter and organic material. *F. enigmaticus* structures broke off very quickly, particularly at C.O.P.1. In June, water turbidity gradually decreased, and at C.O.P.1 the first *brightening response* since December of the previous year was observed. Scrape samples also revealed small, apparently juvenile individuals of *Amphibalanus improvisus* growing on the calcareous tubes of *F. enigmaticus* (Figure 6B), which had not been observed in March. Scrape samples and ROV footage showed that the substrate was predominantly colonised by *Amphibalanus improvisus*. The closer inspection of scrape samples from 04 September 2023 (C.O.P.1.) revealed conspicuously numerous small, partially membranous tubes attached to existing larger ones (shown in Figure 6C). At

C.O.P.2, new, adult colonies of *F. enigmaticus* were also found in scrape samples taken on 17 September 2023.

Fig. 6 A pole (around the site C.O.P.1) with knoll-shaped colonies of *F. enigmaticus* on the bottom within a 5 m radius (A), scrape samples of *F. enigmaticus* colonies with juvenile individuals of *Amphibalanus improvisus* (C.O.P.1, 22 June 2023) (B) and juvenile individuals of *F. enigmaticus* (C.O.P.1, 04 September 2023) (C).

Microscopic examinations identified an associated fauna that uses *F. enigmaticus* reef structures as habitat. Specimens of the Zuiderzee crab *Rhithropanopeus harrisii* (GOULD, 1841) were frequently observed within the structures. Additionally, colonies of the bryozoan *Conopeum seurati* (CANU, 1928) were detected on the calcareous tubes. In an uninhabited tube of *F. enigmaticus*, individuals of the bristle worm *Alitta succinea* (LEUCKART, 1847) were also documented. During subsequent fieldwork on distribution, *Amphibalanus improvisus* was again found growing on the colonies, and in the vicinity of the colonies, the common starfish *Asterias rubens* Linnaeus, 1758 and *Mytilus edulis* settled.

During laboratory examinations of live samples in December 2023, the animals became more active as the temperature increased, and the tentacle crown gradually emerged from the tube opening. Individuals were then carefully removed from their tubes and subsequently examined microscopically. At measured water temperatures of 16–18 °C, spherical structures were observed around the tentacle crown, which in size and shape could correspond to eggs of *F. enigmaticus* (Figure 7). After 24 hours, a tentacle crown with an operculum protruded from almost all tubes. However, mechanical disturbance of the sample container or artificial shading caused the animals to retract abruptly into their tubes. This sudden withdrawal, as previously suspected, reveals the white calcareous tube opening. In large colonies, this then appears as a colour change from brown to white. In contrast to shading, an increase in light intensity using a dimmable lamp had the opposite effect: the animals extended their tentacle crowns further out of the tubes.

Fig. 7 Suspected egg-laying of *F. enigmaticus* observed with a fluorescence filter under the microscope during laboratory investigations in December 2023.

