Rapid Communication

First record and spread of the long-wristed hermit crab *Pagurus longicarpus* Say, 1817 in the North Frisian Wadden Sea (Germany)

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Abstract

The long-wristed hermit crab *Pagurus longicarpus* is native to the East Coast of North America from the Gulf of Mexico to the Gulf of St. Lawrence. Here we present the first record of this species in the German Wadden Sea. Sixty-one individuals of *P. longicarpus* were found during a regular beam trawl survey at nine stations in the Meldorf Bight in late August 2020. The identity of the new species was confirmed by DNA barcoding of mitochondrial subunit I of cytochrome *c* oxydase (COI). The northward spread up to Hallig Hooge was documented in 2021, with a total of 122 *P. longicarpus* found at 12 stations. *Pagurus longicarpus* was found in 2.5 m to 18.0 m depth at salinities of 24.89 to 30.43 PSU and temperatures ranging from 16.46 °C to 22.22 °C. We compared these parameters with the environmental conditions in its native range by using data from the Global Biodiversity Information Facility (GBIF) and the GIS database MARSPEC. The results revealed that environmental conditions in the North Frisian Wadden Sea closely fits those in the native range of *P. longicarpus*. Different size classes and sexes were identified, including ovigerous females, indicating a reproducing population in the North Frisian Wadden Sea. The species was most likely introduced via ballast water transport and seems to be already well established.

Key words: North Sea, monitoring, invaders, introduced species, invasion, epifauna, Demersal Young Fish Survey

Introduction

Pagurus longicarpus, the long-wristed or long-clawed hermit crab, is a small hermit crab attaining a maximum body length of around 2.5 cm in adult individuals (~ 1.3 cm cephalothorax length) (Rupert and Fox 1988). Coloration is highly variable and appears to depend on the sampling location. In its native range overall coloration ranges from beige to off-white to greenish-grey to brown. A notable feature is that the upper surface of all walking legs and chelipeds is iridescent even in preserved specimens (Provenzano Jr. 1959). The chelipeds of *P. longicarpus* are unequal, and the right is much larger than the left. The right, enlarged cheliped is long, slender and approximately cylindrical in shape giving the hermit crab its name and typically making it distinguishable from co-occurring hermit crabs (Williams 1984).

Pagurus longicarpus is a common shallow-water hermit crab along the East Coast of North America from the Gulf of Mexico to the Gulf of St. Lawrence. Within its native range it has been reported in a variety of habitats including beaches, harbours and channels from the intertidal up to 200 m depth. The species has been found on sand, sand/mud and hard substrate as well as in seagrass beds and salt marshes (Williams 1984; Wilber 1989; Strasser and Price 1999). However, *P. longicarpus* has not yet emerged as a successful invader. The species has been rarely recorded outside its native range, and no evidence for sustainable populations exist in European waters. A single individual of *P. longicarpus* was found by divers at the coast of Selsey (English Channel) in 2013 at a water depth of 2.35 m (GBIF.org 2020). However, it was not possible to properly validate this sighting.

The present paper reports the first record of *P. longicarpus* in the Meldorf Bight in the German Wadden Sea in 2020 and a further spread to the north in 2021. We investigate the ecological tolerance of *P. longicarpus* and discuss the origin and pathways of introduction as well as the reproduction patterns of the species in the North Frisian Wadden Sea.

Materials and methods

Sampling

Samples were taken during the Demersal Young Fish Survey (DYFS), which is a regular beam trawl survey carried out annually in the German Wadden Sea since 1972 (ICES 2021). The main goal of this survey is the determination of recruitment indices of important commercially exploited fish species, mainly for plaice and sole, and is coordinated by the International Council for the Exploration of the Seas (ICES 2021). Further, this survey targets the abundance and distribution of brown shrimp (*Crangon crangon*) in the area. The DYFS covers areas within the 12 nautical mile zone along the whole German North Sea coast (Figure 1).

Sampling took place on chartered shrimp vessels and the research vessel Clupea from August to September in 2020 and 2021. The gear in use was a 3 m beam trawl equipped with rubber bobbins and a mesh size of 20 mm (stretched mesh) in the codend. Fifteen-minute standard tows were carried out at a towing speed of 2–4 knots over ground with a mean distance of approximately 0.75 nautical miles. All species of the beam trawl catches were identified on the vessel to the lowest possible taxonomic level. Unidentified species were preserved in 96% alcohol for identification in the laboratory, including the individuals which were later identified as the long-clawed hermit crab *Pagurus longicarpus*. Depth, temperature and salinity measurements were conducted with an autonomous CTD data logger attached to the gear (NKE WiSens CTD 50). In the laboratory, size measurements of 62 *P. longicarpus* were carried out by measuring the propodus and carpus lengths as well as propodus widths of the right chelipeds

