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Spread of the invasive shell-boring annelid *Polydora websteri* (Polychaeta, Spionidae) into naturalised oyster reefs in the European Wadden Sea

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Abstract

With globally growing aquaculture activities, the co-introduction of parasites alongside large-scale movements of commercial species poses an increasing risk for marine ecosystems. Here, we present the first record of the shell-boring polychaete *Polydora websteri* Hartman in Loosanoff and Engle, 1943 in invasive Pacific oysters *Crassostrea* (*Magallana*) *gigas* (Thunberg, 1793) in the European Atlantic Ocean. In October 2014, mud blisters in the shells of wild Pacific oysters and specimens of a spionid polychaete were observed in close proximity to a commercial oyster farm at the island of Sylt (Germany) in the European Wadden Sea. Subsequent investigations indicated that these blisters only occurred near the farm and that no other mollusc species were affected. Morphological and molecular analysis identified the polychaete as *Polydora websteri*, a species that nowadays widely occurs around the globe, but likely is native to the Asian Pacific. Later sampling activities detected *P. websteri* also at other locations around Sylt as well as in the Dutch part of the Wadden Sea at the island of Texel. The number of polychaetes in the oysters was, however, relatively low and mostly below 10 individuals per oyster. Together, this evidence suggests that *P. websteri* is currently extending its range. As the introduction of *P. websteri* may have severe ecological and economic implications, this study aims to alert others to look for *P. websteri* at Western European coasts within farmed or wild Pacific oysters to further document its spread.

Keywords Aquaculture · Co-introduction · *Crassostrea gigas* · Mud blister · Parasitism

Introduction

Global trade has increased enormously during the last decades resulting in an unparalleled introduction of species across the planet (Vitousek et al. 1996; Mack et al. 2000). Besides transport in vessel ballast water or as hull fouling on ships, direct and indirect introductions via aquaculture activities are the most important invasion vectors for marine ecosystems (Katsanevakis et al. 2013). The latter occur mainly via the deliberate import of commercial species and the subsequent transfer of farmed specimens between aquaculture sites. For example, the culture of marine molluscs has frequently been described as a gateway for species introductions as it is often accompanied by large-scale stock movements (Wolff and Reise 2002; Ruesink et al. 2005; McKindsey et al. 2007). Some species, such as the Pacific oyster *Crassostrea* (*Magallana*) *gigas* (Thunberg, 1793), have been repeatedly translocated into new environments and are nowadays traded and cultured globally (Ruesink et al. 2005; Lucas 2019). Consequently, associated organisms that live in or on the oysters, such as sessile and boring species or parasites, have also unintentionally been introduced outside their native range (Elton, 1958; Goedknegt et al. 2016; Feis et al. 2019). One group of organisms that is likely to be co-introduced with commercial molluscs are shell-boring polychaetes, of which polydorins are the most common group (Blake 1969;

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Boonzaaier et al. 2014). These worms are known to penetrate mollusc shells and form burrows therein (Simon and Sato-Okoshi 2015). In cases of heavy infestations, shells are severely damaged by the boring activity of the worms which may negatively affect host condition as the hosts divert energy from growth to shell repair (Kent 1979; Lleonart et al. 2003). In addition, shell damage reduces shell strength which in turn can lead to increased predation by crabs and other predators (Ambariyanto and Seed 1991; Buschbaum et al. 2007).

A polydorin species often co-introduced with cultured molluscs is *Polydora websteri* Hartman in Loosanoff and Engle, 1943 (Simon and Sato-Okoshi 2015; Rice et al. 2018). This species causes mud-filled blisters inside mollusc shells. These so-called mud blisters are the result of the polychaete's feeding activity that leads to the accumulation of detritus, mud, and faecal particles inside the burrow and the production of additional shell layers by the host to cover the burrow of the intruding worm. The polychaete is considered a serious pest in commercial marine aquaculture throughout the globe, as mud blisters decrease the market value of the infested molluscs (Whitelegge 1890; Lunz 1941; Loosanoff and Engle 1943; Bailey-Brock and Ringwood 1982; Ogburn et al. 2007).

