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Research Article

Distribution and ecology of the recently introduced tanaidacean crustacean *Sinelobus vanhaareni* Bamber, 2014 in the northern Baltic Sea

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Abstract

The non-indigenous tanaidacean crustacean *Sinelobus vanhaareni* Bamber, 2014 was first found in northern Europe in 2006 and has since spread to the northern Baltic Sea. Here, we surveyed the distribution of the species in different habitats in southwestern Finland, focusing on vegetated macroalgal and seagrass habitats (i.e., *Fucus vesiculosus* beds and *Zostera marina* meadows). We also evaluated its potential impacts by synthesizing current knowledge on the traits and ecology of the species, and identified knowledge gaps. We found that *S. vanhaareni* is now present throughout most of the southwestern Finnish coast, in a number of vegetated and non-vegetated substrates down to 25 m depth. Furthermore, the presence of egg-brooding females in most areas also confirms that the population is self-sustaining. The species is especially abundant in shallow macroalgal belts and eelgrass meadows, which are critical habitats for biodiversity, ecosystem functioning, and ecosystem service provisioning, highlighting the need to understand the effects of *S. vanhaareni* in these important ecosystems. Its presence on boat hulls and in marinas and harbours suggests that recreational boating may be a major spread vector, while drifting macroalgal fragments may also contribute to regional spread. At this stage of invasion, we found high overlap in epifaunal community composition in sites where *S. vanhaareni* was present and sites where it was absent. Based on the functional traits of *S. vanhaareni* and closely related species, we infer that it is likely part of the detritus-based pathway in benthic food webs. However, additional sampling and experiments are necessary to determine the true extent of its distribution and to quantify trophic links (through stable isotope analysis, gut content analysis, and experimental trials) to fully understand its effects on communities and trophic networks in the northern Baltic Sea.

Key words: Tanaidacea, Tanaididae, non-indigenous species, trophic interactions, functional traits, *Fucus vesiculosus*, *Zostera marina*

Introduction

The spread of non-indigenous species has become increasingly common in marine and estuarine ecosystems globally, mostly due to increased human activity and maritime transport throughout the 20th century (Ruiz et al. 1997; Leppäkoski and Olenin 2001). The Baltic Sea is no exception, as the total number of introduced or cryptogenic (i.e. of unknown origin) species is currently estimated at 140, of which approximately 78 have established permanent populations (Ojaveer et al. 2017). Furthermore, invasion rates



Figure 1. *Sinelobus vanhaareni* individual (male, approx. 2 mm length) from the Åland Islands, northern Baltic Sea. Photo credit: Heidi Herlevi.

in the region have accelerated since the 1950s as maritime transport and shipping activities have grown (Leppäkoski and Olenin 2000; Leppäkoski et al. 2002). During the latest assessment period (2011–2016) of core indicators of the ecological status of the Baltic Sea, twelve new species were recorded (HELCOM 2018), including the tanaidacean *Sinelobus vanhaareni* (Bamber 2014; Figure 1).

This tanaidacean was first noted in Europe in 2006, in the Netherlands and Belgium (van Haaren and Soors 2009). At the time, it was identified as *Sinelobus stanfordi* Richardson, 1901, a widely distributed cosmopolitan species, which was believed to be the sole member of the genus *Sinelobus*. In 2009–2010, it was subsequently observed in several locations in the German North Sea (Brzana et al. 2019), Dutch Wadden Sea (Gittenberger et al. 2010) and Estonian Baltic Sea (G. Reisalu *pers. comm.*). Multiple additional observations of the species have since been made throughout the North and Baltic Seas (Estonia, France, Finland, Germany, Latvia, Lithuania, Netherlands, Poland; AquaNIS 2015), and it has established dense breeding populations in some areas such as in the Gulf of Gdańsk (Brzana et al. 2019). Re-examination of the genus has since revealed multiple species within the genus *Sinelobus* (e.g. Bamber 2008, 2014;

Rishworth et al. 2018), and the species present in northern Europe was named *Sinelobus vanhaareni* (Bamber 2014). Both its origin and initial mode of introduction to northern Europe remain unknown. However, it was never sighted in the Baltic Sea prior to 2010 despite intensive coastal ecological research in the area, and it is officially listed as a non-indigenous species in the Baltic Sea by HELCOM (HELCOM 2018) and by countries in which it has been sighted (e.g. by the Finnish Advisory Board for Invasive Alien Species, appointed by the Ministry of Agriculture and Forestry; www.vieraslajit.fi).

Relatively little is known about *S. vanhaareni*, or its congener *S. stanfordi*. The genus *Sinelobus* belongs to the family Tanaididae in the order Tanaidacea (Sieg 1980; Bamber 2014; Anderson 2016). These small tube-dwelling malacostracan crustaceans are characterised by a prominent pair of clawed chelipeds and the presence of a marsupium (brood pouch) in which the larvae develop and emerge without a dispersive larval phase (Johnson and Attramadal 1982; Błażewicz-Paszkowycz et al. 2012). Tanaidaceans are found in a wide range of habitats, including but not limited to stromatolites (Rishworth et al. 2019), wood (Błażewicz-Paszkowycz et al. 2015), shallow coral reefs (García-Madrigo et al. 2005), deep-sea corals (Jakiel et al. 2015), plant roots (Hendrickx and Ibarra 2008; Slivak et al. 2013), vegetated and bare soft sediments (Ferreira et al. 2015; Kassuga et al. 2017), turf algae (Rishworth et al. 2018), and natural and artificial hard substrates (Bamber 2012; Brzana et al. 2019; Rumbold et al. 2015). We assume that the basic morphological and reproductive characteristics of tanaidaceans are present in *S. vanhaareni*, but species-specific data on its life history, habitat preference, and diet are lacking, making it difficult to determine its ecological role in the northern Baltic Sea.