3.2 Small-Scale Distribution Analysis in the Lower Warnow River

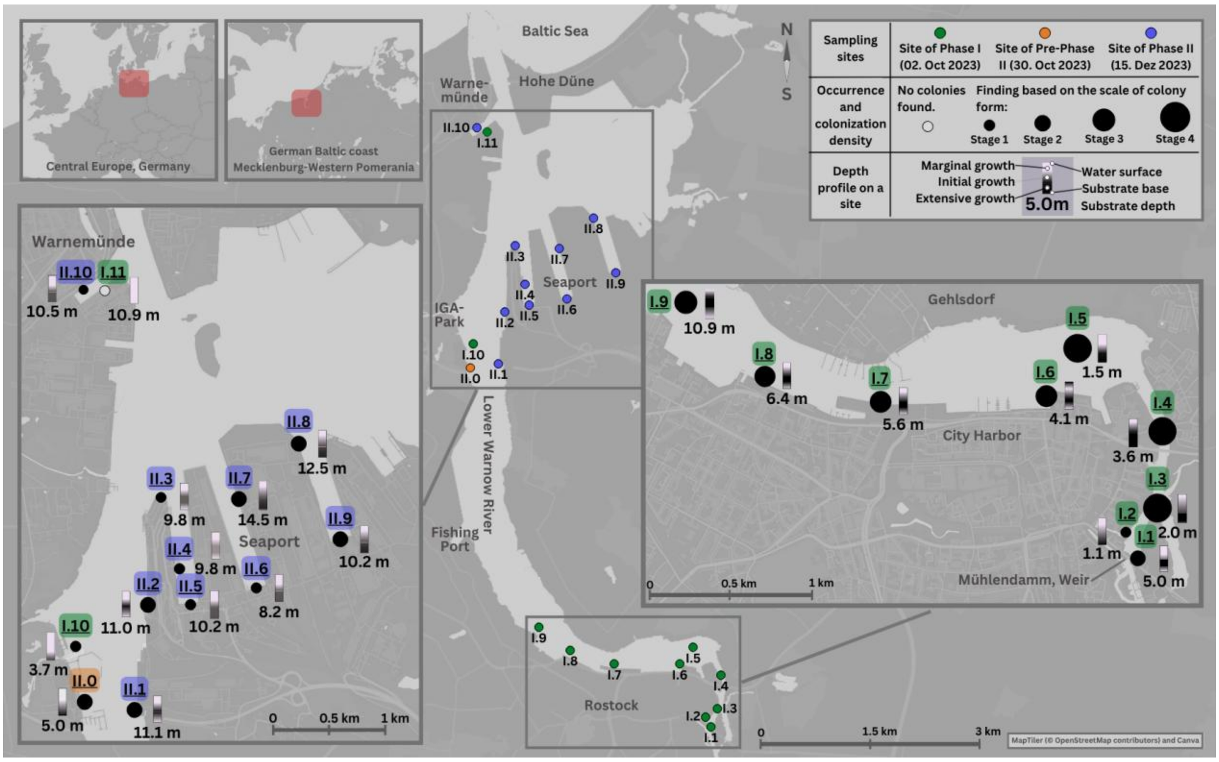

Fig. 8 Map of survey sites and results for the distribution analysis in the Lower Warnow River. MapTiler (© OpenStreetMap contributors).

During Phase I, *F. enigmaticus* was detected at all sites (I.1 to I.10) except Warnemünde (I.11) (highlighted in Figure 8). However, fouling and colony forms varied considerably along the Lower Warnow River. While at sites I.1 and I.2 near the weir, *F. enigmaticus* fouling formed only small, localised groupings, which at sites I.3 to I.5

colonies were observed to cover almost the entire substrate surface. The predominant colony form there, Stage 4, was characterised by directly adjacent tube openings forming a homogeneous surface, despite differences in thickness and extent of the colony structures (Figure 9A).

At sites I.6 to I.9, the appearance of the colonies changed, even though the geographical distance to the previous sites was small and the fouling form corresponded to Stage 3. There, the calcareous tubes grew more independently from each other, with greater spacing between openings, giving the colonies a distinctly more "spiky" appearance (shown in Figure 4 at Stage 3 and Figure 9B, C). Additionally, knoll- and cauliflower-like structures were observed (Figure 9B, C), protruding markedly from the substrate and reaching diameters of up to 2 m. Massive fouling at sites I.3 to I.9 began at depths of 1–2 m. Only at site I.6 was an unusual fouling band found within the uppermost 10 cm of the water column (Figure 9D, E), characterised by a high density of small calcareous tubes. At site I.9, fouling extended to the bottom at a depth of 10.9 m (as shown in Figure 10). In the lower 5 m, however, dense fouling decreased, tubes grew closer to the substrate, and colonies corresponded to Stage 2. At sites I.10 and I.11, *Amphibalanus improvisus* and *Mytilus edulis* dominated, with *F. enigmaticus* only occasionally detected growing on the associated fauna at site I.10. The non-detection of *F. enigmaticus* at site I.11 is attributable to ROV camera issues. It was resolved by the sampling at site II.10. Water temperatures measured on the survey day ranged between 17.8 °C and 16.8 °C at the surface and bottom, without distinct vertical differences. Salinity in the depths ranged between 8.40 and 18.0, with surface salinity values mostly lower, at 4.60–12.24.

