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ORIGINAL ARTICLE

On the occurrence of *Diogenes pugilator* in the German Bight (Crustacea: Decapoda Diogenidae)

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Abstract The occurrence of *Diogenes pugilator* in the German Bight has been examined since 2005. The steady onshore and offshore presence confirms that this southern species has established sustaining populations. The morphometric features are comparable to that of other populations in the adjacent Atlantic Ocean.

Keywords *Diogenes pugilator* · Hermit crab · German Bight · New records · Recent occurrence

Introduction

Invasions of warm water species into the southern North Sea and the German Bight have been very obvious events during the last decade. Such spreads have been recorded for a number of animal groups (Franke and Gutow 2004; Beermann and Franke 2011 for Amphipoda; Franke et al. 1999 for an isopod; Beare et al. 2004 for fish). Long-term studies and observations are necessary, though missing in many cases, in order to get an idea on the dynamics of such invasions. The present study deals with a hermit crab, *Diogenes pugilator*, that is present in the German Bight since 2004 and onshore occurrences of which have been regularly observed since then, especially in the summer months.

Diogenes pugilator is a typical Mediterranean–Atlantic faunal element, which is very abundant in the Mediterranean Sea and the adjacent north-eastern Atlantic Ocean where it ranges from the south-western North Sea through the British Channel to the Cape Verde Islands. It has also been recorded from the northern Red Sea. Throughout its range, the species is characteristic for shallow sandy beaches where it occurs in shallow water. The deepest records are from 40 m, but this is rather exceptional and even deeper ones are certainly erroneous (d'Udekem d'Acoz 1999). *Diogenes pugilator* is clearly a warm water element that has penetrated deeper into the North Sea during recent years (d'Udekem d'Acoz 1997). The present study summarises the data of the specimens collected in the period 2005–2013 from and off the Eastern Frisian Island of Wangerooge and presents morphometric details. Before this, it had already been found around the offshore island of Helgoland (Franke and Gutow 2004), from off Borkum Island (Pätzold and Stamm 2012), and from an unspecified locality at the East Frisian coast (Gehrmann 2009), later specified as off Neuharlinger Siel (Gehrmann 2011), and onshore at the Islands Baltrum and Norderney (Gehrmann 2011), Wangerooge as well as in the Jade Bay (both Türkay 2008).

Materials and methods

The onshore samples were collected from the northern and north-western beach of the Eastern Frisian Island of Wangerooge, the offshore ones from "Langes Riff" a shallow bank off the north coast of Wangerooge and from the Jade Bay. The details of the material examined are presented in Table 1.

The offshore work was performed during routine trawling surveys in the German Bight with R. V. Senckenberg. The gear used for sampling was a 2-m-broad beam-trawl equipped with a tickler chain. The net had a minimum mesh size of 1 cm in the cod end. The seabed was trawled at a distance of 1 nautical mile and at a speed of 2 knots. The catch was sorted on board ship in order to

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Table 1 Details of the material of *D. pugilator* examined for this study, SMF refers to catalogue numbers of the Senckenberg collection