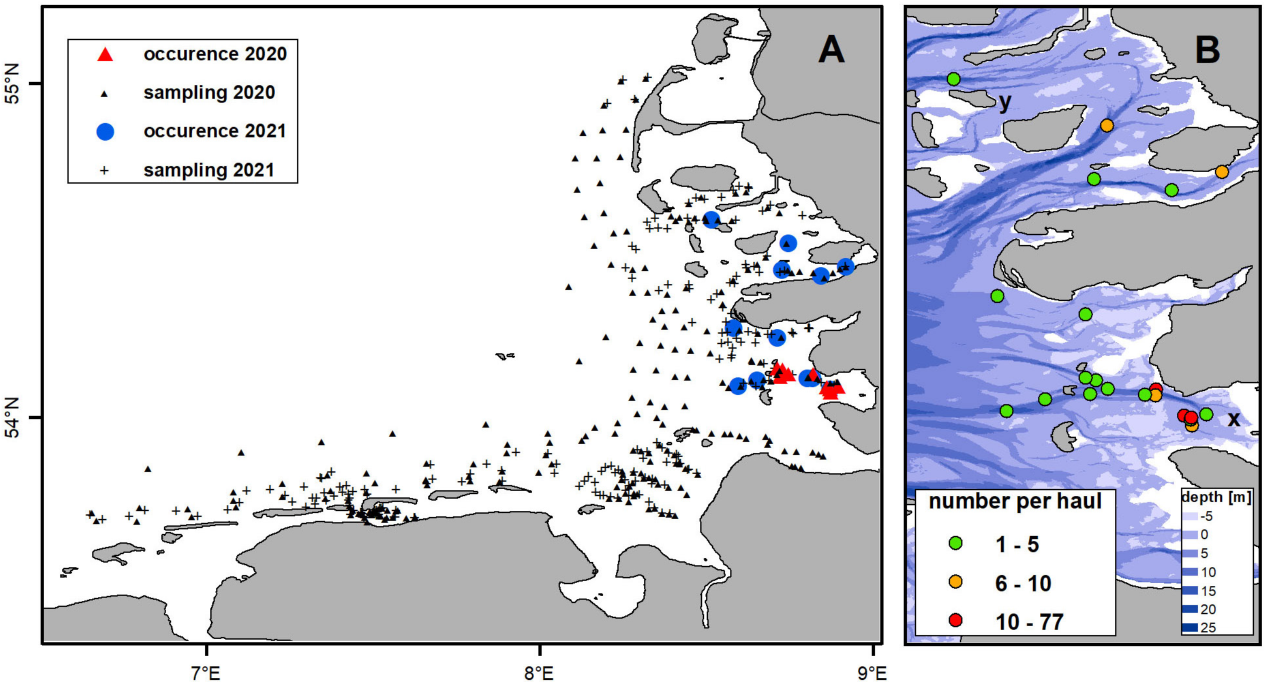

Figure 1. (A) Sampling sites of the Demersal Young Fish Survey (DYFS) along the German coast in 2020 and 2021. Sites where *Pagurus longicarpus* was found are noted as either red triangles (2020) or blue circles (2021). Black crosses and triangles indicate sites with no occurrences. (B) Number of *P. longicarpus* individuals per haul from Meldorf Bight (x) to Hallig Hooge (y). The bathymetry from −5 m below chart datum to 25 m is shown in blue (for details see Supplementary material Table S1).

(12 males / 5 females from 2020; 24 males / 21 females from 2021). Females were identified by paired gonopores on the first segment of the 2nd pair of walking legs. Linear regressions were used to analyse relationships between propodus length vs. carpus length and propodus length vs. propodus width in order to minimize measuring efforts for future studies.

DNA Barcoding

Muscle tissue samples were taken from the legs of two individuals preserved in 96% ethanol and was prepared by mincing on a petri dish with a sterile scalpel. Tissues were incubated overnight at 56 °C in a Proteinase K and lysis buffer solution. The DNA extraction was completed using the NucleoSpin Tissue Kit (Macherey-Nagel, Düren, Germany) according to manufacturer instructions.

A fragment of the sequence coding for the subunit I of the cytochrome *c* oxydase (COI) was amplified using the primers jgLCO1490 (5'TITCIAC IAAYCAYAARGAYATTGG3') and jgHCO2198 (5'TAIACYTCIGGRTGI CCRAARAAYCA3') (Geller et al. 2013). The OCRAll amplification was performed with the AccuStart™II PCR Supermix (Quantabio, Beverly, Massachusetts, USA) in a final volume of 25 µL containing 1 µL of each primer (10 pmol/µL) and 1–2 µL of DNA template. PCR products were visualized via electrophoresis on an 1.5% agarose gel. For each successful PCR, 10 µL of PCR product were purified with a 2.5 µL mix containing exonuclease I (20 U/µL) and alkaline phosphatase (1 U/µL) using an incubation of 15 min at 37 °C and 20 min at 75 °C. All purified PCR products were sequenced in both forward and reverse directions by Macrogen Inc. (Amsterdam, the Netherlands) using M13 universal primers.

Forward and reverse sequences were assembled using Geneious (v. R10, Biomatters, Auckland, NZ) and reciprocally verified to generate a complete contig of the sequenced fragment. All sequences were then exported in FASTA format and uploaded into BOLD's species identification engine (Ratnasingham and Hebert 2007) for taxonomic assignment (consulted in September 2021). The comparison against available data was performed using only barcode records longer than 500 bp with species level identification.