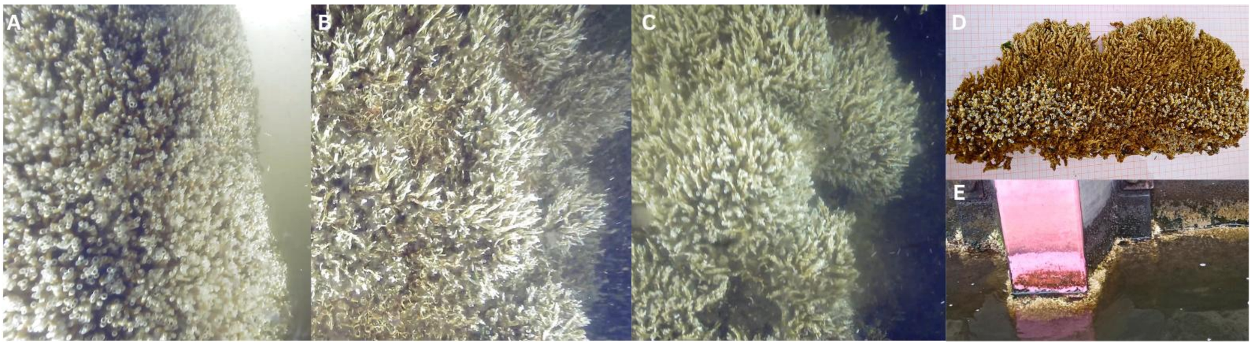

Fig. 9 ROV images of homogeneous Stage 4 colonisation on wooden substrate (A) and spiny as well as spherical reef structures of Stage 3 on metal substrates (B, C); surface colonisation at site I.6 (D, E).

Since the last *F. enigmaticus* individuals were found at site I.10, this was initially assumed to be the boundary of mass distribution. Initial scrape samples in Pre-Phase 2 confirmed this assumption: at depths up to 3.5 m – similar to I.10 – only individual tubes between *Mytilus edulis* and *Amphibalanus improvisus* were observed. However, ropes attached to jetties extending down to 5 m provided a new picture. After retrieval, it was found that only scattered tubes were present down to 4 m, but from 4 m depth onwards, a continuous settlement of *F. enigmaticus* began again. This indicated that a clear boundary of mass distribution could no longer be assumed; rather, observations suggested that *F. enigmaticus* retreated into deeper water layers towards the mouth.

Due to the greater depths, sampling in Phase 2 was conducted in Rostock seaport. Here, *F. enigmaticus* was clearly detected at all sites in the seaport and in

Warnemünde, down to a water depth of 14.5 m (Figure 8). In addition to *F. enigmaticus*, *Mytilus edulis* and *Amphibalanus improvisus* were also present at all sites, with *Asterias rubens* occurring at sites II.3 and II.8. In the upper 4–5 m, *F. enigmaticus* was absent or only present locally at all sites. At sites II.1 and II.2, grouped, partly free-standing colony structures of Stage 2 occurred below 5 m, growing almost continuously between *Mytilus edulis* and *Amphibalanus improvisus* (Figure 10). At sites II.3 to II.6, tubes occurred only sporadically and close to the substrate below 4 m (Stage 1). In general, colonisation was limited mainly to substrate areas free of associated fauna. At sites II.7 to II.9, Stage 2 colonies with spaghetti-like tubes growing over and alongside each other were found, which appeared extensive at greater depths due to the marked decrease in *Mytilus edulis* and *Amphibalanus improvisus* fouling. Here, surface coverage was not due to closely packed tube openings, as at sites A.3 to A.5, but to tubes running parallel to the substrate. At site II.10, the first small tubes of *F. enigmaticus* were observed from a depth of 3 m, growing individually, scattered, and flat on the substrate (Stage 1) at greater depths. Measured bottom temperatures at stations II.1 to II.10 ranged between 6.7 °C and 7.6 °C, thus higher than surface temperatures (4.1 °C–6.4 °C). Salinity differences between surface and depth were generally small, e.g., 9.27–10.14 at site II.8. Only sites II.1 to II.3 showed higher differences, with e.g. 5.20–15.63 (II.1).