Polydora websteri is deemed to be native to Asian coasts (Rice et al. 2018) but has also been reported from several locations all over the world including Australia, New Zealand, Hawaii, Brazil, the Atlantic and Pacific coasts of North America, and the Black Sea in Europe (Read 2010; Surugiu 2012; Sato-Okoshi and Abe 2013; Barros et al. 2017; Ye et al. 2017; Rice et al. 2018; Martinelli et al. 2020). Since it is often associated with economically important mollusc species that are cultured globally, such as *C. gigas*, it is possible that the polychaete will extend its range along coastal areas in the future.

In Europe, Pacific oysters have been cultured for several decades as alternative to the native European flat oyster *Ostrea edulis* Linnaeus, 1758, which was driven to extinction due to overexploitation in many European coastal areas by the 1950s (Troost 2010). The first *C. gigas* were deliberately introduced to several locations along the European Atlantic coast for cultivation purposes in the 1960s and 1970s in the belief that water temperatures were too cold to allow for natural reproduction of the oysters (Troost 2010). This assumption proved to be wrong and wild Pacific oyster populations established along much of the European shoreline (see reviews of Troost 2010, Herbert et al. 2016). This was also true for the Wadden Sea, where oysters mostly settled on epibenthic beds of blue mussels *Mytilus edulis* Linnaeus, 1758, and led to the creation of persisting mixed populations of mussels and oysters (Waser et al. 2016, Reise et al. 2017b, van der Meer et al. 2019). The oyster populations of the Wadden Sea originate from two different sources (Moehler et al. 2011). One population stems from oyster farms in the Dutch Delta, from which individuals were deliberately brought to Texel in the Dutch Wadden Sea in the late 1970s and later spread throughout large parts of the Wadden Sea (Troost 2010). The other population in the northern Wadden Sea descends from an oyster farm at Sylt in the German Wadden Sea (Reise 1998, Moehler et al. 2011), which started importing *C. gigas* from the British Isles in 1986.

In the Wadden Sea, molluscs like common periwinkles *Littorina littorea* (Linnaeus, 1758), blue mussels, and Pacific oysters are heavily infested by the small native shell-boring polychaete *Polydora ciliata* (Johnston, 1838). This is easily recognizable by tiny U-shaped burrows lacking dark inclusions. In contrast, in October 2014, Pacific oysters with dark blisters inside the shell (see Fig. 1a) were observed at Blidselbucht (Site 2, see Fig. 2) at northern Sylt adjacent to the only commercial oyster farm of that region. The blisters harboured polydorin worms (Fig. 1b–d) that were of unknown identity and apparently new to the Wadden Sea area. Subsequently, mollusc shells, in particular of Pacific oysters, were investigated for signs of this polychaete throughout the Wadden Sea. Our results represent the first records of *P. websteri* in the Wadden Sea and along the European Atlantic coastline.

Material and methods

After the first sighting of the newly introduced polydorin species, several locations along the eastern coastline of the German Wadden Sea island Sylt and one location at the coast of the Dutch Wadden Sea island Texel were investigated for blisters in live Pacific oysters and in empty oyster shells during autumn 2014. Similarly, other potential hosts, such as mussels and periwinkles, were examined for infestations of this polychaete at Blidselbucht. In some cases, blisters of live oysters and empty shells were opened to check whether they harboured polydorin worms. The polydorins were morphologically inspected and compared with descriptions of species known to occur in the European Atlantic Ocean (Radashevsky 2012). Since our specimens did not match any of these descriptions, they were also compared with descriptions of polydorins from the Asian Pacific Ocean (Sato-Okoshi 1999), where Pacific oysters originate from.

In subsequent years, oysters were not systematically screened, but gaping shells of recently died oysters were inspected for blisters during other sampling activities throughout the entire Wadden Sea (see Fig. 2), and locations with putative positive records were noted. Blisters provide useful information concerning the geographical spread of the polychaete, albeit only of advanced stages of infestation. Thus, recently infested oysters harbouring worm burrows still lacking mud blisters were missed out.