Station	Position	Depth (m)	Gear	Date	Specimens	SMF
LR-050602 Ku	53°49.770′N 7°50.095′E–53°49.466′N 7°51.513′E	12.9–15	BMT	02.06.2005	3♂	30450
LR-050810 Ku	53°49.342′N 7°53.056′E–53°48.859′N 7°54.643′E	12.5–12.9	BMT	10.08.2005	10♂ 4♀ 2 ov ♀	30452
LR-051004 Ku	53°48.820′N 7°54.571′E–53°49.158′N 7°53.085′E	11.5–12	BMT	04.10.2005	2♂	30688
LR-051031 Ku	53°49.277′N 7°53.283′E–53°48.732′N 7°54.93′E	11.8–12.8	BMT	31.10.2005	30♂ 20♀ 5 ov ♀	44370–44372
LR-060728-2 Ku	53°49.395′N 7°52.498′E–53°48.899′N 7°53.863′E	10.7–14	BMT	28.07.2006	53♂ 6♀ 19 ov ♀	31206, 31828
LR-080729 Ku	53°49.454′N 7°52.087′E–53°49.106′N 7°53.572′E	12.4–15.4	BMT	29.07.2008	72♂ 23♀ 14 ov ♀	33296
LR-080729 RD2	53°49.142′N 7°53.479′E–53°49.142′N 7°53.479′E	12.9–12.9	RD	29.07.2008	5♂	33297
LR-090126 Ku	53°49.113′N 7°53.479′E–53°49.479′N 7°51.954′E	13.9–16.4	BMT	26.01.2009	5♂	34665, 34666
LR-090203 Ku	53°49.488′N 7°52.106′E–53°40.096′N 7°53.65′E	13.8–16.5	BMT	03.02.2009	1♀	34668
LR-090816 Ku	53°49.673′N 7°51.737′E–53°49.2′N 7°52.616′E	11.5–13.7	BMT	16.08.2009	207♂ 85♀ 136 ov ♀	43293, 43294
LR-120723 Ku	53°49.673′N 7°51.737′E–53°49.2′N 7°52.616′E	11.5–13.7	BMT	23.07.2012	1♂ 2♀	43716, 44374
LR-130730 Ku	53°49.092′N 7°53.921′E–53°49.418′N 7°52.333′E	11.8–14.2	BMT	30.07.2013	5♂ 2♀ 1 ov ♀ 2 juv	44373
LR-130827 Ku	53°49.112′N 7°53.830′E–53°49.409′N 7°52.353′E	11.4–13.9	BMT	27.08.2013	2♂ 1♀	44675
W'ooge-N-beach	53°47.517′N 7°55.083′E	0		02.09.2006	26♂ 34 ov ♀	31840, 31841
W'ooge-N-beach	53°47.517′N 7°55.083′E	0		14.09.2006	2♂	31207
W'ooge-N-beach	53°47.517′N 7°55.083′E	0		09.06.2007	109♂ 39♀ 114 ov ♀	43290, 43291
W'ooge-W-beach	53°47.725′N 7°51.950′E	0		22.05.2009	5♂ 4♀	43292
D65-200702-1 Ku	53°34.045′N 8°11.166′E–53°34.922′N 8°10.969′E	10.8–11.2	BMT	13.02.2007	2♂ 1♀	31711
D65-200702-4 Ku	53°34.930′N 8°10.995′E–53°34.093′N 8°11.154′E	10.3–11.6	BMT	14.02.2007	1♂	31712
D65-200702-5 Ku	53°34.030′N 8°11.177′E–53°34.885′N 8°10.975′E	9.7–11.3	BMT	14.02.2007	1♂	31713
D65-200702-6 Ku	53°34.056′N 8°11.155′E–53°34.911′N 8°10.978′E	11.6–12.9	BMT	14.02.2007	1 juv	31714
D65-200702-7 Ku	53°34.926′N 8°10.977′E–53°34.052′N 8°11.157′E	12.4–13.6	BMT	14.02.2007	2♂ 1♀ 1 juv	31715
D65-200702-8 Ku	53°34.018′N 8°11.147′E–53°34.908′N 8°10.959′E	11–12.1	BMT	14.02.2007	1♀	31716
D65-200702-11 Ku	53°34.902′N 8°10.961′E–53°34.048′N 8°11.159′E	12.7–14	BMT	14.02.2007	1♂	31717
D65-200702-13 Ku	53°34.038′N 8°11.190′E–53°34.906′N 8°10.985′E	9.4–10.8	BMT	15.02.2007	1♀	31718
D65-200702-14 Ku	53°34.008′N 8°11.194′E–53°34.914′N 8°10.989′E	10.8–12.3	BMT	15.02.2007	2♂	31719
D65-200702-16 Ku	53°34.984′N 8°10.572′E–53°34.101′N 8°11.144′E	11.6–13.3	BMT	15.02.2007	1 juv	31720
D65-200711-9 Ku	53°33.950′N 8°11.205′E–53°34.89′N 8°10.994′E	10.1–11.4	BMT	27.11.2007	1 ov ♀	32310

record larger megafauna. The onshore samples were taken during regular shore collecting along the north and west beach of the Eastern Frisian Island of Wangerooge.

The hermit crab specimens studied in this paper were preserved in 70 % ethylic alcohol and taken back to the home laboratory where they were separated from their shells, sexed and their carapace measurements were taken with an accuracy of one digit after the point.