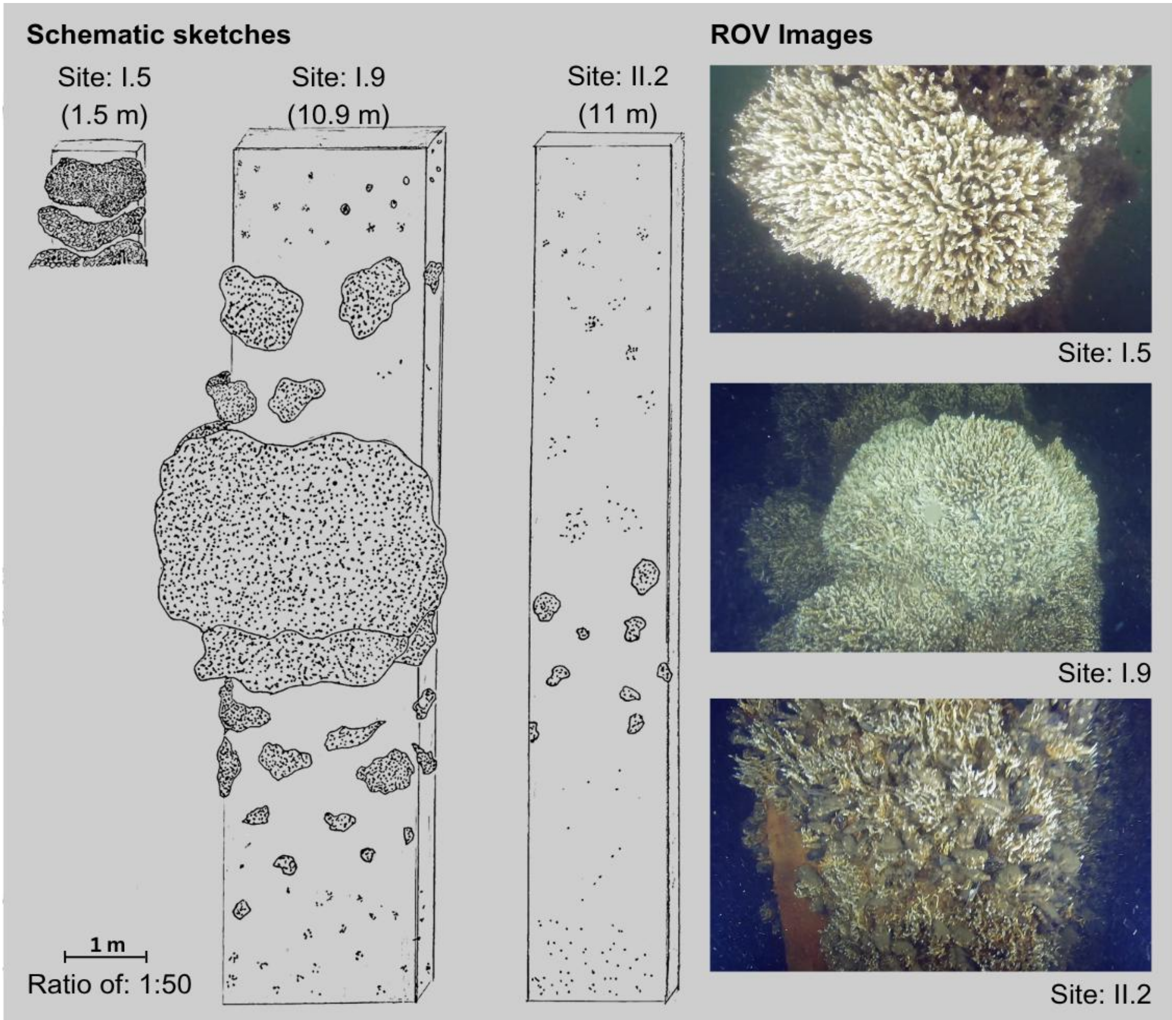

Fig. 10 Schematic sketches of substrate colonisation at selected sites along the Lower Warnow River and their corresponding ROV images.