Sinelobus vanhaareni was found in Finnish waters for the first time in 2016, in the western Gulf of Finland (Finnish Biodiversity Information Facility, Supplementary material Table S1, Figure 2). It has been present since at least 2013 in Muuga Harbour, near Tallinn (G. Reialu *pers. comm.*), on the Estonian coast of the Gulf of Finland. This may be its point of introduction to Finland, due to heavy recreational boating and commercial shipping between Estonia and Finland in this area. Since 2016, several individuals have occasionally been reported in the Gulf of Finland, Archipelago Sea, and Bothnian Sea during water and benthos monitoring programmes (Räisänen 2018; Holmberg et al. 2020; Räisänen and Koivunen 2020; Vahtera et al. 2020), but no dedicated research or monitoring for the species exists. However, following numerous sightings in 2019–2020, there is an increased interest in understanding the potential impacts of this rapidly spreading non-indigenous species. Our aims in this study were to (1) describe the current distribution and density of *S. vanhaareni* in different habitats along the Finnish coast, (2) determine whether invertebrate communities in vegetated habitats (*Fucus vesiculosus* Linnaeus, 1753 and

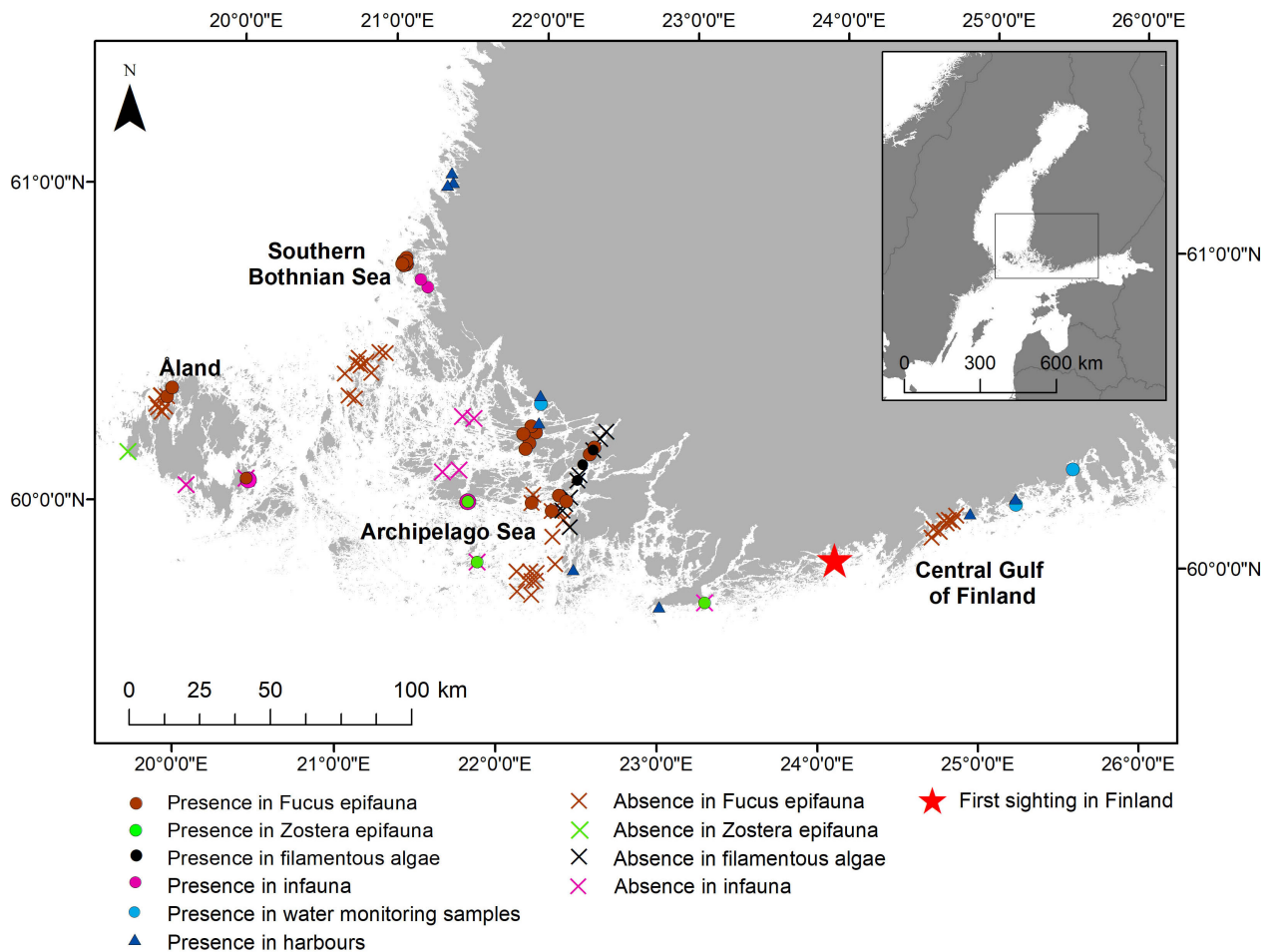


Figure 2. A map of the study area indicating sites where *Sinelobus vanhaareni* was present (including samples taken in this study and reports from other sources in blue; see Table S1) and where it was absent from samples taken in the course of this study (see “Field sampling” section in methods). Different colours indicate the studied habitat, a filled circle or triangle indicates presence of *S. vanhaareni* and a cross indicates absence of *S. vanhaareni*. The red star indicates the location of the first reported sighting in Finland.

Zostera marina Linnaeus, 1753) differ in the presence and absence of *S. vanhaareni*, and (3) synthesize current knowledge and identify knowledge gaps in the traits and ecology of the species to assess potential impacts on communities and trophic networks.

Materials and methods

The data in this study were collected using a number of different sampling methods across the southern and southwestern Finnish coast and Åland Islands (Table 1, Figure 2). These samples were collected as part of several ongoing research projects studying the biodiversity of coastal habitats. We supplemented this data with sightings reported on the online portals of the Finnish Advisory Board for Invasive Alien Species (www.vieraslajit.fi) and the Finnish Biodiversity Information Facility (www.laji.fi), published reports of benthos and water monitoring from municipalities, and as-of-yet unpublished data from ongoing monitoring efforts of boats, marinas, and harbours by the environmental NGO “Keep the Archipelago Tidy” Association and the Finnish Environment Institute SYKE.

Table 1. Summary of sampling efforts and methods used in this study. See Table S1 for details of sites in which *Sinelobus vanhaareni* were found and for additional sightings in Finland from other sources.