The most stable size measurement is that of the carapace shield, from the tip of the rostrum to the midline if

the cervical furrow, because this region is well calcified and does not show any deformations. The total carapace length (TL) from the tip of the rostrum to the posterior end along midline is less reliable, because the branchial flaps and the posterior region of the carapace are less calcified and deformed at occasions. This measurement was, however, taken when no deformation was obvious in order to get a conversion factor for comparison with older measurements in the literature. Therefore, the numbers of values for TL have been less than those for the carapace shield. Of 1,063 specimens examined, the TL could be only measured reliably in 191 ones (= nearly 18 %), but this number was enough in order to calculate conversion factors.

Results

Diogenes pugilator was found by us for the first time in October 2005 while trawling on "Langes Riff" off the north coast of Wangerooge and every year after that, from 2006 on also in the intertidal zone of the island until 2009. For 2010 and 2011, there are no records in spite of intensive trawling and shore collection. In 2012 and 2013, the species appeared again on Langes Riff. In the Jade Bay, it was only collected regularly during routine trawling in February 2007.

While on the first occasion (October 2005) on Langes Riff, no further notes were taken, as the specimens were accidentally discovered when looking through trawl samples, in August of the same year, the whole catch was sorted for small-sized hermits. Of the 61 hermits of comparable size 16 (= 26 %) were identifiable to *D. pugilator*, the remaining 45 were young *Pagurus bernhardus*. This shows that *Diogenes* was already quite abundant by that time and it has been caught regularly after that.

The general sex ratio is quite even, 546 males and 517 females were collected in the whole period. This equal sex distribution does not change much seasonally; at least there are no obvious seasonal patterns visible.

Ovigerous females have been collected in June–October, in the Jade Bay also once in November. Of the remaining months, there are only samples from January, February and May, in which the females were non-ovigerous. In the months in which berried females were collected, these accounted for about 60 % of the total numbers with some variations in the period, but without any significant differences between the months of that period. Females were already ovigerous from a shield length (SL) of 1.4 mm on and to a SL of 3.5 mm. There were still non-ovigerous females beyond that size (up to 3.6 mm shield length).

The two lengths of the carapace (SL vs. total length) have a linear relationship with a slope of $m = 1.9424$ (Fig. 1). If the three outlier values, most probably caused by deformed branchial flaps of the carapace, are omitted, the conversion factor rises to 1.9595, which can be taken as the more probable value. There are no significant differences between males and females in this respect.

If the whole-size data set is pooled, the measurements result in a normal distribution (Fig. 2) with a median carapace shield value of 2.5 mm and a standard deviation (SD) of 0.51. In order to detect morphometric differences between the sexes and with reference to non-ovigerous versus ovigerous females, a data distribution analysis was performed. The resulting box–whisker plots (Fig. 3a, b) show that the median value of the SL of males (2.7 with a SD of 0.571) is superior to that of females (2.4 with a SD of 0.392), but the difference is not significant. Also, males have been found to grow larger than females (maximum SL 4 vs. 3.6 mm).