3.3 Survey along the Baltic Sea coastline

During the survey along the Baltic Sea coastline, *F. enigmaticus* was detected exclusively at three sites (S.12 to S.14) within the Lower Warnow River as well as at its mouth (Figure 11 and Table 3). At all other sampling sites along the Baltic Sea coast and in the Bodden waters, no specimens were found despite consistent application of the methodology (Figure 11).

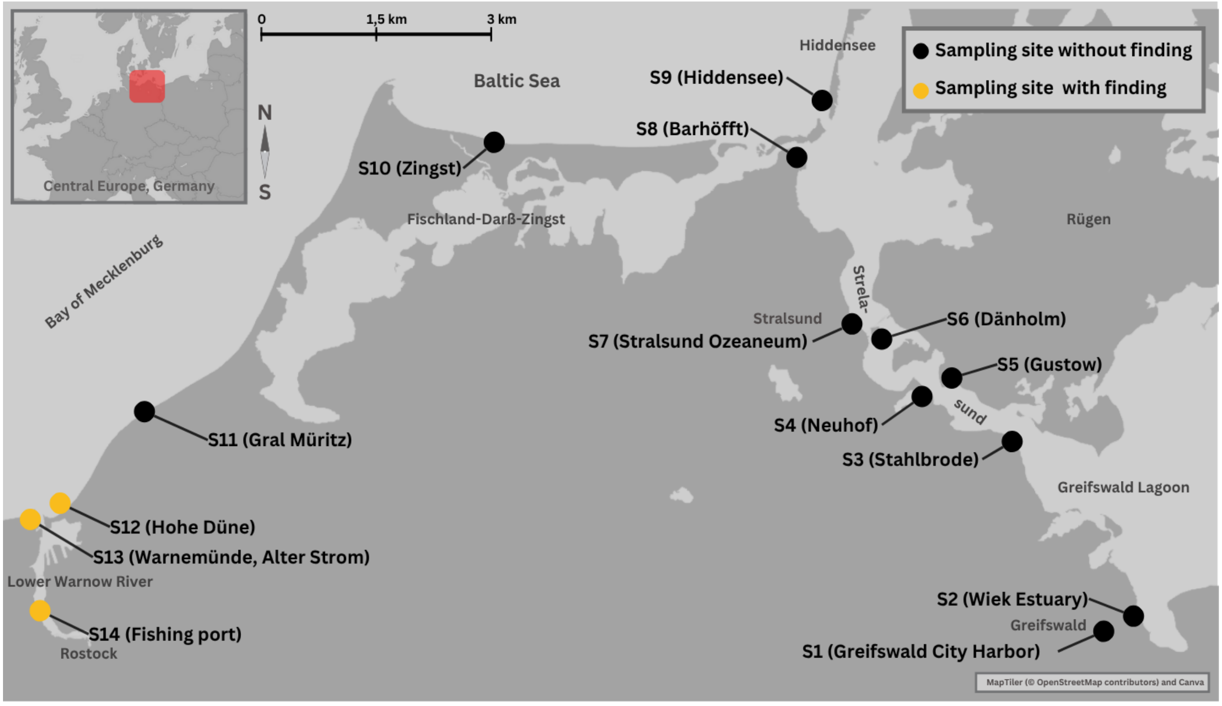

Fig. 11 Map of sampling sites and findings during the survey along the Baltic Sea coastline. MapTiler (© OpenStreetMap contributors).