Year	Area(s)	Habitat	Sampling method	Sites sampled	Sites with <i>S. vanhaareni</i>	Used in community analysis?
Infaunal sampling						
2018, 2019	Åland	Mud, unvegetated	Infauna grab	5	2	No
2019	Archipelago Sea, Bothnian Sea	Mixed sediment, sparse vegetation	Infauna core	6	2	No
2020	Åland, Archipelago Sea, Gulf of Finland	Sand, <i>Zostera marina</i>	Infauna core	4	1	No
Epifaunal sampling						
2018	Åland	Rock, <i>Fucus vesiculosus</i>	By hand	1	1	No
2020	Archipelago Sea	Rock, filamentous algae	By hand	9	3	No
2020	Åland, Archipelago Sea, Bothnian Sea, Gulf of Finland	Rock, <i>Fucus vesiculosus</i>	Mesh bag	55	19	Yes
2020	Åland, Archipelago Sea, Gulf of Finland	Sand, <i>Zostera marina</i>	Mesh bag	4	3	Yes

Field sampling

In 2018 and 2019, we sampled infauna at 5 sites in the Åland Islands (2 eastern and 3 southern) with an Ekman bottom grab (3 replicates, 0.0289 m², sieved at 0.5 mm) from unvegetated soft sediments (2–5 m depth). The sampling was done twice each year, in June and in August.

In July 2019, we sampled infauna using a bottom corer (5 replicates, Ø 10.5 cm, 10 cm deep, sieved at 0.5 mm) from soft sediments (1–3 m depth) with sparse macrophyte cover (*Myriophyllum spicatum*, *Potamogeton perfoliatus*, *Stuckenia pectinata*, *Z. marina*) at 6 sites in the Archipelago Sea and southern Bothnian Sea.

In July 2020, we sampled epifauna associated with filamentous algae (mostly composed of *Cladophora glomerata* and *Ulva intestinalis*) on hard substrates at 9 sites in the Archipelago Sea. The algae were collected randomly by hand at 0.5 m depth at each site. We measured the dry weight of the algae in each sample.

In July 2020 we also sampled epifauna associated with bladderwrack *F. vesiculosus* on hard substrate in the central Gulf of Finland (8 sites), Archipelago Sea (from inner to outer archipelago, altogether 24 sites), northeastern and western Åland Islands (10 and 7 sites, respectively), and southern Bothnian Sea (6 sites). The samples were taken from 0.5–1 m depth using mesh bags (mesh size 0.5 mm) and sieved through a 0.5 mm sieve. 6 replicates in total were taken at each study site, 3 from the sheltered and 3 from the exposed sides of small rocky islands. We measured *F. vesiculosus* wet weight of each sample and estimated the *F. vesiculosus* dry weight using dry weight:wet weight ratio (based on a ratio measured for 10 random *F. vesiculosus* thalli).

In August–September 2020, we sampled epifauna (9–10 replicates, Ø 20 cm mesh bags, mesh size 0.5 mm) and infauna (5 replicates, Ø 10.5 cm corer, sieved at 0.5 mm) from 4 eelgrass (*Z. marina*) meadows on soft substrate in

the Gulf of Finland, the Archipelago Sea, and the Åland Islands. For the epifauna samples, we also measured *Z. marina* aboveground (i.e. shoot) dry weight of each sample.

For all field sampling methods, we calculated the mean density of *S. vanhaareni* in each site and reported densities (Table S1) relative to sampling area (individuals m⁻²) and to vegetation dry weight (individuals g dw⁻¹) for epifaunal samples. Salinity throughout the study areas is relatively stable (ca. 5–6), and, while sampling of different habitats was conducted at different time points, sampling within a habitat type was always conducted during the same season. Thus, the effect of salinity, temperature and successional state of the community should have had minor effects on the community composition within each substrate type.

Community analyses

To assess whether epifaunal community composition differed between locations with and without *S. vanhaareni*, we compared the community composition in *F. vesiculosus* (n = 170 from 29 sites) and *Z. marina* (n = 38 from 4 sites) habitats sampled in 2020 (see *Field sampling* above). The *F. vesiculosus* and *Z. marina* communities were analysed separately. We excluded data from areas where *S. vanhaareni* was completely absent in the *F. vesiculosus* analysis (southeastern Åland Islands, outer Archipelago Sea, central Gulf of Finland) (Figure 2). If *S. vanhaareni* was present in some sites within an area, all were included. In the *Z. marina* analysis, there were only four sites, so all were included. We considered the following taxa in the analysis: *S. vanhaareni*, Amphipoda (mostly *Gammarus* spp.), Isopoda (*Idotea* spp. and *Jaera* spp.), *Rhithropanopeus harrisi*, *Praunus* spp., *Palaemon* spp., Mysidae, Copepoda, Ostracoda, *Cerastoderma glaucum*/*Parvicardium hauniense*, *Limecola balthica*, *Mytilus trossulus*, *Bithynia tentaculata*, Hydrobiidae/*Potamopyrgus antipodarum*, *Limapontia* sp., *Radix* spp., *Theodoxus fluviatilis*, *Piscicola geometra*, Polychaeta, Oligochaeta, Nematoda, *Cyanophthalma obscura*, Turbellaria, Chironomidae, Coleoptera, Trichoptera, *Macropoda* sp., Collembola, and Arachnida.

Community analyses were conducted in PRIMER-E v6 (Clarke and Gorley 2006) on the abundance of each taxon in each sample separately for *F. vesiculosus* and *Z. marina* habitats. The data were square root transformed, and the resemblance matrices were calculated based on Bray-Curtis similarity. Differences between communities with and without *S. vanhaareni* were analyzed with ANOSIM. Global-R in ANOSIM indicates how similar communities are on a scale from 0 to 1, with 1 indicating complete dissimilarity and values < 0.2 indicating a high degree of similarity and overlap (Clarke and Gorley 2006). The differences in community composition were visualized in multidimensional scaling (MDS) plots. Due to the technical limitation of multivariate analyses, the nested structure of the data

Table 2. Functional and ecological traits of *Sinelobus vanhaareni*, related species *S. stanfordi* and southern Baltic tanaidacean *Heterotanais oerstedii*. The level of verification indicates whether/which type of information exists for *S. vanhaareni*, or if it is inferred from other species.

