First record of Say's mud crab *Dyspanopeus sayi* (Smith, 1869) from the Seudre estuary (Marennes-Oléron, French Atlantic coast)

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Abstract

The Say's mud crab *Dyspanopeus sayi* (Smith, 1869), native to the Atlantic coast of North America, was reported for the first time in the Seudre estuary (Marennes-Oléron Bay, south-west France). In all, twenty-four crabs were collected from subtidal shelly, muddy bottoms located in the polyhaline part of the estuary in April and October 2007, and subsequently in October 2012. The specimens were identified according to their distinctive morphological characters. A critical review of the available literature clarified its European Atlantic range and supported the view that this is actually the first record for the French Atlantic coast. Life history traits of *D. sayi*, as well as vector(s) of introduction into the Seudre estuary, remain to be elucidated but they are likely to be involved with the Marennes-Oléron shellfish trade.

Keywords: non-native species; Decapoda; *Dyspanopeus sayi*; Seudre; Marennes-Oléron

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Premier signalement du Décapode *Dyspanopeus sayi* (Smith, 1869) dans l'estuaire de la Seudre, bassin ostréicole de Marennes-Oléron, côte atlantique française

Résumé

Le Décapode Brachyoure *Dyspanopeus sayi* (Smith, 1869) natif de la côte atlantique nord-américaine est signalé pour la première fois dans le secteur polyhalin de l'estuaire de la Seudre qui débouche au sud-est du bassin conchylicole de Marennes-Oléron. Au total, 24 individus ont été récoltés en avril et octobre 2007 puis en octobre 2012 dans des sédiments subtidaux hétérogènes envasés. Les critères morphologiques distinctifs de l'espèce ont permis son identification. La répartition géographique Manche-Atlantique de l'espèce est clarifiée via une analyse exhaustive et critique de la littérature. Celle-ci confirme la présente signalisation comme étant la toute première pour les côtes atlantiques françaises. Des interrogations demeurent sur la dynamique de population de l'espèce dans l'estuaire de la Seudre et sur le(s) vecteur(s) de son introduction dans cet écosystème, mais qui sont probablement en lien avec le dynamisme de son activité conchylicole.

Mots-clés : espèce introduite ; Décapodes ; *Dyspanopeus sayi* ; Seudre ; Marennes-Oléron

Introduction

Dyspanopeus sayi (Smith, 1869) is a small decapod brachyuran species native to the Atlantic coast of North America, from Chaleur Bay, Canada (Williams, 1984; Squires, 1990; Brunel *et al.,* 1998) to the Florida Keys, south-eastern United States (Abele, 1972; Sheridan, 1992; Felder *et al.,* 2009). The first report of *D. sayi* outside its native range was in Swansea, Wales (Naylor, 1960), where it was presumably accidentally introduced by shipping during the 1950's (Ingle, 1997; Minchin *et al.,* 2013). The species was located in Queen's Dock, the marine waters of which were artificially warmed (hottest outflow ca. 20 °C above ambient) by effluents from the Tir John power station (Naylor, 1960; Naylor, 1965). The power station operated from June 1935 until March 1976 (Walker, 2007) but electricity production, based on anthracite duff and then oil burning, was reduced by at least twice after November 1960 (Naylor, 1965). Naylor (1960) together with Ingle (1980) and Clark (1986) hypothesised that *D. sayi* could spread into suitable British marine habitats given its natural thermic tolerance. As a matter of fact, the species was still recorded in large numbers in Queen's Dock between October 1976 and February 1977, when the waters had returned to ambient thermic conditions (Bullimore *et al.,* 1978). However, there is no published evidence that *D. sayi* extended beyond Queen's Dock, and established self-sustaining populations elsewhere, leading to the conclusion, that in Great Britain, it is a non-established introduced species (Eno *et al.,* 1997; Minchin & Eno, 2002; Minchin *et al.,* 2013).