Hydrographic measurements indicate a pronounced salinity gradient from the Wiek estuary in Greifswald (5.02) to Hohe Düne in Rostock (9.61), with salinity increasing abruptly from the Darßer Schwelle (site 8, Barhöft) and continuing to rise westward (Table 1). Water temperature in the shallow Bodden waters around Rügen was higher (22.89 °C at S5 in Gustow) than in the maritime coastal sections between Hiddensee and Rostock (e.g. 19.06 °C at S11 in Graal Müritz).

Structurally, the sampled sites differed considerably: while the Lower Warnow River is characterised by a high density of anthropogenic substrates, hydraulic engineering structures along the coastal sections between Rostock and Hiddensee are scarcely present. Harbours such as those in Stralsund, Greifswald, and Rügen do provide hard substrates locally, but at greater geographical distances and lower concentrations than in the Lower Warnow River. The known associated fauna of the serpulid worm, particularly *Amphibalanus improvisus* and *Mytilus edulis*, occurs more frequently between Rostock and Hiddensee. Beyond this area, *Amphibalanus improvisus* dominates as virtually the main fouling benthic species.

4 Discussion

Since *F. enigmaticus* is cosmopolitan and occurs primarily in countries with year-round higher temperatures (Dittmann et al. 2009), the question of overwintering has so far hardly arisen. With its spread into regions experiencing distinctly colder temperatures at certain times of the year, the question gains relevance and was addressed for the first time in the Lower Warnow River in this study. Despite its massive occurrence in late summer 2020 (Hille et al. 2021), a die-off of the population and a new introduction in the following year could not previously be ruled out. In particular, due to the first record in 2016 and disappearance of the species between 2016 and 2019 (IfAÖ 2020), this hypothesis had to be considered. Through a one-year investigation at two sites (C.O.P.1 and C.O.P.2), overwintering and thus a closed life cycle of *F. enigmaticus* in the river can now be assumed. Crucial to this was the *brightening response* described for the first time in this study (Figure 5). Although this is based on a natural defence reflex of the worms, whereby they abruptly retract their branchial crown into the calcareous tube, the resulting distinct visual change in large colonies is conclusive evidence that individuals are alive and active. It can therefore be concluded for the evaluation of ROV footage that the *brightening response* can be regarded as a reliable indicator of active *F. enigmaticus* individuals. Conversely, if only dark spots are visible in the tubes, it can be assumed that the individuals have withdrawn and are inactive. This facilitates the identification of living specimens during visual field surveys with the ROV and may also be relevant for future research. The absence of the phenomenon in samples from C.O.P.1 and C.O.P.2 from December onwards suggests that colonies of *F. enigmaticus* had ceased their filtration activity. The observation of a black closure of the calcareous tube, together with a water temperature of 4.8 °C (C.O.P.2) in February (corresponding to a measurement of 4.6 °C by the local authority StALU MM at a nearby station), makes a permanent retraction of *F. enigmaticus* into its tube during the winter months likely. The high proportion of inhabited tubes 77 % (C.O.P.1) and 50 % (C.O.P.2) in samples collected from late February and early March, when water bodies in Central Europe generally reach their lowest temperatures, indicates that cold-induced extinction of *F. enigmaticus* colonies in the Lower Warnow River did not occur during the study period. With the first observation of the *brightening response* in continuously monitored colonies at site C.O.P.1 in June, overwintering of *F. enigmaticus* in this river section was proven. Although colonisation by juvenile *Amphibalanus improvisus* (Figure 6B) on the calcareous tubes increases competitive pressure, samples from September (shown in Figure 6C) demonstrate that *F. enigmaticus,* after reproduction, has the potential to overgrow existing associated fauna and establish populations across large areas. In vivo examinations of individuals also revealed that spawning occurs without delay once the reproduction temperature of 16–18 °C is reached, as Hille et al. (2021) had already indicated for the Lower Warnow River.