Trait	Modality	Level of verification for <i>S. vanhaareni</i> , or from another species	Reference
Maximum size	3 mm	<i>S. vanhaareni</i> .	Bamber 2014
Longevity	< 1 year	<i>H. oerstedii</i> . Unverified for <i>S. vanhaareni</i> .	Bückle Ramírez 1965
Reproductive technique	Sexual	All tanaidaceans are egg brooders with direct development within the marsupium.	Błażewicz-Paszkowycz et al. 2012
Sexual differentiation	Gonochoric	Some tanaidaceans (e.g. <i>H. oerstedii</i>) can be hermaphroditic (Bückle Ramírez 1965), but this has not been reported in <i>S. vanhaareni</i> .	Bamber 2014
Developmental technique	Ovoviviparous	All tanaidaceans are egg brooders with direct development within the marsupium.	Błażewicz-Paszkowycz et al. 2012
Reproductive frequency	Annual protracted	<i>H. oerstedii</i> . In <i>S. stanfordi</i> , frequency depends on latitude (continuous in low latitudes, annual in high latitudes). In <i>S. vanhaareni</i> , we observed brooding females from July-September but no sampling has been conducted outside of this period.	Bückle Ramírez 1965; César and Becerra 2019; this study
Living habit	Tube dweller	<i>S. stanfordi</i> ; tubes also observed for <i>S. vanhaareni</i> .	Gardiner 1975; Moore and Eastman 2015; this study
Environmental position	50% Infaunal, 50% Epibenthic/epifaunal	<i>S. vanhaareni</i> (in seagrass, more abundant epifaunally than infaunally).	This study
Depth	0–25 m	<i>S. vanhaareni</i> .	This study, Räsänen 2018; Brzana et al. 2019; Holmberg et al. 2020; Räsänen and Koivunen 2020; Vahtera et al. 2020
Habitat	Vegetation, sand, mud, clay, natural and artificial hard substrates	<i>S. vanhaareni</i> .	This study; Brzana et al. 2019
Feeding position	50% Surface 50% subsurface	<i>H. oerstedii</i> . Likely similar for <i>S. vanhaareni</i> .	Bückle Ramírez 1965
Diet	75% Detritivorous 12.5% Herbivorous 12.5% Carnivorous	<i>Sinelobus</i> sp., <i>H. oerstedii</i> . Likely similar for <i>S. vanhaareni</i> .	Bückle Ramírez 1965; Heiman et al. 2008; Rishworth et al. 2018
Resource capture method	Jawed	All tanaidaceans.	Bamber 2014
Mobility	Semi-mobile	All tanaidaceans.	Bamber 2014
Movement type	50% Crawler 50% Tube dweller	<i>H. oerstedii</i> . Likely similar for <i>S. vanhaareni</i> .	Bückle Ramírez 1965
Dispersal potential	Non-disperser	All tanaidaceans are egg brooders with direct development within the marsupium.	Błażewicz-Paszkowycz et al. 2012
Pelagic phase	No	All tanaidaceans are egg brooders with direct development within the marsupium.	Błażewicz-Paszkowycz et al. 2012

was ignored, and all samples from each site were considered independently in the analyses (but taken into account when interpreting the data).

Functional traits

To assess the potential impacts of *S. vanhaareni* on ecosystem functioning and trophic networks, we undertook a literature review to determine functional traits and information on trophic links. As we found little literature on this species, we also collected trait data on the closely related *S. stanfordi* and the southern Baltic species *Heterotanais oerstedii* Krøyer, 1842. We selected traits related to life history, habitat, reproduction, dispersal, and trophic relationships (Table 2), based on previous studies of

infaunal functional traits in the Baltic Sea (e.g. Törnroos and Bonsdorff 2012). Life history, reproduction and dispersal traits provide information on the potential spread of the species, while traits linked to habitat give insight about which habitats are likely affected and the potential physical effects of the species on habitats (e.g. bioturbation, nutrient cycling, etc.). Lastly, trophic traits provide insight on the potential impacts of the species on trophic networks.

Results

Distribution and abundance

Sinelobus vanhaareni was present throughout the southwestern Finnish coast in 2018–2020, including the Gulf of Finland, Archipelago Sea, southern Bothnian Sea, and Åland Islands, with the highest densities (up to 1500 individuals m⁻²) observed in epifaunal samples from vegetated habitats including *Z. marina* and *F. vesiculosus* (Table S1, Figure 2). In 2020, the population of *S. vanhaareni* in these vegetated habitats was concentrated in the eastern parts of the inner and middle Archipelago Sea and in the southern Bothnian Sea (Figure 2). Individuals were also found in several other shallow hard- and soft-substrate habitats, including mud, sand, and among filamentous algae growing on rocks (Table S1, Figure 2). These included adult individuals of both sexes, including egg-brooding females in all areas. Additional sightings were also noted from deeper (10–25 m) benthic habitats (mud and clay) in five coastal municipalities (Helsinki, Naantali, Porvoo, Rauma, Turku; Räisänen 2018; Holmberg et al. 2020; Räisänen and Koivunen 2020; Vahtera et al. 2020; Turkki 2021) and from small boats, hard surfaces, and fouling plates in six marinas and harbours (Hanko, Kasnäs, Raisio, Ruoholahti, Satava, Vuosaari; O. Outinen and J. Vuolamo *pers. comm.*).

Community analyses

Epifaunal community composition in *F. vesiculosus* differed significantly between communities with and without *S. vanhaareni*, but the differences between these communities were negligible due to high overlap (ANOSIM Global R = 0.175, $p < 0.001$), which was also visible on the MDS plot (Figure 3A). The epifaunal community composition in *Z. marina* also differed significantly between communities with and without *S. vanhaareni*, but contrary to *F. vesiculosus*, this difference was notable (ANOSIM Global R = 0.513, $p < 0.001$) and clearly visible on the MDS plot (Figure 3B). However, this effect was likely driven by differences in overall community structure between the sampled sites (ANOSIM Global R = 0.926, $p < 0.001$), and not driven solely by the presence of *S. vanhaareni*. As the majority of samples (9 of 11) that contained *S. vanhaareni* were from the same site, additional data would be needed to properly assess if there are differences in community structure due to *S. vanhaareni* presence at a much larger geographical scale.