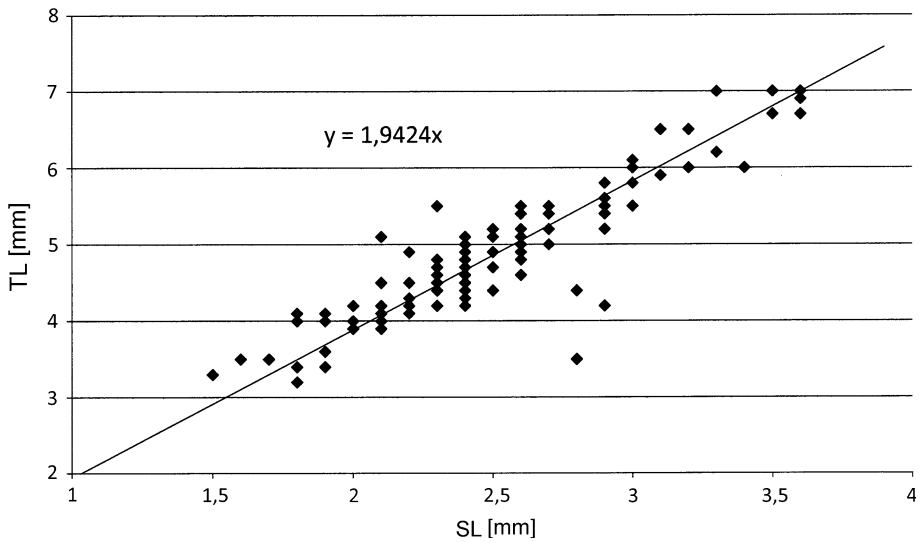

Fig. 1 Relation of TL to SL in *D. pugilator* from the German Bight

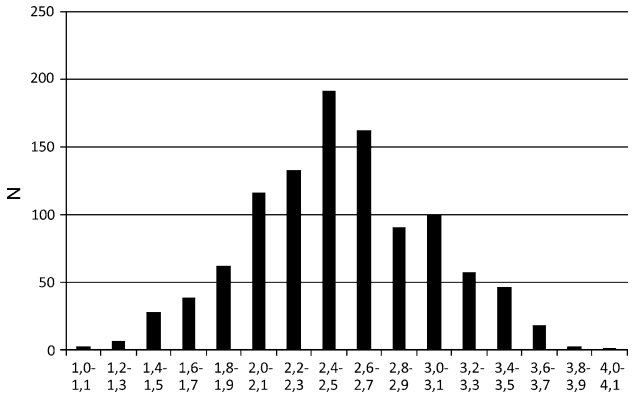

Fig. 2 Frequencies (*N*) of size classes (in mm) in the examined data set

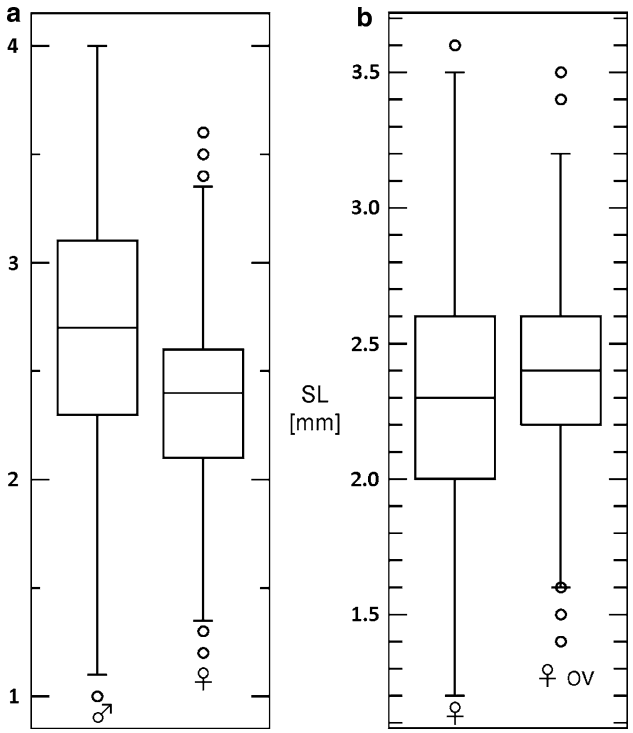

Fig. 3 Box–whisker plots. Size distribution of SL in **a** males and females, **b** non-ovigerous versus ovigerous females

The size distribution of 0.2-mm classes in the different sampling months of the period with a minimum number of specimens has been plotted in Fig. 4. It is evident that in October 2005, the population mainly consisted of small specimens, growing larger through July and September of the same year. In February 2007, only very small specimens could be collected in low numbers. In June of the same year, the size was increased again to 2.71 mm. Similar sizes and size distributions could be recorded in July 2008 and August 2009. The corresponding average and median lengths are included in Fig. 4.

Shells utilised by the examined populations of *D. pugilator* belong to seven gastropod species. The absolute and relative numbers are presented in Table 2 together with shell usage at the Western Frisian Islands. As expected, the most commonly utilised shell was that of *Littorina littorea*. Besides this, *Nassarius reticulatus* is also quite common, even in the intertidal population on the beach. This and the presence of other shell species in the onshore beach population show that the hermit crabs actively transport shells from the sublittoral into the intertidal zone. All species in Table 2 have also been found washed ashore during shore collections at Wangerooge Island, but most of them were quite rare and were only found a few times. It is therefore surprising to see the relative dominance of sublittoral shells as those of *N. reticulatus* used by the beach population of *Diogenes*.