Environmental conditions in the native distribution range of Pagurus longicarpus

We used data from the Global Biodiversity Information Facility (GBIF) and the GIS database MARSPEC to analyse the environmental conditions in the native distribution range of *Pagurus longicarpus* in order to compare them with the conditions in the German Wadden Sea. The GBIF query resulted in 917 distribution records of *P. longicarpus* that were restricted to records made after the year 1950, because these records have validated coordinates and no geospatial issues (GBIF.org 2020). MARSPEC is a high-resolution GIS database of climatic and geophysical spatial data layers derived from *in situ* and satellite observations of the global ocean (Sbrocco and Barber 2013). The data were provided as ESRI raster grids at a 30 arc-second spatial resolution (1 km grids) and used a common land mask. One geophysical layer and four climatic layers were used to describe the environmental conditions for the *P. longicarpus* native range: depth of the seafloor (m), sea surface salinity of the freshest and saltiest months (psu) and sea surface temperature of the coldest and warmest months (°C). Climatic data were derived from long-term monthly climatological means obtained from remotely sensed and in situ oceanographic observations (see Sbrocco and Barber 2013 for further details). All spatial analyses and maps were made with ESRI ArcMap 10.5. If the depth records were also included in the GBIF data, we used the observed GBIF depths instead of those from the modelled MARSPEC database. It should be mentioned, however, that the analysis provides only a rough idea of the environmental conditions in *P. longicarpus*' native range, especially since the temporal scales of the GBIF and MARSPEC data do not align completely.

Results and discussion

The only hermit crabs identified previously from the Demersal Young Fish Survey (DYFS) have been *Pagurus bernhardus* and *Diogenes pugilator*. In August 2020, unusual hermit crabs were found in the Meldorf Bight near Büsum during the DYFS (Figure 1). Due to the unique shape and iridescent color, especially of the carpus of the right claw, it was obvious that these

Figure 2. *Pagurus longicarpus* Say, 1817**:** Dorsal view of individual with 11mm propodus length (left). In situ picture of *P. longicarpus* showing the prolonged, iridescent carpus of the right cheliped (right). Photographs by Hermann Neumann.

Table 1. Results of the taxonomic assignment using the BOLD reference database. BOLD sample ID and GenBank Accession number are provided as a reference for the first best match.

GenBank Accession Nr.	Best Match on BOLD	Genetic Similarity (%)	BOLD sample ID/ GenBank Accession Nr.	Barcode Index Number (BIN)
OL630911	*Pagurus longicarpus*	99.85	L164AR1-10	BOLD:AAA5534
OL630912	*Pagurus longicarpus*	100	AF483138	BOLD:AAA5534

hermit crabs could not be assigned to either of the two previously known species (see Figure 2). However, exact identification of the new encountered species was initially difficult. Therefore, we applied DNA barcoding to two individuals of the unidentified hermit crab, which revealed the occurrence of *Pagurus longicarpus* in the study area (Table 1). Barcodes of both specimens were 661 bp long and were matched with high confidence (> 99%) to numerous sequences of *P. longicarpus* published in previous studies (Young et al. 2002; Radulovici et al. 2009) or publicly available on BOLD. The remaining individuals were identified following the barcoding analysis by using the keys of Williams (1984) and Strasser and Price (1999). In total, 61 *P. longicarpus* individuals were identified at 9 stations in the Meldorf Bight during the DYFS in 2020 (Figure 1). In 2021, the total number of *P. longicarpus* caught in the DYFS increased and individuals were found in more northward locations up to Hallig Hooge. *Pagurus longicarpus* was reported from 12 stations during the 2021 DYFS survey. A total of 122 individuals were sampled, with the highest number of individuals still occurring in the Meldorf Bight (Figure 1). The records of spread were not a result of increased sampling effort in 2021 since the northern areas were also intensively sampled during the 2020 DYFS survey.