Fig. 1 *Crassostrea gigas* infested with *Polydora websteri* collected from Blidselbucht at Sylt in the German Wadden Sea. **a** Inner surface of infested valves of *C. gigas* showing mud blisters caused by *P. websteri*; **b** close up of an opened mud blister inhabited by *P. websteri*; **c** overview of a single specimen of *P. websteri*; and **d** black lines on the sides of the palps of *P. websteri*. Photo copyrights: Dagmar Lackschewitz

Fig. 2 Sampling locations where Pacific oysters, mussels, and periwinkles were studied for presence of *Polydora websteri* in the Wadden Sea from 2014 onwards. Locations where individuals or blisters of *P. websteri* were recorded are represented by squares, while circles indicate negative records. The inserts show the two sampling areas in the northern (Sylt) and southern (Texel) Wadden Sea, where an initial survey in 2014 took place and where *P. websteri* was recorded. For sampling dates (year, month) and numbers of investigated Pacific oysters, oyster shells, mussels, or periwinkles, see Table 1. The year dates next to the smaller circles in the overview map indicate the last visit to a respective location with a negative record. The dashed lines represent country borders
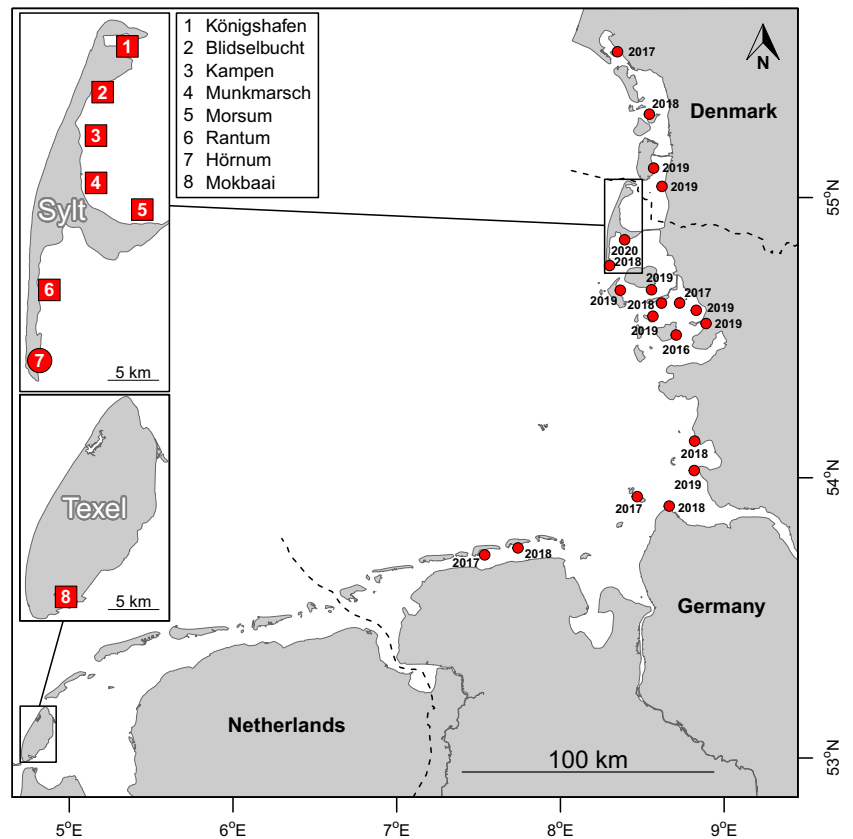
Fig. 3 Phylogenetic tree based on mitochondrial COI sequences. Tree topology is based on Kimura-2-parameter distance matrix and rooted with a sequence of *Pseudopolydora dayii* as outgroup. Bootstrap support out of 1000 replicates is shown for branches with > 95% support. Accession numbers are given for each sequence. Origin of the sequences is given for the *P. websteri* clade, and sequences generated in this study are shown in bold
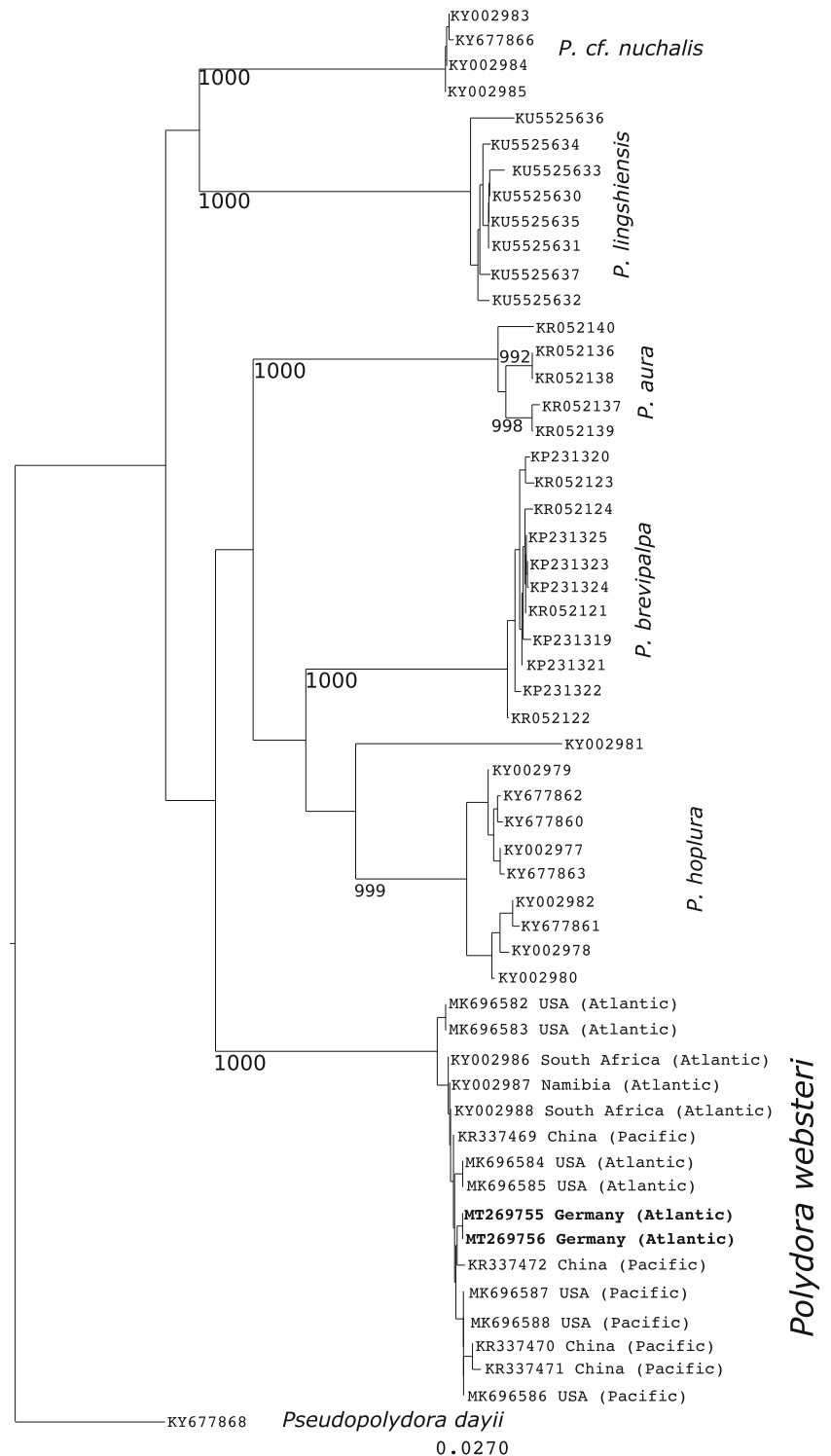
In March 2017, nine Pacific oysters gathered from Blidselbucht were examined to assess the number of blisters per individual oyster, and in late summer/early autumn 2017, a systematic survey was conducted at the two Wadden Sea islands Sylt and Texel. On Sylt, mussels and oysters were sampled at Blidselbucht in August 2017 and on Texel at Mokbaai in October 2017 (Fig. 2). Overall, 41 Pacific oysters (Sylt = 19, Texel = 22) and 229 blue mussels (Sylt = 79, Texel = 150) were randomly collected from the intertidal zone. All collected individuals were incubated overnight in a