Discussion

Diogenes pugilator has been collected in the south-western North Sea as early as 1899 (Laporte et al. 1985). Together with its regular occurrence in the British Channel, it has to be considered as an autochtonous element in this region. There have, however, apparently always been pulses that brought the species deeper into the North Sea. The first one was noted around 1937, another one in 1984 (Laporte et al. 1985). The first invasion extended to the coast of South Holland across the Rhine delta with the northernmost record from Katwijk an Zee (Holthuis 1950; Wolf and Sandee 1971). Since this time, the entire Belgian coast must have been populated by this hermit crab, as can be concluded from the list of records published by Laporte et al. (1985) and in which a good deal dates back to the period between 1937 and 1950 (identification years which do not necessarily correspond exactly to the year of collecting). As expected, there are also a good number of records from around 1984. In recent years, the species has spread farther towards the east. In 1995, it occurred at the Western Frisian Island of Ameland (d'Udekem d'Acoz 1997). In 2007, it had reached Schiermonnikoog (van Peursen 2008). Franke and Gutow (2004) noted its occurrence around Helgoland in 2002. This record was based upon few specimens dredged from the edge of the Helgoland Trench at 20–30 m depth, which is not typical for the species. In 2008, there was a mass occurrence at the dune island of Helgoland (H.-D. Franke, Helgoland, personal communication). Our collection of specimens from off Wangerooge and ashore after 2005 confirms the onshore establishment of the species in the German Bight, where it is evidently a recent invader like a number of other warm water elements.

The colonisation success and the eastward move of this species are well documented, especially in the Belgian and