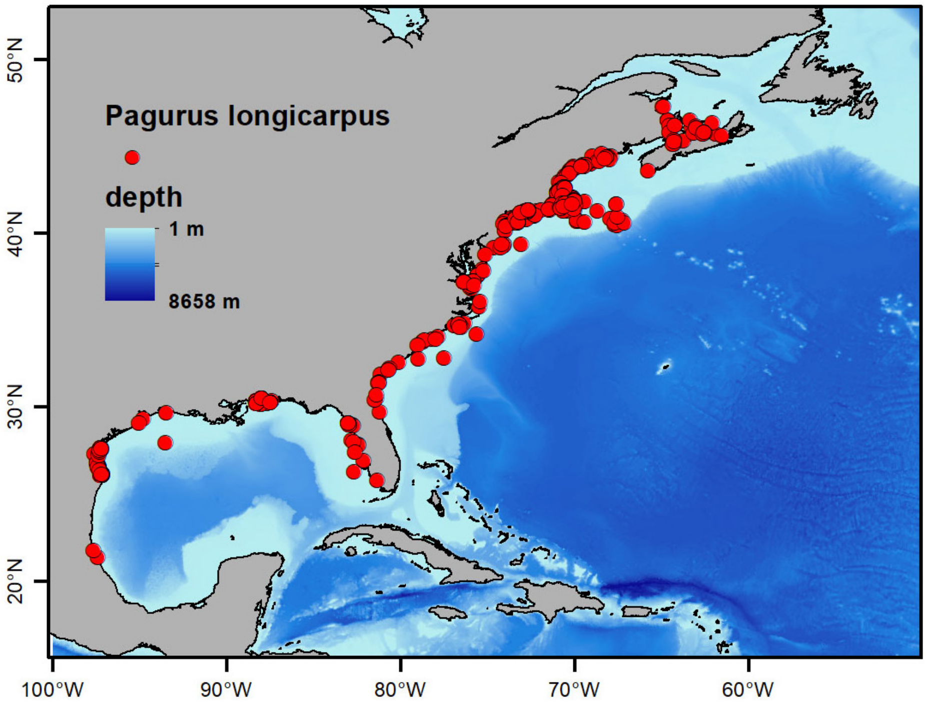

Figure 3. Native distribution of *Pagurus longicarpus* (red circles) along the East Coast of North America based on GBIF data.

Pagurus longicarpus is native to the East Coast of North America from the Gulf of Mexico to the Gulf of St. Lawrence (e.g. Provenzano Jr. 1959; Young 1978; Williams 1984; Abele and Kim 1986), which is consistent with the distribution records extracted from GBIF (Figure 3). The populations in its native range have been subdivided into a western Atlantic and Gulf of Mexico population based on morphological and genetic differences (Young et al. 2002). Our barcoding results showed a high similarity with the sequences of the western Atlantic population suggesting that the introduced individuals (or larvae) of *P. longicarpus* originated from this population. Sequence analysis is regularly used in population genetics to estimate population structure and reconstruct sources of haplotypes in different populations, often using neutral markers like mitochondrial COI used in this study. In particular, this method is used to identify source populations for invasion biology studies (Kelly et al. 2006). However, our hypothesis of the possible origin of these individuals being from the western Atlantic Ocean needs to be confirmed by additional genetic and morphological studies.

Since the distance across the Atlantic is too far for a natural range expansion, it is likely that the introduction of *P. longicarpus* was caused by global shipping. The most likely vector is larval transport via ballast water, which has been considered one of the most important factors for species introduction into the North Sea in recent decades (Gollasch 2002; Gollasch and Nehring 2006; Seebens et al. 2016; Bailey et al. 2020). Like many crustaceans, *P. longicarpus* has planktonic larval stages that spend 2–3 weeks in the water column and are easily taken up and released during

Table 2. Environmental conditions (depth, temperature, salinity) where *Pagurus longicarpus* was found in its native range based on occurrence data from the Global Biodiversity Information Facility (GBIF; see Figure 3) and German Wadden Sea (see Figure 1).

	East Coast of North America		German Wadden Sea	
	min	max	min	max
depth [m]	0.1	310	2.5	18
temperature [C°]	1.05	29.61	16.46	22.22
salinity [psu]	27.42	37.14	24.89	30.43

ballasting/deballasting procedures and thus may allow for long-distance dispersal (Roberts Jr. 1970; Hänfling et al. 2011). A plausible scenario is therefore, that larvae originated from ships entering or leaving Hamburg port or anchoring near Helgoland awaiting entrance to Hamburg port. Assuming this, larvae could have easily reached the Meldorf Bight and settled there due to favourable circulation patterns of surface currents in the German Bight (Stanev et al. 2015; Meyerjürgens et al. 2019). Current drift of larvae can also explain the northward spread of *P. longicarpus* up to Hallig Hooge within one year. Such yearly, stepwise spread along the German coast has already described for the Pacific oyster *Crassostrea gigas* (Wehrmann et al. 2000) and the Angular Crab *Goneplax rhomboides* (Neumann et al. 2013). Considering the residual current velocities given by Wehrmann et al. (2000) (4.5 nm/day) and the prevailing NE flow of currents in the German Bight, larvae could have been easily transported from Meldorf Bight to Hallig Hooge (30–35 nm) within their pelagic phase of 2–3 weeks (Roberts Jr. 1970). However, human-mediated transport, e.g. via shipping, cannot be completely ruled out for the observed northward spread of *P. longicarpus*. As mentioned above, a single individual of *P. longicarpus* was found by divers along the coast of Selsey (English Channel) in 2013. We were not able to validate this finding yet. However, we do not believe that the Meldorf Bight population originates from the English Channel. In this case, step-stone populations of *P. longicarpus* would mostly likely have already been discovered between the Channel and Meldorf Bight. To our knowledge, none of these populations exist, and we can rule out the area between Borkum and Cuxhaven by our own sampling.