Moreover, there have been no reports of *D. sayi* along the continental north-eastern Atlantic coast over the last four decades of the twentieth century (Leppäkoski *et al.,* 2002). *D. sayi* was not listed from both regional seas (Baltic Sea and North Sea) and national coasts

i.e. Norway to France. For the latter, Goulletquer *et al.* (2002) gave details about non-native fauna along the English Channel, Brittany and Bay of Biscay coasts. Ten years later, a similar conclusion was given by Noël (2011) in an European synopsis included in the first global overview of alien marine crustaceans all over the world (Galil *et al.,* 2011). It should also be noted that the absence of *D. sayi* from all 1990-2010's surveys in north-eastern European marine waters could not be attributed to gaps in taxonomic knowledge as the genus *Neopanope* = *Dyspanopeus* and related species *D. sayi* had been described early in British (Allen, 1967; Ingle, 1980; Clark, 1986; Hayward & Ryland, 1990) and European faunas (Noël, 1992). Today, the ecological roulette (Carlton & Geller, 1993) with *D. sayi* is operating again along the north-eastern Atlantic coast, since the species is newly reported from the polyhaline section of the Seudre estuary located south-east to the Marennes-Oléron Bay (south-west France). In April and October 2007, the specimens first collected were determined as small xanthid crabs. Further examination of new specimens sampled in October 2012 allowed all of them to be identified at specific level as *D. sayi*.

This study had three objectives: 1) summarize the current morphological characters useful for the specific distinction of the two closely related species known within the genus *Dyspanopeus* (Martin & Abele, 1986), 2) critically examine the current geographic distribution of *D. sayi* in the north-east Atlantic and North Sea in the available European literature, which includes several inaccuracies and 3) document the presence of *D. sayi* in the Seudre estuary as the first record for the French Atlantic coast.

Material and methods

Study area

The Seudre estuary is a narrow 25 km long coastal inlet, surrounded by a vast system of fresh, brackish and marine wetlands, including saltmarshes, marine ponds and intertidal mudflats submitted to a macrotidal regime. Marine ponds are used for fish and shellfish farming in shallow "claires", where oysters are traditionally placed for fattening (Hinard, 1923; Grelon, 1978; Goulletquer & Héral, 1997). The Seudre estuary is located south-east of the Marennes-Oléron Bay (figure 1), which is the main oyster centre in France (Goulletquer & Héral, 1997). Half of trading companies linked to oyster farming in Marennes-Oléron Bay are located within the Seudre estuary (Masson, 1997). The freshwater discharge of the Seudre River (watershed area 380 km) averaged 1 $m^3 s^{-1}$ with a maximal discharge of 24 $m^3 s^{-1}$ during the highest winter floods (http://www.hydro.eaufrance.fr). The salinities of the middle estuary ranged from 27-31 down to 12-17 according to the rainfall regime (Bouquet, 2003). Although most of sediments from "claires" and tidal flats are muddy (Hinard, 1923), sandy gravelly muds with a significant shelly fraction occurred throughout the channel and its tributaries (Ruckebusch, 1949; Sauriau *et al.,* 2013).

Field benthic sampling and sample processing

Surveys conducted in the Seudre estuary were part of the 2007-2012 monitoring program of transitional waters, supervised by both Ifremer and Agence de l'Eau Adour-Garonne, under the scope of the European Water Framework Directive (WFD, 2000/60/EC). Samples were collected at two sites Mornac-sur-Seudre (middle estuary) and La Tremblade - La Cayenne

(lower estuary). For each site, intertidal and subtidal soft-bottom stations (figure 1) were sampled in April 2007 and then in October in the years 2007, 2008, 2009 and 2012. At each station, five replicates were randomly collected from the vessel "Estran - La Rochelle University" using a van Veen grab sampler (0.1 m^2). Samples were sieved through a 1 mm mesh size and fixed with 4 % buffered formalin solution in sea water. Samples were then stored in 70 % ethanol after identification. Carapace width (CW, as measured at the widest points between the fifth anterolateral spines across the carapace) and carapace length (CL, as measured between the front to the posterior edge of the carapace in the midline) were measured at the nearest 0.1 mm with Mitutoyo vernier callipers.