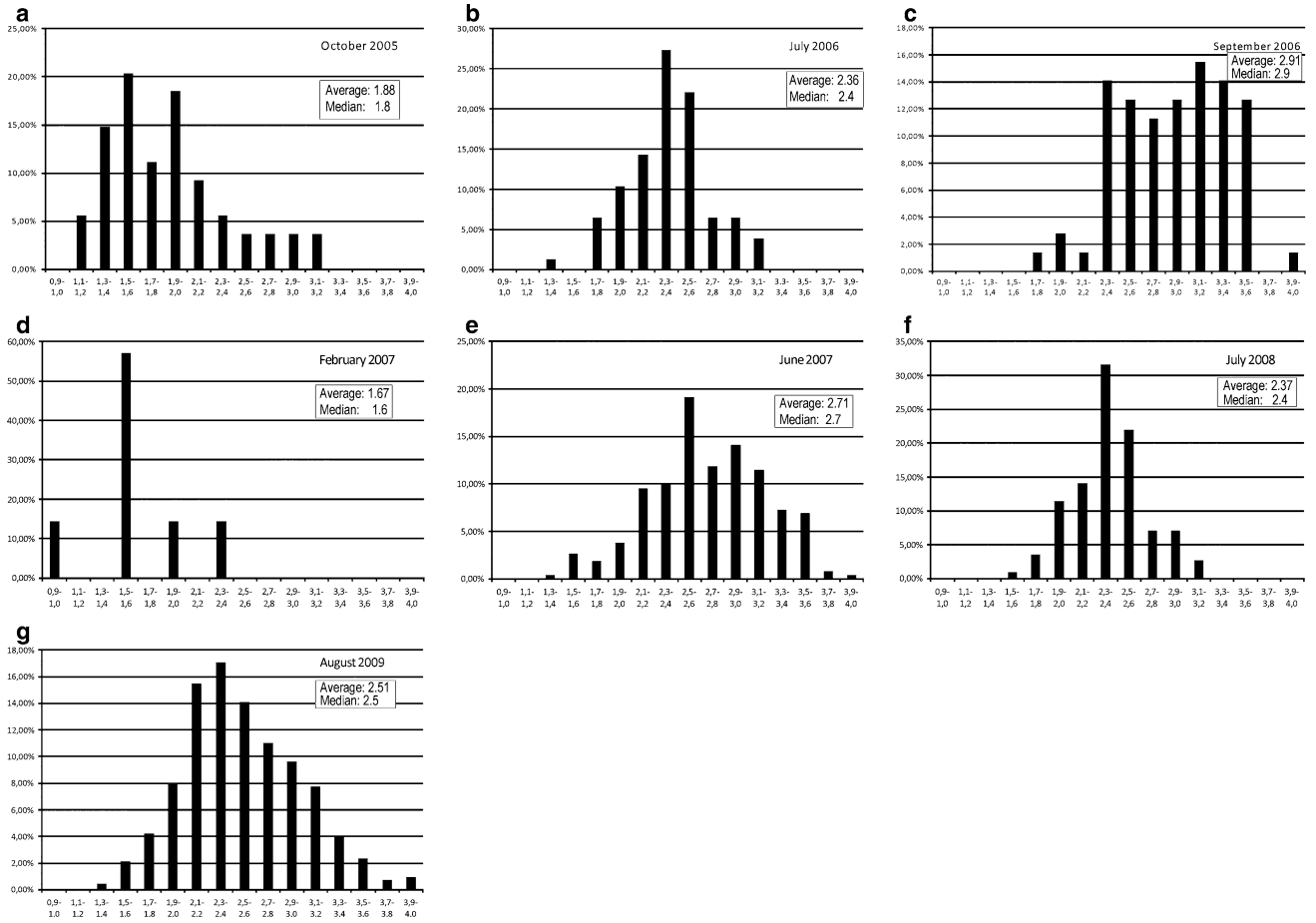

Fig. 4 Frequencies (in %) of size classes (in mm) in different samples. **a** October 2005; **b** July 2006; **c** September 2006; **d** February 2007; **e** June 2007; **f** July 2008; **g** August 2009. Average and median values of the shield in mm

Table 2 Mollusk shells utilised by *D. pugilator* at the beach of Wangerooge and Langes Riff together with presence–absence data for the more western Dutch Islands

	LR-090816	Wangerooge, beach	Schiermonnikoog	Terschelling	Texel
Littorina littorea	265	189	X	X	X
Nassarius reticulatus	32	47	X	X	X
Euspira nitida	31	16	X	X	X
Turritella communis	17	2		X	
Propebela turricula	14	4	X	X	
Buccinum undatum	5	5		X	
Epitonium clathrus	4	1		X	
Littorina cf *saxatilis*	3	1		X	
Euspira catena		3		X	
Aporrhais pespelecani			X	X	
Epitonius turtonis			X	X	
Gibbula magus				X	
Littorina sp.				X	
Nassarius cf. *incrassatus*				X	
Nassarius pygmaeus				X	
Nucella lapillus				X	

Data for Schiermonnikoog from Van Peursen (2008), for Terschelling from Doeksen (2003), Knol (2005) and van Peursen (2008), for Texel from de Wolf and de Wolf (2002)

Dutch literature. It is also evident that in cold winters, the eastern populations diminished or even faded but were replaced by subsequent invasions. This is also true for the more southern occurrences and was especially noted in the area of Oostende for the winters 1995/1996 and 1996/1997 after which the species had disappeared but was back in 1998 (Kerckhof 1998). Still, the move forward towards the east seems unbroken. The temperature sensibility of this species is also clearly visible in our data set. The water temperatures of the area in front of Spiekeroog, Wangerooge and the Jade mouth in the period of January–February have been plotted for all years since 2005 (Fig. 5). The moving average line shows an increase in the average temperature in the coldest months from 2005 to 2007, then it drops again to a minimum in 2011, increasing towards 2012. If this development is compared to the records of the species in the different years of the period and to the size distributions in Fig. 4, a correlation can be seen. The largest beach sample was taken in 2007. Of the offshore samples, the one in 2009 was the largest, when the minimum average temperatures of the year were only a bit lower than the ones in 2005. Numbers of specimens were also quite high in 2005–2008. After the minimum of average temperature in 2010–2011 the species had disappeared, but was present again in 2012–2013. In this late period, however, there were no specimens on the beach in contrast to around the time with higher temperature minima. These results also show that the specimens occurring on the beach are more affected by lower temperatures than the sublittoral ones. This means that these last ones might form a reservoir for specimens surviving through the winter. This is further confirmed by the fact that specimens could also be collected in January and February 2009 at Langes Riff and in the Jade Bay.