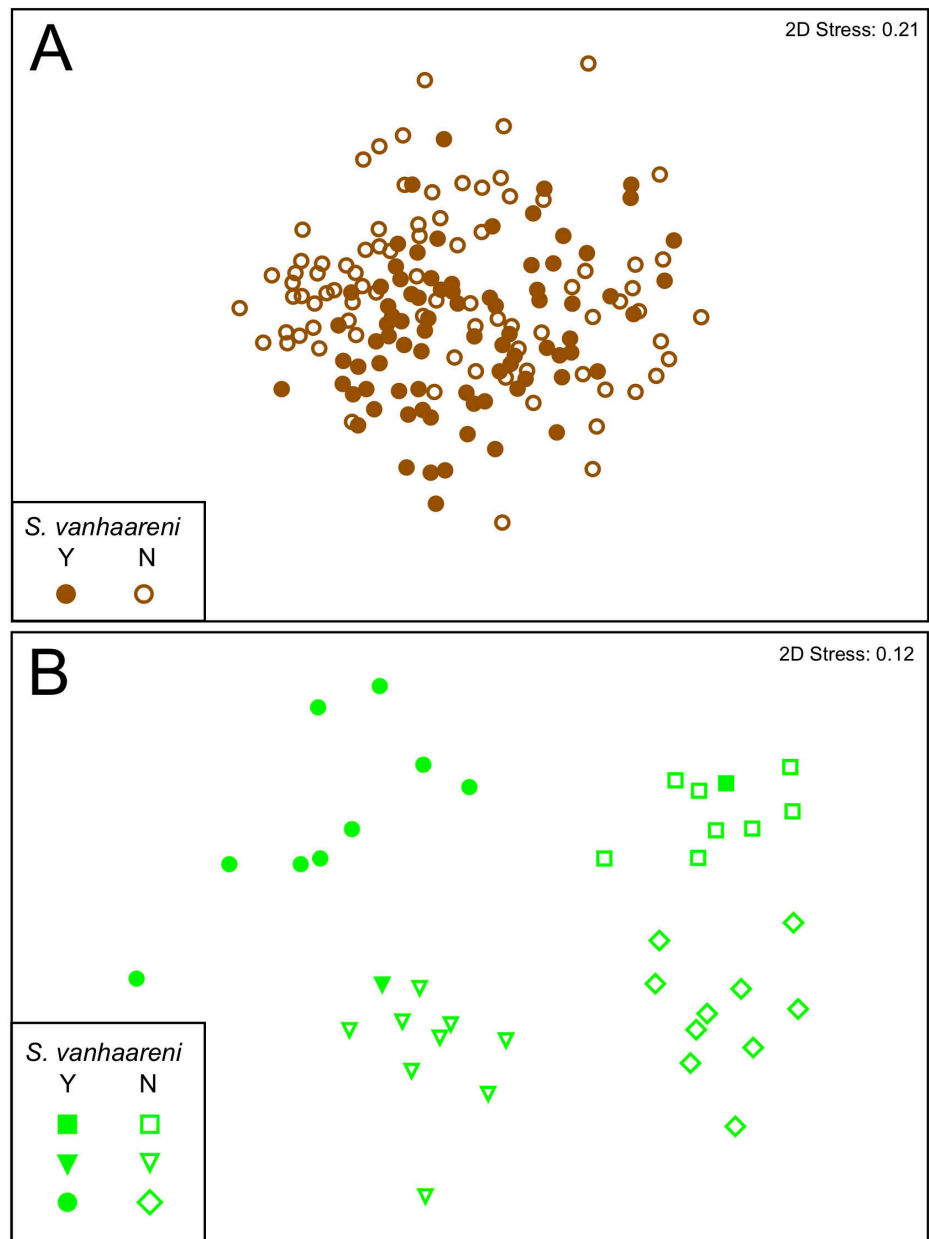


Figure 3. Multidimensional scaling (MDS) plots visualizing the epifaunal community composition in (A) *Fucus vesiculosus* and (B) *Zostera marina* habitats. Filled symbols (Y) indicate the presence of *S. vanhaareni* and open symbols (N) indicate its absence. In panel B, different symbols indicate different sites (squares: Fårö, triangles: Tvärminne, circles: Ängsö, diamonds: Hinderbengtsviken). Note the lack of open circles, indicating that *S. vanhaareni* was present in all Ängsö samples, and the lack of filled diamonds, indicating that it was absent in all Hinderbengtsviken samples. Almost all (9 of 11) of the samples where *S. vanhaareni* was present were from Ängsö, and thus the grouping of *S. vanhaareni* communities is mainly due to the differing community composition between the study sites.

Functional traits

We found that basic morphological and reproductive traits of tanaidaceans were well documented, and this study reported, for the first time, the distribution and abundance of *S. vanhaareni* across different habitats and depths in the northern Baltic Sea (Table 2). However, the literature review revealed that several important gaps remain, particularly relating to life span, reproductive frequency, and trophic interactions.

Discussion

Since being first reported in Finland in 2016 near Inkoo in the western Gulf of Finland (Finnish Biodiversity Information Facility), the non-indigenous tanaidacean *Sinelobus vanhaareni* is now present throughout the southern and southwestern Finnish coast, from the central Gulf of Finland and throughout the Archipelago Sea up to the Bothnian Sea and Åland Islands. Egg-brooding females were observed in all sampled areas in July–September 2020 (Figure S1), indicating that the species is reproducing in Finnish waters and that the population is likely self-sustaining. However, we found no small juvenile individuals. Either the eggs hatch later in the season, or the newly-hatched juveniles were too small (< 0.5 mm) to be included in our samples. Year-round sampling using a smaller mesh size would be needed to fully understand the life cycle and phenology. As the species has little dispersal capacity due to its small size and lack of pelagic larval phase, human-mediated vectors have probably contributed to spread of this magnitude. Shipping, in particular ballast water and hull transfer, is an important vector for non-indigenous marine species (Ojaveer et al. 2017) and has been noted as a vector for another tanaidacean *Tanais dulongii* (Rumbold et al. 2015). Brzana et al. (2019) suggested that spread of *S. vanhaareni* throughout the southern Baltic Sea has likely occurred through fouling on ship hulls. This is also likely to be the case in Finland, though we suggest that recreational boating, which is very popular in the area, may also be a major spread vector, as multiple individuals have been found on small boat hulls and hard surfaces in harbours and marinas (J. Vuolamo *pers. comm.*). The high abundance of *S. vanhaareni* on the brown alga *Fucus vesiculosus* suggests that drifting fragments of *F. vesiculosus* (Rothäusler et al. 2015) could also contribute to the spread of the species along the coast.

Tanaidaceans are widely distributed and have been recorded from a number of different habitats, substrates, and depths in different parts of the world (García-Madrigal et al. 2005; Hendrickx and Ibarra 2008; Bamber 2012; Slivak et al. 2013; Błażewicz-Paszkowycz et al. 2015; Ferreira et al. 2015; Kassuga et al. 2017; Jakiel et al. 2015; Rumbold et al. 2015; Rishworth et al. 2018, 2019). In this study, we found that *S. vanhaareni* also occupied a broad range of infaunal and epifaunal habitats, including mud, clay, sand, filamentous algae, *Z. marina* shoots, and *F. vesiculosus* thalli. In *Z. marina* meadows, *S. vanhaareni* seems to be more abundant as epifauna on vegetation than as infauna in the sediment. This suggests that the species benefits from the habitat complexity offered by aboveground vegetation which provides refuge, food, and shelter from disturbances (e.g. Pihl 1986; Boström and Bonsdorff 2000). Its presence across multiple habitat types, substrates, and depths, including artificial substrates in human environments and anoxic and oil-polluted sediments (e.g. Holmberg et al. 2020), also suggests a high degree of persistence and tolerance to environmental conditions.