solution of one-part ethanol 96% and twenty parts seawater (similar to the 1:20 solution of phenol and seawater used by Handley (1995)) to drive the boring polychaetes out of the shells. The efficiency of the solution had been tested on five oysters, whose shells were completely broken after treatment and carefully investigated for *P. websteri* presence. In all broken oyster shells, no individuals of *P. websteri* were found in addition to the ones that had left the shells overnight. All polydorins were identified and counted per individual mussel or oyster. Prevalence was calculated as the proportion of infested oysters and mussels in each sample. In summer 2018, another sample of 30 Pacific oysters taken at Blidselbucht was inspected for blisters.

Molecular identification

Morphological characteristics of some polydorin species display high variability, which may compromise the species identification based on morphological characteristics (e.g. Sato-Okoshi and Abe 2013). In order to confirm the species identity, two individuals collected from Blidselbucht in early 2019 that showed the same morphological characteristics as previously collected specimens were used for molecular species identification based on cytochrome c oxidase I (mtCOI) as a molecular marker. DNA of both specimens was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. A ~ 680 bp fragment of COI was amplified using the annelid primers X1-F2 C C W G A T A T R G C A T T C C C   a n d   X 1 - R 2 GCKARYCADCTAAATACTTTAA (Ye et al. 2017) in a PCR reaction containing 10 μl of 2x Hot Star Polymerase Mastermix (Qiagen, Hilden, Germany), 1.5 μl of each primer (5 μM), and 2 μl of DNA extract in 20 μl reaction volume. Cycling consisted of 5′ hot start activation at 95 °C, followed by 35 cycles of 50″ at 94 °C, 50″ at 50 °C annealing and 1′30″ extension at 72 °C before ending the reaction with a final extension of 10′ at 72 °C. The PCR products were purified using the Qiaquick DNA purification kit (Qiagen, Hilden, Germany), and 75 ng of the purified products were sequenced from both ends by Eurofins Genomics (Ebersberg, Germany). Forward and reverse reads were assembled using CLC Genomics Workbench v. 8.5 (Qiagen, Hilden, Germany), manually curated and trimmed of primer sequences. The obtained sequences were aligned together with other *Polydora* sequences retrieved from GenBank using muscle (Edgar, 2004). A phylogenetic neighbour joining tree was constructed based on a Kimura-2-parameter distance matrix rooted with the COI sequence of *Pseudopolydora dayii* (GenBank accession: KY677868), and the resulting tree topology was tested against 1000 bootstrap replicates using the software Seqotron v1.0.1 (Fourment and Holmes 2016).

Results

Morphological characteristics

The spionid worms found in blisters of Pacific oysters were generally about 40–50 mm long when alive or anaesthetised in a MgCl$_2$-solution, with the largest specimen anaesthetised measuring 60 mm. Specimens preserved in ethanol shrank to < 20 mm. The most striking characteristics in live animals were thin black lines along the feeding grooves of the palps (see Fig. 1d). In the majority of specimens examined, they appeared as continuous dark lines but could also consist of non-continuous bands or were missing in a few cases. These lines started to fade out when the animals were preserved in ethanol or formalin. Apart from that, there was no dark body pigmentation. The prostomium was bilobed and more or less incised. Two pairs of eyes were in trapezoidal arrangement, while an occipital antenna was absent. The caruncle seemingly extended up to the third segment. Chaetiger 1 only showed neuropodial setae with the notopodial setae missing. Chaetiger 5 was elongated compared with adjacent segments. Its major modified spines were falcate with a lateral flange on the concave side, and the companion chaetae were hastate and showed partly frayed tips. From chaetiger 7 onwards, hooded hooks with constrictions on the shafts were present. Also from chaetiger 7, branchiae continued almost to the rear end. The pygidium was generally disc-like with a distinct dorsal gap but in some specimens tended to be more cup-shaped.

All these characteristics combined did not match up with polydorin species known from the European Atlantic (Radashevsky 2012), suggesting that the species was new to the area. Instead, the morphological features generally corresponded to descriptions of *Polydora websteri* (Radashevsky 1999; Sato-Okoshi 1999; Read 2010; Sarugiu 2012; Barrows et al. 2017; Ye et al. 2017).

Molecular identification

The COI sequences of the investigated specimens were 679 bp in length (GenBank accessions: MT269755, MT269756). Both sequences clustered with the other sequences assigned to *Polydora websteri* and were separated with high bootstrap support from the other *Polydora* species (i.e. *P. hoplura*, *P. brevipalpa*, *P. aura*, *P. lingshiensis*, and *P. nuchalis,* Fig. 3). Therefore our molecular identification matches the morphological identification indicating that also the other specimen that were not subjected to molecular identification were correctly assigned to *P. websteri*. Within the *P. websteri* clade, the sequences generated from the specimens used here were located in a cluster of similar sequences that were isolated from worms collected in the Pacific (China, USA) as well as in the Atlantic Ocean (Namibia, South Africa,

USA). The global distribution of sequence origins within this cluster further supports the recent global spread of this species (Martinelli et al. 2020).