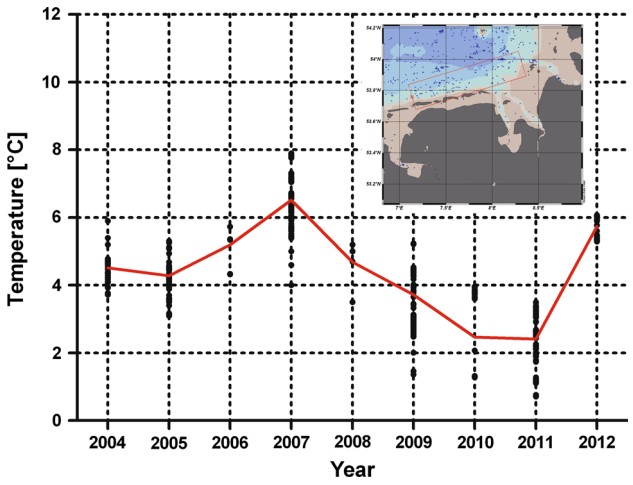

Fig. 5 Water temperatures for the area marked in the *inlay map* (from off Langeoog to Weser estuary) for the months of January to February of the years 2004–2012. All data pooled for a given year and average value calculated (*red line*). Data from ICES Oceanography data portal, downloaded October 2013; plot prepared and processed with the program Ocean Data View V4 (Schlitzer 2013) (color figure online)

As to the reproductive activity, Manjón-Cabeza and García-Raso (1998) observed ovigerous females throughout the year and continuous recruitment. In our data set, ovigerous females are restricted to the second half of the year, getting rarer from October on. This points towards a stronger seasonality in the North Sea populations. To date, there is only one record of larvae in the Helgoland plankton (Greve et al. 1996), which refers to specimens collected on 02.12.1994 (W. Greve, Hamburg, personal communication). This record is long before the species got established in the German Bight, but confirms the reproductive season in the second half of the year. Subsequent Plankton sampling at Helgoland Roads has not resulted in any further records of larvae of *Diogenes* (Jasmin Renz, DZMB, Hamburg). This means that the local population of Wangerooge may have only a very local discharge of larvae. It is not known how recruitment works at this location and from where the larval supply comes.

The life cycle of *D. pugilator* has been analysed with reference to populations of the south-western Atlantic coast of Spain by Manjón-Cabeza and García-Raso (1998). They estimated the maximum longevity as 2 years, but most of the cohorts lived only for 1 year. Our results also indicate a rapid growth within 1–2 years (Fig. 4a–c). The size distribution from October 2005 to September 2006 shows a clear increase in size. In February 2007 (Fig. 4d), again only small specimens are present, while in June (Fig. 4e) of the same year, the median size is again similar to that in July 2006. In the summers of the following years (2008, 2009), sizes are like the ones in summer 2007. All this confirms that the life cycle and the longevity of the German populations are similar to those recorded from Spain.

With reference to the growth dependent size parameters, the examined North Sea population exhibits slightly higher values than those of the Spanish populations analysed by Manjón-Cabeza and García-Raso (1998). In these last ones, the mean value of the SL is 2.34 mm with a SD of 0.71 in males and 2.19 mm with a SD of 0.57 in females. In contrast, the maximum SL is smaller in the North Sea population than in the Spanish ones (5.45 vs. 4.0 mm). Dolbeth et al. (2006) give maximum sizes of 8.6 mm of SL in a Portuguese population, which seem much larger than any measures known from the literature. Indeed, in the Fig. 3, "cephalothoracic length" is given as a measure on the x-axis, which would correspond to a SL of 4.39 mm if the conversion factor calculated in this paper is used. In another morphometric study on this species (Codreanu and Balcesco 1968), a mean value of the TL of 5.53 mm with a SD of 0.065 is given for males and 4.69 mm with a SD of 0.037 for females from

Arcachon (French Atlantic coast). These figures correspond to median shield lengths of 2.82 and 2.39 mm, respectively. This again corresponds roughly with the measurements of the North Sea specimens.

The shells used by *D. pugilator* at and off Wangerooge have also been detected at the Western Frisian Islands' populations, with most species at Terschelling (Table 2), but this is certainly due to more intensive collecting and recording.

Conclusions

From the present data set, it gets clear that the *D. pugilator* populations of the German North Sea coast show similar characteristics to the ones analysed from more southern regions of the NE Atlantic. There is no indication of lower fitness as it is sometimes seen at the margins of the distribution of a species. This means that *D. pugilator* is meanwhile fully established in the southern German Bight and has the prospect of spreading further east and north. Offshore populations seem to be quite stable and serve as a reservoir for recolonisation of shallower environments, also after cold winters.

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