As communities with and without *S. vanhaareni* were highly overlapping, we found no evidence (using a space-for-time approach) that it has significantly altered the macrofaunal community composition associated with *F. vesiculosus*, at least at this stage of spread. However, we were unable to assess this in other habitats such as *Z. marina*, as it was only abundant in one site. Similarly, shifts in meiofaunal community composition could not be tested here, as the sampling methodology did not target small meiofaunal species below 0.5 mm. The effects of *S. vanhaareni* in different habitats definitely merit further attention, as its high abundance in some sites suggests potential for altering ecosystem functioning and/or trophic networks as it continues to spread. Due to the low native biodiversity of the Baltic Sea, non-indigenous species have previously introduced novel traits and trophic links, leading to shifts in ecosystem functioning, community structure, and trophic interactions (Kotta et al. 2006; Packalén et al. 2008; Aarnio et al. 2015; Jormalainen et al. 2016). The magnitude of a non-indigenous species' impacts is highly context-dependent (Thomsen et al. 2011), depending on the species in question, the recipient community, and environmental conditions in the recipient habitat. Determining the traits and trophic links of a new non-indigenous species is therefore the first step in evaluating its potential impacts.

However, as with the majority of non-indigenous species in the Baltic Sea (Ojaveer et al. 2021), studies quantifying or even documenting the effects of *S. vanhaareni* on Baltic food webs are lacking. To our current knowledge, there are no records of *S. vanhaareni* trophic interactions or any studies on its role in the food web using e.g. gut contents analysis (visual or molecular approaches) or stable isotope analysis in any areas. However, inference based on its functional traits, phylogeny, and distribution in different habitats, as well as documented trophic interactions of related species in other parts of the world, suggests that *S. vanhaareni* in the Baltic Sea is: (i) Likely part of the detritus-based pathway in benthic food webs in shallow coastal areas (and possibly to depths of down to 25 m) and plays a role in meiofaunal community structure due to its small size. (ii) Feeding mainly on detritus and associated microorganisms (e.g. algal particles, nematodes; Bückle Ramírez 1965; Heiman et al. 2008; Rishworth et al. 2018). Although *S. vanhaareni* increases the taxonomic diversity of the community, as there are no other tanaidacean species in the northern Baltic Sea, it is likely contributing to the functional redundancy of small epifaunal and infaunal invertebrate detritivorous consumers, such as amphipods and polychaetes, rather than increasing functional richness. It could thus potentially have an indirect positive effect on macrophyte growth by feeding on epiphytic microalgae and detritus (Hughes et al. 2004). (iii) Likely a prey/food item for small benthic feeding fish and crustacean species, such as gobies, juvenile flounder, sticklebacks, perch, shrimp, etc., which feed on other small crustaceans such as amphipods (see

Nordström et al. 2015 and references therein). Beyond trophic interactions, *S. vanhaareni* could also potentially affect ecosystem functioning, sediment dynamics and small-scale biogeochemistry in soft substrates, through its tube-building and bioturbation activities in a similar way to infaunal amphipods (Rhoads and Boyer 1982).

Determining the actual distribution of this species, along with confirming and quantifying the trophic links above (through stable isotope analysis, gut content analysis, and experimental trials) are key to addressing knowledge gaps and understanding its effects on Baltic Sea communities and trophic networks. Public observations of conspicuous invasive species in Finland are usually readily reported to online portals, providing a reliable source of information on their distribution and spreading rates. However, as *S. vanhaareni* is small and inconspicuous, there are very few public observations. Therefore a dedicated monitoring programme would be necessary to determine the true distribution of this species and assess its impacts. Monitoring of harbours, ship hulls, and ballast water for non-indigenous species in the Baltic Sea is underway in the ongoing COMPLETE project (<https://balticcomplete.com/>), but based on the data collected here, we suggest that a monitoring programme targeting this species should also include a wide variety of natural habitats and artificial substrates along a large depth gradient (at least 0–25 m).

Conclusions

Though small and inconspicuous, *S. vanhaareni* has quickly become more frequently observed since its initial recorded sighting in Finnish waters, with its spread possibly aided by recreational boating and drifting algal fragments. The species now occurs in a variety of habitats and environments, from unvegetated sediments down to 25 m depth, to seagrass and algal habitats in shallower waters. *Sinelobus vanhaareni* also seems persistent and tolerant to a wide range of environmental conditions, as it has been recorded in environments with clear human impacts such as boat hulls, marinas, and anoxic and oil-polluted sediments. It is likely part of the detritus-based pathway in the food web, but several functional traits and trophic connections are still unverified. Thus, its potential effects on coastal ecosystems are uncertain, opening up many avenues for further research into the ecological role of this species in the northern Baltic Sea.

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Authors' contribution

KG and HR conceptualized the study. KG, HH, TS, SS-L, HR designed the sampling protocols and methods. All authors participated in data collection. JW, MCN, TS, HR analysed the data. KG, HH, MCN, TS, SS-L, HR wrote the manuscript and all authors participated in editing and finalising the manuscript.