Infestation prevalence and dose

In total, 271 Pacific oysters and 130 single shells of dead oysters were observed systematically for *P. websteri* infestation. In 2014, the period where the polychaete was first recorded in the Wadden Sea, blisters of *P. websteri* could only be detected in oysters from Blidselbucht, while oysters at other investigated locations showed no signs of *P. websteri* infestation (Table 1). There were also no indications that *P. websteri* infected other species, like mussels and periwinkles (Table 1). The prevalences at Blidselbucht in autumn 2014 were 80–90% in alive Pacific oysters and 60–70% in gaping valves of recently died oysters.

As of 2016, Pacific oysters showing mud blisters were also found at the northern end of Sylt at Königshafen (location 1), Kampen (location 3), and Munkmarsch (location 4, Table 1, Fig. 2). In 2020, blisters were furthermore observed close to the causeway connecting Sylt with the mainland at Morsum (location 5) and at the southern end of Sylt near Rantum (location 6, Table 1, Fig. 2). In autumn 2017, blisters in Pacific oysters and specimens of *P. websteri* were found at the island of Texel in the Dutch Wadden Sea. At the other locations throughout the Wadden Sea (Fig. 2), no blisters were found in all shells of dead and gaping Pacific oysters. All six of the new records showed rather low occurrences of *P. websteri* (prevalence on Texel 14% and very few oysters featuring blisters at the other locations at Sylt (Table 1, Reise pers. obs.), compared with the area around the oyster farm at Blidselbucht, where the prevalence was found to be relatively high with 42% and 77% in 2017 and 2018, respectively (Table 1). With respect to the infection dose of individual oysters sampled in autumn 2017, the average intensity of *P. websteri* in the oysters was 3.18 ± 3.43 SD, with the highest record of 11 individuals of *P. websteri* in an oyster from Blidselbucht (Table 2). Considering the number of blisters per oyster, a maximum of 12 blisters was observed in a 15.5-cm-long oyster (Table 2).

Table 1 Locations as well as year and month (beginning with first record) at which Pacific oysters, mussels, and periwinkles were investigated in the Wadden Sea from 2014 onwards

Location	Code	Year	Month	Species	n	Oysters with *P. websteri*	Prevalence	Pathology
Blidselbucht, Sylt	2	2014	10	Oysters	10	8	80%	Blisters, live worms
Blidselbucht, Sylt	2	2014	10	Single shells of dead oysters	20	12	60%	Blisters
Königshafen, Sylt	1	2014	11	Oysters	40	0	0	
Blidselbucht, Sylt	2	2014	11	Oysters	55	48	87%	Blisters, live worms
Blidselbucht, Sylt	2	2014	11	Single shells of dead oysters	110	80	73%	Blisters
Blidselbucht, Sylt	2	2014	11	Mussels	45	0	0	
Blidselbucht, Sylt	2	2014	11	Periwinkles	12	0	0	
Kampen, Sylt	3	2014	11	Oysters	40	0	0	
Hörnum, Sylt	7	2014	11	Oysters	13	0	0	
Mokbaai, Texel	8	2014	11	Oysters	30	0	0	
Königshafen, Sylt	1	2015	4	Oysters	NA	1	NA	Blisters
Kampen, Sylt	3	2016	1	Oysters	NA	1	NA	Blisters
Munkmarsch, Sylt	4	2016	7	Oysters	NA	3	NA	Blisters
Blidselbucht, Sylt	2	2017	8	Oysters	19	8	42%	Blisters, live worms
Blidselbucht, Sylt	2	2017	8	Mussels	79	0	0	
Mokbaai, Texel	8	2017	10	Oysters	22	3	14%	Blisters, live worms
Mokbaai, Texel	8	2017	10	Mussels	150	0	0	
Blidselbucht, Sylt	2	2018	7	Oysters	30	23	77%	Blisters
Rantum, Sylt	6	2020	4	Oysters	NA	4	NA	Blisters
Morsum, Sylt	5	2020	5	Oysters	12	4	25%	Blisters