The overlap of the GBIF records with the MARSPEC data revealed a very broad range of environmental conditions in which *P. longicarpus* can survive. The analysis revealed that, in the native range, the species occurred at depths from 0.1 m to 310 m with temperatures and salinities ranging from 1.05 °C to 29.61 °C and 27.42 psu to 37.14 psu, respectively (Table 2). However, this does not necessarily imply that *P. longicarpus* is exposed to such extremes in nature since we used the annual max./min. values of temperature and salinity at the corresponding GBIF locations, and the species could escape these conditions by migration or other means. In the North Frisian Wadden Sea, *P. longicarpus* was found in depths from 2.5 to 18 m at salinities of 24.89 to 30.43 psu and temperatures ranging from 16.46 to 22.22 °C (Table 2), which largely correspond to the conditions in its native range, even if we consider the high variability of temperature and salinity in the Wadden Sea. *Pagurus longicarpus* has broad salinity and temperature tolerances; often, this species inhabits tide pools with extreme conditions in its native range (Biggs and McDermott 1973; Sherman and Eichrodt 1982). However, Sherman and Eichrodt (1982) found that low temperature-low salinity conditions were stressful for *P. longicarpus* resulting in higher mortality, swelling and motor impairment. Additionally, *P. longicarpus* migrates into deeper water in autumn when the temperature drops below 10 °C and begins spring inshore migration as the water temperature rises above 5 °C (Rebach 1974; McDermott 1999). Interestingly, this migration pattern occurred at two locations independently at the same temperatures (Rhode Island waters and Cape May peninsula, New Jersey, USA). It can be assumed that *P. longicarpus* will display migratory behavior in the Wadden Sea as well to avoid high seasonal fluctuations in abiotic conditions. Young (1978) found that *P. longicarpus* is intolerant of water loss and that the species is rarely, if ever, exposed to air during low tide, which fits our observed minimum depth where we have found the species. This is contrasted by McDermott (1999) who stated that *P. longicarpus* occurred intertidally in shallow depressions in the mid-Atlantic, USA region. Systematic sampling in the intertidal of the North Frisian Wadden Sea is necessary to clarify whether the species also occurs intertidally. Sediment data were not taken during our survey. However, sediments in the Meldorf Bight are heterogenous consisting mainly of fine-sand to silty sediments with coarser sands at hydrodynamically exposed areas and finer deposits at sheltered areas (Ricklefs and Asp Neto 2005). These are bottom conditions that *P. longicarpus* also finds in its natural environment, where the species occurs on a variety of sediments and habitats (Young 1978; Wilber 1989).

Fifteen males and 6 females were identified in 2020, while 39 males and 73 females were identified in 2021. This results in two contrasting male-female ratios of 2.50 in 2020 and 0.53 in 2021. The reasons for these differences are unclear, but we do not necessarily see a causal relationship here. Possibly the number of samples in 2020 was simply too low for a representative result. McDermott (1999) calculated a male-female ratio of 0.87 from 9034 samples from the Herefort Inlet estuary (Cape May peninsula, USA), which is similar to our result from 2021. No juveniles (one year classes) were found in our study whose shield length should have been < 2 mm (McDermott 1999, shield length = distance between the rostrum and the cervical groove). However, all of the females found in 2020 and 2021 were ovigerous, which indicates a reproductive population and thus an establishment of *P. longicarpus* in the North Frisian Wadden Sea.

Reproduction patterns of *P. longicarpus* can vary along the native range. The main reproduction period of *P. longicarpus* in New Jersey (Cape May peninsula, Hereford Inlet estuary, USA) was in the spring (McDermott 1999),