Ethics and permits

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References

- Aarnio K, Tömroos A, Björklund C, Bonsdorff E (2015) Food web positioning of a recent coloniser: the North American Harris mud crab *Rhithropanopeus harrisi* (Gould, 1841) in the northern Baltic Sea. *Aquatic Invasions* 10: 399–413, <https://doi.org/10.3391/ai.2015.10.4.04>
- Anderson G (2016) Tanaidacea - Thirty Years of Scholarship, Version 2.0. <https://aquila.usm.edu/tanaids30/3> (accessed 14 January 2021)
- AquaNIS (2015) Information system on Aquatic Non-Indigenous and Cryptogenic Species. Version 2.36+, www.corpi.ku.lt/databases/aquanis (accessed 21 January 2021)
- Bamber RN (2008) Tanaidaceans (Crustacea: Peracarida: Tanaidacea) from Moreton Bay, Queensland. *Memoirs of the Queensland Museum* 54(1): 143–218
- Bamber RN (2012) A re-assessment of *Hexapleomera* Dudich, 1931 (Crustacea: Tanaidacea: Tanaididae), with designation of three new species. *Zootaxa* 3583: 51–70, <https://doi.org/10.11646/zootaxa.3583.1.4>
- Bamber RN (2014) Two new species of *Sinelobus* Sieg, 1980 (Crustacea: Tanaidacea: Tanaididae), and a correction to the higher taxonomic nomenclature. *Journal of Natural History* 48: 2049–2068, <https://doi.org/10.1080/00222933.2014.897767>
- Błażewicz-Paszkowycz M, Bamber R, Anderson G (2012) Diversity of Tanaidacea (Crustacea: Peracarida) in the world's oceans - how far have we come? *PLoS ONE* 7: e33068, <https://doi.org/10.1371/journal.pone.0033068>
- Błażewicz-Paszkowycz M, Kobyłecka E, Jennings RN (2015) Redescription of wood-associated tanaidacean *Protanais birsteini* (Kudinova-Pasternak, 1970) and its relationship within the Tanaididae. *Deep Sea Research Part II, Topical Studies in Oceanography* 111: 333–342, <https://doi.org/10.1016/j.dsr2.2014.10.006>
- Boström C, Bonsdorff E (2000) Zoobenthic community establishment and habitat complexity - the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. *Marine Ecology Progress Series* 205: 123–138, <https://doi.org/10.3354/meps205123>
- Brzana R, Marszewska L, Normant-Saremba M, Błażewicz M (2019) Non-indigenous tanaid *Sinelobus vanhaareni* Bamber, 2014 in the Polish coastal waters - an example of a successful invader. *Oceanological and Hydrobiological Studies* 48: 76–84, <https://doi.org/10.1515/ohs-2019-0008>
- Bückle Ramirez LF (1965) Untersuchungen über die Biologie von *Heterotanais oerstedii* Kröyer (Crustacea, Tanaidacea). *Zeitschrift für Morphologie und Ökologie der Tiere* 5: 714–782, <https://doi.org/10.1007/BF00406235>
- César II, Becerra RV (2019) Biologic and ecologic aspects of *Sinelobus stanfordi* (Richardson, 1901) (Crustacea, Tanaidacea) in the Martín García Island Natural Reserve, Río de la Plata, Argentina. *Annual Research & Review in Biology* 31: 1–14, <https://doi.org/10.9734/arrb/2019/v3i1i330048>
- Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E Ltd, Plymouth, UK, 189 pp

- Ferreira AC, Ambrosio ES, Rodrigues Capítulo A (2015) Population ecology of *Sinelobus stanfordi* (Crustacea: Tanaidacea) in a temperate southern microtidal estuary. *New Zealand Journal of Marine and Freshwater Research* 49: 462–471, <https://doi.org/10.1080/00288330.2015.1089914>
- García-Madrigal MDS, Heard R, Suárez-Morales E (2005) Records of and observations on Tanaidaceans (Peracarida) from shallow waters of the Caribbean coast of Mexico. *Crustaceana* 77: 1153–1177, <https://doi.org/10.1163/1568540043166137>
- Gardiner LF (1975) A fresh and brackish water Tanaidacean *Tanais stanfordi* Richardson, 1901, from a hypersaline lake in the Galapagos Archipelago, with a report on West-Indian specimens. *Crustaceana* 29: 127–140, <https://doi.org/10.1163/156854075X00144>
- Gittenberger A, Rensing M, Stegenga H, Hoeksema B (2010) Native and non-native species of hard substrata in the Dutch Wadden Sea. *Nederlandse Faunistische Mededelingen* 33: 21–75
- Heiman KW, Vidargas N, Micheli F (2008) Non-native habitat as home for non-native species: comparison of communities associated with invasive tubeworm and native oyster reefs. *Aquatic Biology* 2: 47–56, <https://doi.org/10.3354/ab00034>
- HELCOM (2018) Trends in arrival of new non-indigenous species HELCOM core indicator 2018. HELCOM core indicator report, 20 pp
- Hendrickx M, Ibarra S (2008) Presence of *Sinelobus stanfordi* (Richardson, 1901) (Crustacea: Tanaidacea: Tanaidae) in coastal lagoons of western Mexico. *Nauplius* 16(2): 79–82
- Holmberg J, Anttila-Huhtinen M, Raunio J (2020) Porvoon edustan merialueen yhteistarkkailun vuosiraportti 2019. Laajat tutkimukset. Kymijoen vesi ja ympäristö ry. Nro 294/2020, 192 pp
- Hughes AR, Bando KJ, Rodriguez LF, Williams SL (2004) Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach. *Marine Ecology Progress Series* 282: 87–99, <https://doi.org/10.3354/meps282087>
- Jakiel A, Stępień A, Józwiak P, Serigstad B, Błażewicz-Paszkowycz M (2015) First record of Tanaidacea (Crustacea) from a deep-sea coral reef in the Gulf of Guinea. *Zootaxa* 3995: 203–228, <https://doi.org/10.11646/zootaxa.3995.1.18>
- Johnson SB, Attramadal YG (1982) Reproductive behaviour and larval development of *Tanais cavolinii* (Crustacea: Tanaidacea). *Marine Biology* 71: 11–16, <https://doi.org/10.1007/BF00396987>
- Jormalainen V, Gagnon K, Sjöroos J, Rothäusler E (2016) The invasive mud crab enforces a major shift in a rocky littoral invertebrate community of the Baltic Sea. *Biological Invasions* 18: 1409–1419, <https://doi.org/10.1007/s10530-016-1090-9>
- Kassuga AD, Marafon-Almeida A, Masunari S (2017) Population structure of *Sinelobus cf. stanfordi* (Crustacea, Tanaidacea) from Pinheiros River mangrove, Guaratuba Bay, southern Brazil. *Journal of the Marine Biological Association of the United Kingdom* 97: 243–247, <https://doi.org/10.1017/S0025315416000242>
- Kotta J, Kotta I, Simm M, Lankov A, Lauringson V, Pöllumäe A, Ojaveer H (2006) Ecological consequences of biological invasions: three invertebrate case studies in the north-eastern Baltic Sea. *Helgoland Marine Research* 60: 106–112, <https://doi.org/10.1007/s10152-006-0027-6>
- Leppäkoski E, Olenin S (2000) Non-native species and rates of spread: lessons from the brackish Baltic Sea. *Biological Invasions* 2: 151–163, <https://doi.org/10.1023/A:1010052809567>
- Leppäkoski E, Olenin S (2001) The meltdown of biogeographical peculiarities of the Baltic Sea: the interaction of natural and man-made processes. *AMBIO* 30: 202–209, <https://doi.org/10.1579/0044-7447-30.4.202>
- Leppäkoski E, Gollasch S, Gruszka P, Ojaveer H, Olenin S, Panov V (2002) The Baltic - a sea of invaders. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1175–1188, <https://doi.org/10.1139/f02-089>
- Moore PG, Eastman LB (2015) The tube-dwelling lifestyle in crustaceans and its relation to feeding. In: Tiel M, Watling L (eds), *Lifestyles and Feeding Biology*. Oxford University Press, New York, USA, pp 35–77
- Nordström MC, Aarnio K, Törnroos A, Bonsdorff E (2015) Nestedness of trophic links and biological traits in a marine food web. *Ecosphere* 6: 161, <https://doi.org/10.1890/ES14-00515.1>
- Ojaveer H, Olenin S, Narščiūsis A, Florin A-B, Ezhova E, Gollasch S, Jensen KR, Lehtiniemi M, Minchin D, Normant-Saremba M, Stråke S (2017) Dynamics of biological invasions and pathways over time: a case study of a temperate coastal sea. *Biological Invasions* 19: 799–813, <https://doi.org/10.1007/s10530-016-1316-x>
- Ojaveer H, Kotta J, Outinen O, Einberg H, Zaiko A, Lehtiniemi M (2021) Meta-analysis on the ecological impacts of widely spread non-indigenous species in the Baltic Sea. *Science of The Total Environment* 786: 147375, <https://doi.org/10.1016/j.scitotenv.2021.147375>
- Packalén A, Korpinen S, Lehtonen KK (2008) The invasive amphipod species *Gammarus tigrinus* (Sexton 1939) can rapidly change littoral communities in the Gulf of Finland (Baltic Sea). *Aquatic Invasions* 3: 405–412, <https://doi.org/10.3391/ai.2008.3.4.5>
- Pihl L (1986) Exposure, vegetation and sediment as primary factors for mobile epibenthic faunal community structure and production in shallow marine soft bottom areas. *Netherlands Journal of Sea Research* 20: 75–83, [https://doi.org/10.1016/0077-7579\(86\)90063-3](https://doi.org/10.1016/0077-7579(86)90063-3)
- Räisänen R (2018) Rymättylän ja Velkua merialueiden yhteistarkkailututkimus. Vuosiraportti 2017. Lounais-Suomen vesi- ja ympäristötutkimus Oy. Nro 144-18-7080, 77 pp