The results of the present study on the distribution and habitat requirements of the species in the Lower Warnow River reveal a more detailed and differentiated picture than previous publications have provided. The strongest colonisation according to the applied scale with the highest density, substrate coverage, and abundance was recorded at sites I.3 to I.5 in the city harbour (summarised in Figure 8). This suggests that colonies in this section are exposed to optimal habitat conditions. In contrast to the findings of Hille et al. (2021), the site with the highest abundance is therefore not Bramow (comparable to site C.O.P.1). Sites I.6 to I.9 are also characterised by massive colonisation, which, however, often appears spikier or forms outgrowths from the substrate at certain points. It is plausible that this difference depends on the nature of the substrates. While wooden substrates, such as at sites I.3 to 1.5, promote uniform, dense, and extensive colonisation (Figure 9A), metallic, partly corroded surfaces appear to favour locally spherical outgrowth colonies (Figure 9B, C). The occurrence of *F. enigmaticus* colonies growing around a pole near site C.O.P.1 on the bottom (Figure 6A) was unique within the scope of this study. They likely can only establish there because hard substrates, such as shells and stones, are scattered around the pole. This example highlights the importance of hard substrates for the settlement of *F. enigmaticus*, which apparently cannot find sufficient support on loose sediment to construct its tube.

The settlement depths of 1–4 m (Hille et al. 2021), with a preferred colonisation depth of 3–4 m (Weitzel, 2021), already documented for *F. enigmaticus* in the Lower Warnow River, are correct for the sites sampled in these studies, but remain incomplete for the river ecosystem as a whole. At sites with Stage 3 and Stage 4 colonies, the worm was found in mass occurrences and fully covering the substrate from a water depth of 1–6 m (Figure 8). Above 1 m depth, tubes occurred only sporadically or in small clusters. The single surface growth (Figure 9D, E) at site I.6 cannot be explained. While Stage 3 colonisation was still found at C.O.P.1, colony density decreased rapidly and markedly towards the river mouth. Colony forms of Stage 1 to Stage 2 often occurred only from a depth of 5 m onwards and extended down to 14.5 m (shown in Figure 8, sites of Phase 2). As the occurrence extended to the bottom at all sites, it can be assumed that *F. enigmaticus* may also occur at depths greater than 14.5 m. Investigations at site II.0 demonstrated for the first time that retreat into deeper waters is an adaptation to altered habitat conditions towards the river mouth. This colonisation in greater depth could be confirmed between sites II.1 and II.10.

The sites with Stage 1 to Stage 2 colonies (precise reference to sites) are strongly influenced by the nearby marine environment of the Baltic Sea, which entails higher average salinity values and increased water and current movement. The decreasing difference between surface and bottom towards the mouth indicated increasing vertical mixing of the water column (Table 2). Long-term measurements (4–10 measurements per year) between 2014–2023 from StALU MM show that despite the fluctuations typical for an estuary, the mean salinity at a measurement point in the seaport was 15.2, higher than the 13.0 recorded in the city port. Since *F. enigmaticus* can tolerate salinities of 1–55 (Skaer 1974) and trochophore (larval) development can take place from 6 onwards (Straughan 1972), this factor does not seem to directly explain the differences in colony forms. Furthermore, colonies may find it more difficult to settle above a water depth of 5 m, where the greatest current influence occurs, possibly due to increased water movement. Calcareous tubes appeared increasingly only at depths greater than 5 m, and abundance further increased with depth. This results in greater substrate adhesion of the calcareous tubes (Figure 4, schematic colonisation sketch Stage 1 and 2), as structures projecting orthogonally from the substrate could easily break off due to water movement.

Smaller tube sizes and lower population densities can also be explained by increased space and food competition with more frequently occurring marine associated fauna such as *Asterias rubens* and *Mytilus edulis* (Figure 10, ROV image of site II.2). The finding of predators (site II.3) such as the round goby *Neogobius melanostomus* (Pallas, 1776) in the harbour area may also explain reduced colony formation. The likewise invasive *Neogobius melanostomus* occurs preferentially in the vicinity of artificial substrates in harbours (Wiesner 2005), with polychaetes potentially forming part of their diet (Skabeikis & Lesutiene 2015). Whether the presence of this species in areas with lower settlement densities of *F. enigmaticus* is related or merely coincidental, and whether it also occurs in river sections with higher polychaete abundance, could not be definitively determined. Visual surveys of the sites further show that *F. enigmaticus*, through its extensive coverage, leaves little substrate available for other fouling organisms such as *Amphibalanus improvisus* and *Mytilus edulis*, allowing for the assumption of competitive displacement. At the same time, the reef-like colony structures of *F. enigmaticus* create habitat on otherwise artificial, structurally heterogeneous, and ecologically difficult-to-utilise substrates such as sheet piling or piles. Laboratory investigations of the study confirm this through the discovery of individuals seeking shelter within (*Alitta succinea*) or between (*Rhithropanopeus harrisii*) the calcareous tubes.