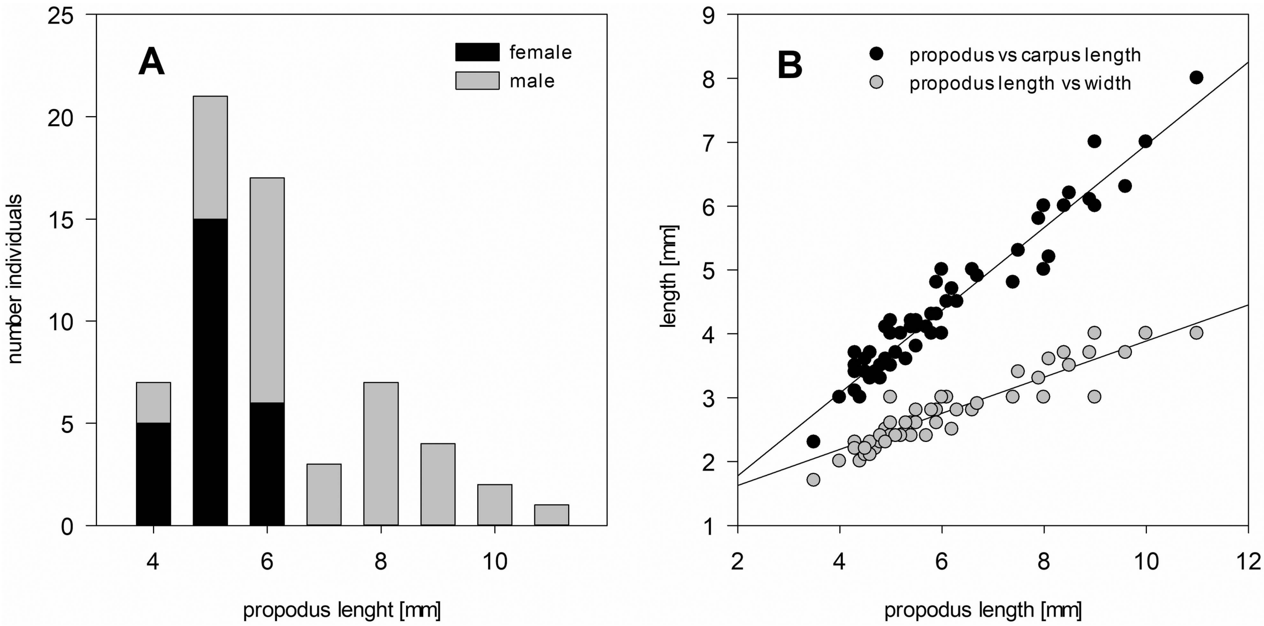

Figure 4. Results of morphometric measurements. (A) Length distribution of propodus (right cheliped) and (B) linear relationships of propodus length vs. carpus length (black) and propodus length vs. propodus width (grey).

but it was in fall/winter in two populations in Florida, USA (Wakulla Beach and Bay Mouth Bar, Gulf of Mexico) (Wilber 1989). In New Jersey, McDermott (1999) found ovigerous hermit crabs from late March to October with a sharp peak in April (70.6–96.4%) followed by a noticeable decline from May to August, with very few ovigers in September and October (4 among 849 crabs). In Florida, Wilber (1989) found a distinct peak of ovigerous hermit crabs (70–90%) in October through December, followed by a sharp decline through May. Monthly sampling would be necessary to make any clear statement about reproduction patterns of *P. longicarpus* at the North Frisian coast. However, we found 100% ovigerous females in late August/early September indicating a reproduction pattern that is more similar to the one from the Gulf of Mexico. It can be assumed that the reproduction season is triggered by habitat-specific environmental factors and that *P. longicarpus* has a high plasticity in this regard, which allows it to colonize a wide variety of habitats successfully. But this could also be an indication that the North Frisian *P. longicarpus* originates from the Gulf of Mexico population rather than from the western Atlantic population (see discussion above).

Size measurements of the right cheliped were made for 62 individuals of *P. longicarpus*. Regression analysis revealed strong linear relationships between propodus length and carpus length ($y = 0.6478x + 0.4837$; $R^2 = 0.9073$) as well as propodus length and propodus width ($y = 0.2825x + 1.0622$; $R^2 = 0.7983$) (Figure 4B). Propodus lengths ranged from 4 mm to 11 mm indicating the existence of different size and age classes in the North Frisian *P. longicarpus* population (Figure 4A). Females were generally smaller in size (propodus lengths 4 to 6 mm), which was also found by Biggs and McDermott (1973) in two populations from southern New Jersey, USA.

Pagurus longicarpus has some characteristics that make them successful invaders, e.g., broad environmental tolerances, good dispersal abilities and high reproductive potential (high fecundity and the ability to reproduce more than once per season) (McDermott 1999). The rapid northward spread within one year indicates that further spread along the North Frisian coast is likely. Further spread into the Baltic Sea can also be expected, since secondary spread from species previously introduced to the North Sea is the main introduction pathway into the Baltic Sea (Ojaveer et al. 2017). Possible impacts of the introduction of *P. longicarpus* and whether it become invasive remains speculative. Non-native species generally have the potential to alter ecosystems, which could result in the decline or extinction of native species, global homogenization and the loss of ecosystem functioning and services (Olden et al. 2004; Vilà et al. 2010). One possible competitor for food and space is the native hermit crab *Pagurus bernhardus*. So far, our data show that *P. longicarpus* co-occurs with *P. bernhardus* at 11 stations, indicating possible co-existence, at least for now. In contrast, introduced species could also play a beneficial role in ecosystems by increasing functional redundancy and diversity (Reise et al. 2006; Briggs 2010). This seems to be supported by long-term studies of the Pacific oyster *Crassostrea gigas* and the American razor clam *Ensis directus*, which are well-known invaders in the German Wadden Sea. Neither of them has suppressed any native species yet. Instead, they have increased diversity, served as additional food resource, stabilised the sediment and functioned as sediment traps for organic matter, thereby enhancing food availability for other species (Beukema and Dekker 2010; Markert et al. 2010, 2013; Dannheim and Rumohr 2012). Long-term monitoring programmes such as the DYFS are needed to track the spread and abundance of *P. longicarpus* in future.

Summary and conclusions

This study describes the first records and spread of the long-wristed hermit crab *Pagurus longicarpus* in the North Frisian Wadden Sea (Germany). The species is native to the East Coast of North America and is most likely introduced through ballast water. The identity of the new species was verified by morphological and DNA barcoding approaches. *Pagurus longicarpus* has a high adaptability to a wide range of environmental factors suggesting that the species is able to survive under most coastal and estuarine conditions. We found different age- and size classes as well as ovigerous females, indicating successful reproduction and thus establishment of *P. longicarpus* in the North Frisian Wadden Sea. The study highlights the value of long-term monitoring programmes such as the DYFS beyond their designated tasks. Due to annual sampling of large parts of the German Wadden Sea during the DYFS it was possible to describe the introduction of *P. longicarpus* from the beginning, and it will be possible to track the spread and population structure of this species in the future. However, further investigations would be necessary to clarify the origin of *P. longicarpus*, how it reached the German Wadden Sea and whether it occurs intertidally.