- Räisänen R, Koivunen S (2020) Turun seudun puhdistamo Oy:n Räisionjoen pumppaamon ylivuodon vesistön jälkitarkkailun pohjaeläintutkimus, vuonna 2020. Lounais-Suomen vesija ympäristötutkimus Oy. Nro 301-20-7225, 20 pp
- Rhoads DC, Boyer LF (1982) The effects of marine benthos on physical properties of sediments. In: McCall PL, Tevesz MJS (eds), *Animal-Sediment Relations. Topics in Geobiology*, vol 100. Springer, Boston, MA, USA, pp 3–52, https://doi.org/10.1007/978-1-4757-1317-6_1
- Rishworth GM, Perissinotto R, Bird MS, Pelletier N (2018) Grazer responses to variable macroalgal resource conditions facilitate habitat structuring. *Royal Society Open Science* 5: 171428, <https://doi.org/10.1098/rsos.171428>
- Rishworth GM, Perissinotto R, Błażewicz M (2019) *Sinelobus stromatoliticus* sp. nov. (Peracarida: Tanaidacea) found within extant peritidal stromatolites. *Marine Biodiversity* 49: 783–794, <https://doi.org/10.1007/s12526-018-0851-3>
- Rothäusler E, Corell H, Jormalainen V (2015) Abundance and dispersal trajectories of floating *Fucus vesiculosus* in the Northern Baltic Sea. *Limnology and Oceanography* 60: 2173–2184, <https://doi.org/10.1002/lno.10195>
- Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *American Zoologist* 37: 621–632, <https://doi.org/10.1093/icb/37.6.621>
- Rumbold CE, Obenat SM, Spivak ED (2015) Comparison of life history traits of *Tanais dulongii* (Tanaidacea: Tanaididae) in natural and artificial marine environments of the southwestern Atlantic. *Helgoland Marine Research* 69: 231–242, <https://doi.org/10.1007/s10152-015-0432-9>
- Sieg J (1980) Taxonomische Monographie der Tanaidae Dana 1849 (Crustacea: Tanaidacea). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 537: 1–272
- Slivak NN, Poppe JL, Würdig NL (2013) Population structure of the tanaid *Sinelobus stanfordi* (Richardson, 1901) (Crustacea, Tanaidacea) associated with roots of the water hyacinth *Eichhornia azurea* (Sw.) Kunth. (Liliiflorae, Pontederiaceae), from a coastal lagoon in southern Brazil. *Revista Brasileira de Zootecias* 15: 15–25
- Thomsen MS, Wernberg T, Olden JD, Griffin JN, Silliman BR (2011) A framework to study the context-dependent impacts of marine invasions. *Journal of Experimental Marine Biology and Ecology* 400: 322–327, <https://doi.org/10.1016/j.jembe.2011.02.033>
- Törnroos A, Bonsdorff E (2012) Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species. *Ecological Applications* 22: 2221–2236, <https://doi.org/10.1890/11-2042.1>
- Turkki H (2021) Rauman merialueen pohjaeläintutkimus vuonna 2019. Lounais-Suomen vesija ympäristötutkimus Oy. Nro 116-21-311, 80 pp
- Vahtera E, Räisänen M, Muurinen J (2020) Pääkaupunkiseudun merialueen tila 2018-2019. Helsingin kaupunki. Kaupunkiympäristön julkaisuja 2020:25, 314 pp
- van Haaren T, Soors J (2009) *Sinelobus stanfordi* (Richardson, 1901): a new crustacean invader in Europe. *Aquatic Invasions* 4: 703–711, <https://doi.org/10.3391/ai.2009.4.4.20>

Supplementary material

The following supplementary material is available for this article:

Table S1. Sightings, habitat, sampling methods, and density of *Sinelobus vanhaareni* along the Finnish coast 2016–2020.

Figure S1. *Sinelobus vanhaareni* individuals from *Fucus vesiculosus* samples in the Archipelago Sea.