The absence of *F. enigmaticus* findings during surveys along the coastline between Rostock and Greifswald matches the results of WEITZEL (2021), obtained in the context of the coastal monitoring described there. This study, however, differs in that *F. enigmaticus* was detected for the first time in the marine environment of Hohe Düne (S.12) and Warnemünde, at Alter Strom (S.13). Although occurrences were very sporadic (Figure 11), these sites represent the most maritime records so far within both the current investigation and those by WEITZEL (2021) and HILLE et al. (2021). Given the euryhaline characteristics and the salinity threshold of 6 for larval development identified by STRAUGHAN (1972), a salinity too low at sites S3 to S11 cannot be considered a sufficient explanation for the absence of *F. enigmaticus* (bottom salinities in Table 3). As already seen at sites with reduced abundance in the Lower Warnow River, wave action and current influence along the coastline may exert an even greater impact. However, along the coastal stretch, *F. enigmaticus* cannot retreat to greater depths due to the lack of artificial substrate, which only occurs in shallow waters at harbour or pier facilities (comparison of substrate depths in Figure 8 and Table 3). Additional factors such as oxygen content and nutrient availability, which could not be examined in this study, should also be considered as potential influences.

The absence of *F. enigmaticus* along the Baltic Sea coastline underlines that the specific character of the Lower Warnow River is decisive for the establishment and success of the invasive worm. Both the variability of environmental factors along the river section and the high degree of anthropogenic influence enable its mass proliferation from the ecological optimum in the city port to the settlement at the absolute tolerance limit of *F. enigmaticus* in Warnemünde at the transition to the Baltic Sea. Nevertheless, further eastward expansion of *F. enigmaticus* cannot be entirely ruled out in the future, considering anthropogenic impacts and climate change. The methodological approach of the study, based mainly on visual inspection of substrates with the ROV, can be assessed as efficient and suitable, although with a lower degree of precise quantification, similar to the use of a scale for distinguishing colony forms. In the future, it could be enhanced by automatic, AI-based colony abundance determination and a technical combination of ROV and piling scraper to allow sampling from variable depths without divers.

5 Concluding remarks

The study was able to demonstrate the establishment of the invasive calcareous tubeworm in the Lower Warnow River, to detail its distribution both within the river and eastward along the coastline, and to highlight ecological trends. The investigations into *F. enigmaticus* also exemplify that anthropogenically influenced ecosystems, due to their already degraded ecological condition, exhibit an increased susceptibility to the establishment of invasive species. Whether such success and ecological dominance of *F. enigmaticus* would have been possible in an intact ecosystem with a natural shoreline and without anthropogenically created deep harbour basins, sheet piling, and pier structures remains questionable. Due to the high dominance of *F. enigmaticus* in the ecosystem, it can be assumed that competitive interactions with other species also increase, making biodiversity loss likely. At the same time, the invasive traits of the species create new microhabitats. Assessing the consequences of the establishment of non-indigenous species is often difficult; however, it can be stated that species like *F. enigmaticus* have the potential to strongly alter entire ecosystems like the Lower Warnow River within a short period of time. In light of climate change, increasing anthropogenic interventions in ecosystems, and stronger global interconnectedness, it is becoming ever more important to monitor ecosystem conditions. Regular investigations and monitoring such as in this study are therefore crucial to better assess the influence of non-indigenous and potentially invasive species in the future.

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