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Authors' contribution

HN: research conceptualization, investigation and data collection, data analysis and interpretation, writing – original draft; HH: research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, writing – review and editing; TK: data analysis and interpretation, writing – review and editing; AB: data analysis and interpretation, writing – review and editing.

Ethics and permits

Herewith we acknowledge that we have complied with the institutional and/or national policies governing the humane and ethical treatment of the experimental subjects, and that they are willing to share the original data and materials if so requested. All research pertaining to this article did not require any research permit(s).

References

Abele LG, Kim W (1986) An illustrated guide to the marine decapod crustaceans of Florida, Vol. 8. State of Florida Department of Environmental Regulation, Tallahassee, Florida, USA, 225 pp

Bailey SA, Brown L, Campbell ML, Canning-Clode J, Carlton JT, Castro N, Chainho P, Chan FT, Creed JC, Curd A, Darling J, Fofonoff P, Galil BS, Hewitt CL, Inglis GJ, Keith I, Mandrak NE, Marchini A, McKenzie CH, Occhipinti-Ambrogi A, Ojaveer H, Pires-Teixeira LM, Robinson TB, Ruiz GM, Seaward K, Schwindt E, Son MO, Therriault TW, Zhan A, Hussey N (2020) Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: A 50-year perspective. *Diversity and Distributions* 26: 1780–1797, https://doi.org/10.1111/ddi.13167

Beukema JJ, Dekker R (2010) Increasing species richness of the macrozoobenthic fauna on tidal flats of the Wadden Sea by local range expansion and invasion of exotic species. *Helgoland Marine Research* 65: 155–164, https://doi.org/10.1007/s10152-010-0210-7

Biggs DC, McDermott JJ (1973) Variation in temperatue-salinity tolerance between two estuaine populations of *Pagurus longicarpus* Say (Crustacea: Anomura). *The Biological Bulletin* 145: 91–102, https://doi.org/10.2307/1540350

Briggs JC (2010) Marine biology: the role of accomodation in shaping marine biodiversity. *Marine Biology* 157: 2117–2126, https://doi.org/10.1007/s00227-010-1490-9

Dannheim J, Rumohr H (2012) The fate of an immigrant: *Ensis directus* in the eastern German Bight. *Helgoland Marine Research* 66: 307–317, https://doi.org/10.1007/s10152-011-0271-2

GBIF.org (2020) GBIF Occurrence Download. https://doi.org/10.15468/dl.68rvdd (accessed 23 December 2020)

Geller J, Meyer C, Parker M, Hawk H (2013) Redesign of PCR primers for mitochondrial cytochrome *c* oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. *Molecular Ecology Resources* 13: 851–861, https://doi.org/10.1111/1755-0998.12138

Gollasch S (2002) The Importance of Ship Hull Fouling as a Vector of Species Introductions into the North Sea. *Biofouling* 18: 105–121, https://doi.org/10.1080/08927010290011361

Gollasch S, Nehring S (2006) National checklist for aquatic alien species in Germany. *Aquatic Invasions* 1: 245–269, https://doi.org/10.3391/ai.2006.1.4.8

Hänfling B, Edwards F, Gherardi F (2011) Invasive alien Crustacea: dispersal, establishment, impact and control. *BioControl* 56: 573–595, https://doi.org/10.1007/s10526-011-9380-8

ICES (2021) Working Group on Beam Trawl Surveys (WGBEAM). *ICES Scientific Reports* 3(46), 89 pp

Kelly DW, Muirhead JR, Heath DD, MacIsaac HJ (2006) Contrasting patterns in genetic diversity following multiple invasions of fresh and brackish waters. *Molecular Ecology* 15: 3641–3653, https://doi.org/10.1111/j.1365-294X.2006.03012.x

Markert A, Esser W, Frank D, Wehrmann A, Exo K-M (2013) Habitat change by the formation of alien *Crassostrea*-reefs in the Wadden Sea and its role as feeding sites for waterbirds. *Estuarine, Coastal and Shelf Science* 131: 41–51, https://doi.org/10.1016/j.ecss.2013.08.003

Markert A, Wehrmann A, Kroencke I (2010) Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). *Biological Invasions* 12: 15–32, https://doi.org/10.1007/s10530-009-9425-4

McDermott JJ (1999) Reproduction in the Hermit Crab *Pagurus longicarpus* (Decapoda: Anomura) from the Coast of New Jersey. *Journal of Crustacean Biology* 19: 612–621, https://doi.org/10.2307/1549265

Meyerjürgens J, Badewien TH, Garaba SP, Wolff J-O, Zielinski O (2019) A State-of-the-Art Compact Surface Drifter Reveals Pathways of Floating Marine Litter in the German Bight. *Frontiers in Marine Science* 6: 1–15, https://doi.org/10.3389/fmars.2019.00058

Neumann H, de Boois I, Kroencke I, Reiss H (2013) Climate change facilitated range expansion of the non-native angular crab *Goneplax rhomboides* (Linnaeus, 1758) into the North Sea. *Marine Ecology Progress Series* 484: 143–153, https://doi.org/10.3354/meps10299