For each location, the number of collected mollusc species (mussels, periwinkles, and oysters (alive and dead shells)) is given as well as the number of specimens where *Polydora websteri* was found either based on shell blisters or on the identification of polydorin species (only 2017). Moreover, the prevalence per species and location is given. Note that for locations where only qualitative data exist, only the date of the first record is given. NAs indicate cases that were inspected qualitatively, and hence, no information on the sample size and prevalence exist

Discussion

Our findings constitute the first evidence that the shell-boring polychaete *Polydora websteri* is present in the Wadden Sea and document its expansion to the European Atlantic coast. Previous reports indicated that this species has spread widely around the globe, supposedly distributed by means of shellfish translocations (Simon and Sato-Okoshi 2015; Rice et al. 2018). According to this, previous records of *P. websteri* often stem from farmed oysters (see Simon and Sato-Okoshi 2015). Interestingly, we first detected the polychaete at a site (location 2: Blidselbucht) in close proximity to a commercial oyster farm where juvenile Pacific oysters are imported primarily from a nursery in southern Ireland, supplied by British hatcheries. These oysters of about 50 mm in length are kept on trestles and usually reach marketable size within 2 years, spending winter months indoors to avoid damage by ice. We found *P. websteri* in the direct vicinity of the trestles in discarded and wild Pacific oysters descending from the farm (Reise 1998; Moehler et al. 2011; Reise et al. 2017a). Since this is the site of the first record and still the locality with the highest infestation and there is no other oyster farm in the entire region, we suspect that the establishment of *P. websteri* in the northern Wadden Sea may be related to the oyster imports conducted by that farm. Previous studies indicated that the oyster farm at Sylt served as origin for the co-introduction of other non-indigenous organisms that were formerly not recorded in the Wadden Sea before (Reise 1998; Wolff and Reise 2002). The distant occurrence of *P. websteri* near the island of Texel in the western Wadden Sea with no positive sites in between may have another origin (see below).

Blisters were also recorded at four other locations at the northern end of Sylt and at one location at the southern end. Apart from the site in the tidal basin south of Sylt, which is separated from the northern basin by a causeway connecting the island with the mainland, all locations at Sylt are in close distance to the oyster farm. Besides planktotrophic larvae, *P. websteri* is also capable of producing adelphophagic larvae (Simon 2015) that feed on unfertilised eggs and, therefore, have a short or no planktonic phase. Perhaps, a predominance of this mode of reproduction explains the rather limited dispersal found so far. In order to colonise the southern tidal basin of Sylt, larvae would have to travel southward along the exposed west coast of Sylt and then back into the Wadden Sea, resulting in a minimum distance of 50 km. This would require dispersal by planktotrophic larvae. Alternatively, birds, mussel fishery, or leisure boats with fouling oysters might have served as vectors. Given the limited range extension at Sylt over the past 6 years, natural dispersal from Sylt to Texel, almost 500 km of coastline, seems rather unlikely and a different origin can be assumed. Hull fouling might have been the vector, as there are harbours (navy, ferry) with regular traffic in the Bay where *P. websteri* was observed at Texel.

At the location close to the oyster farm at Sylt, the studied oyster shells generally showed high prevalence of polydorins

Table 2 Overview of the number of blisters (sampled in March 2017) as well as the number of *P. websteri* per live oyster (intensity, sampled in August and October 2017) of individual *P. websteri* encountered in Pacific oysters at Blidselbucht and Mokbaai in 2017

Location	Year	Month	Host length (cm)	number of blisters	intensity of *P. websteri*
Blidselbucht	2017	3	5.5	1	NA
Blidselbucht	2017	3	10	5	NA
Blidselbucht	2017	3	10.5	3	NA
Blidselbucht	2017	3	11	3	NA
Blidselbucht	2017	3	12	2	NA
Blidselbucht	2017	3	13	3	NA
Blidselbucht	2017	3	14	8	NA
Blidselbucht	2017	3	14.5	2	NA
Blidselbucht	2017	3	15.5	12	NA
Blidselbucht	2017	8	5	NA	2
Blidselbucht	2017	8	6.7	NA	1
Blidselbucht	2017	8	7.8	NA	11
Blidselbucht	2017	8	7.9	NA	5
Blidselbucht	2017	8	8.7	NA	1
Blidselbucht	2017	8	9.7	NA	1
Blidselbucht	2017	8	9.7	NA	8
Blidselbucht	2017	8	10.3	NA	1
Mokbaai	2017	10	14.5	NA	1
Mokbaai	2017	10	15.4	NA	1
Mokbaai	2017	10	15.4	NA	3