Ojaveer H, Olenin S, Narščius A, Florin A-B, Ezhova E, Gollasch S, Jensen KR, Lehtiniemi M, Minchin D, Normant-Saremba M (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

Olden JD, LeRoy Poff N, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution* 19: 18–24, https://doi.org/10.1016/j.tree.2003.09.010

Provenzano Jr AJ (1959) The shallow-water hermit crabs of Florida. *Bulletin of Marine Science* 9: 349–420

Radulovici AE, Sainte-Marie B, Dufresne F (2009) DNA barcoding of marine crustaceans from the Estuary and Gulf of St Lawrence: a regional-scale approach. *Molecular Ecology Resources* 9: 181–187, https://doi.org/10.1111/j.1755-0998.2009.02643.x

Ratnasingham S, Hebert PD (2007) BOLD: The Barcode of Life Data System (http://www.barcodinglife.org). *Molecular Ecology Notes* 7: 355–364, https://doi.org/10.1111/j.1471-8286.2007.01678.x

Rebach S (1974) Burying Behavior in Relation to Substrate and Temperature in the Hermit Crab, *Pagurus longicarpus*. *Ecology* 55: 195–198, https://doi.org/10.2307/1934636

Reise K, Olenin S, Thieltges DW (2006) Are aliens threatening European aquatic coastal ecosystems? *Helgoland Marine Research* 60: 77–83, https://doi.org/10.1007/s10152-006-0024-9

Ricklefs K, Asp Neto NE (2005) Geology and morphodynamics of a tidal flat area along the German North Sea coast. *Die Küste* 69: 93–127

Roberts Jr MH (1970) Larval development of *Pagurus longicarpus* Say reared in the laboratory, I. Description of larval instars. *The Biological Bulletin* 139: 188–202, https://doi.org/10.2307/1540136

Rupert E, Fox R (1988) Seashore Animals of the Southeast: A Guide to Common Shallow-Water Invertebrates of the Southeastern Atlantic Coast. University of South Carolina Press, Columbia, South Carolina, 429 pp

Sbrocco EJ, Barber PH (2013) MARSPEC: ocean climate layers for marine spatial ecology: Ecological Archives E094-086. *Ecology* 94: 979–979, https://doi.org/10.1890/12-1358.1

Seebens H, Schwartz N, Schupp PJ, Blasius B (2016) Predicting the spread of marine species introduced by global shipping. *Proceedings of the National Academy of Sciences* 113: 5646–5651, https://doi.org/10.1073/pnas.1524427113

Sherman E, Eichrodt A (1982) The effect of temperature on osmotic responses of the hermit crab *Pagurus longicarpus* say. *Comparative Biochemistry and Physiology Part A: Physiology* 73: 261–265, https://doi.org/10.1016/0300-9629(82)90067-6

Stanev E, Ziemer F, Schulz-Stellenfleth J, Seemann J, Staneva J, Gurgel K-W (2015) Blending surface currents from HF radar observations and numerical modeling: tidal hindcasts and forecasts. *Journal of Atmospheric and Oceanic Technology* 32: 256–281, https://doi.org/10.1175/JTECH-D-13-00164.1

Strasser KM, Price WW (1999) An annotated checklist and key to hermit crabs of Tampa Bay, Florida, and surrounding waters. *Gulf and Caribbean Research* 11: 33–50, https://doi.org/10.18785/grr.1101.06

Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE, partners D (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* 8: 135–144, https://doi.org/10.1890/080083

Wehrmann A, Herlyn M, Bungenstock F, Hertweck G, Millat G (2000) The Distribution Gap is Closed - First Record of Naturally Settled Pacific Oysters *Crassostrea gigas* in the East Frisian Wadden Sea, North Sea. *Senckenbergiana Maritima* 30: 153–160, https://doi.org/10.1007/BF03042964

Wilber TP (1989) Associations between gastropod shell characteristics and egg production in the hermit crab *Pagurus longicarpus*. *Oecologia* 81: 6–15, https://doi.org/10.1007/BF00377002

Williams AB (1984) Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington DC, USA, 550 pp

Young A, Torres C, Mack J, Cunningham C (2002) Morphological and genetic evidence for vicariance and refugium in Atlantic and Gulf of Mexico populations of the hermit crab *Pagurus longicarpus*. *Marine Biology* 140: 1059–1066, https://doi.org/10.1007/s00227-002-0780-2

Young AM (1978) Desiccation tolerances for three hermit crab species *Clibanarius vittatus* (Bosc), *Pagurus pollicaris* Say and *P. longicarpus* Say (Decapoda, Anomura) in the North Inlet Estuary, South Carolina, U.S.A. *Estuarine and Coastal Marine Science* 6: 117–122, https://doi.org/10.1016/0302-3524(78)90047-6

Supplementary material

The following supplementary material is available for this article:

Table S1. Records of *Pagurus longicarpus* in the North Frisian Wadden Sea in 2020–2021.

This material is available as part of online article from:
http://www.reabic.net/journals/bir/2022/Supplements/BIR_2022_Neumann_etal_SupplementaryMaterial.xlsx