NA indicates information that was not registered

and of oysters showing blisters, ranging between 42 and 87%. Similar values are reported from other locations where the polychaete has been introduced. For instance, in Washington State at the US Pacific coast, where *P. websteri* was recently confirmed to be present, 41% of Pacific oysters showed blisters and burrows that in many cases were linked to *P. websteri* (Martinelli et al. 2020). At locations where *P. websteri* is established for several decades, such as along the US Atlantic coast and Hawaii, the polychaete reaches prevalence up to 100% (Rice et al. 2018). In respect to the infestation intensities, the observed numbers of *P. websteri* in oysters from the Wadden Sea seem comparably low. Up to 11 individuals of *P. websteri* and a maximum of 12 blisters were recorded within a single oyster, whereas previous studies report worm numbers exceeding 100 individuals per host in highly infected areas (Simon & Sato-Okoshi 2015; Rice et al. 2018).

Despite a broad range of host species is known for *P. websteri* (Simon and Sato-Okoshi 2015) and other potential host species co-exist with oysters in the Wadden Sea, we only found the polychaete in Pacific oysters. Probably *P. websteri* prefers the relatively thick oyster shells over the much thinner shells of other species, like mussels *Mytilus edulis*. Such a preference for oyster shells has also been reported from the native shell-boring polychaete *Polydora ciliata* infecting mussels and oysters in the Wadden Sea (Goedknegt et al. 2019).

Although the infestation with *P. websteri* in farmed oysters was not explicitly quantified here, it seems that the species currently does not pose a threat to the oyster industry on Sylt (pers. comm. workers of the oyster farm). It is possible that the farmed oysters feature environmental conditions that are less favourable for *P. websteri* compared with the ones encountered at the surrounding wild oysters. For instance, the cultured oysters are kept on trestles about 0.35 m above the surface (Reise 1998), and it is known that tidal exposure reduces the infestation with *P. websteri* (Littlewood et al. 1992; Handley and Bergquist 1997). Furthermore, a lower siltation, which is probably caused by the regular manual turning of the oyster mesh bags to prevent oysters from cementing together, also reduces infestation success of the polychaetes (Clements et al. 2017). However, given that the polychaete is considered a serious pest in commercial marine aquaculture in other regions around the globe (Whitelegge 1890; Lunz 1941; Loosanoff and Engle 1943; Bailey-Brock and Ringwood 1982; Ogburn et al. 2007), further investigations on the spread and population development of *P. websteri* are warranted.

In conclusion, our study shows that the shell-boring polychaete *Polydora websteri* invaded the intertidal of the Wadden Sea. The most parsimonious explanation of its introduction is via imports of Pacific oysters, as individuals of *P. websteri* concentrate in oysters in the vicinity of the oyster culture. The dispersal of the species seems to be rather slow, and specimens are so far only found in wild oysters with relatively low intensities. With publishing the first record at the European Atlantic coast, we intend to alert other investigators and oyster farmers along the Atlantic coastline of Europe to the occurrence of *P. websteri*. Since we know of no direct transfers of Pacific oysters from overseas to the two localities where we encountered this polydorin, we suspect that there are more sites in Western Europe where *P. websteri* has established but remained unnoticed so far.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for animal testing, animal care, and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities. The study is compliant with CBD and Nagoya protocols.

Data availability All data generated or analysed during this study are included in this published article. The sequences of the two *P. websteri* specimens were deposited in GenBank under the accession numbers MT269755 and MT269756.

Authors' contribution All authors contributed to the study conception and design. DL carried out the initial survey in 2014. JK performed the systematic survey in 2017. KR helped with the initial survey and reported on *P. websteri* occurrence in subsequent years. KMW generated and analysed molecular data. AMW compiled the information and wrote the manuscript with significant contributions of all other authors. All authors read and approved the final manuscript.

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