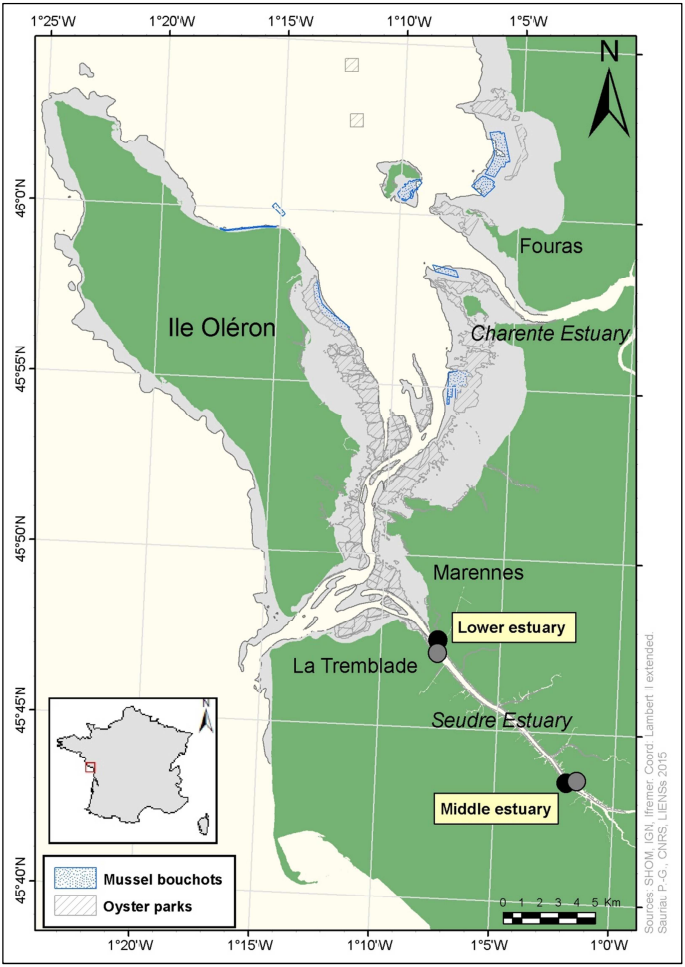

Figure 1: Map of the Marennes-Oléron Bay and location of the two sampling sites Mornac-sur-Seudre (middle estuary) and La Tremblade - La Cayenne (lower estuary) with both subtidal (black circle) and intertidal (grey circle) stations within the Seudre estuary.

Morphological characters

The xanthid crabs were identified using identification keys of Williams (1965), Ingle (1980), Martin & Abele (1986) and Noël (1992, Xanthidae p. 115) together with morphological descriptions by Abele (1972) and Mizzan (1995). Identification problems are numerous and due to successive changes in genus and species names, changes in hierarchy and relevance of morphological characters amongst xanthid identification keys, as well as natural variability of morphological characters submitted to habitat and/or mode of feeding adaptations. The complex armature of male first pleopods (gonopods) is a more conservative character (see the review of Guinot, 1978) for distinction of the genus *Dyspanopeus* and related species (see Martin & Abele, 1986).

Since its first description as *Panopeus sayi* Smith, 1869, the species has been placed in the genus *Neopanope* (Milne-Edwards, 1880) and *Dyspanopeus* (Martin & Abele, 1986). Based on male first pleopod morphology, these authors separated *Neopanope packardii* (Kingsley, 1879) from *N. sayi* (Smith, 1869) and *N. texana* (Stimpson, 1859) creating the new genus *Dyspanopeus* for the two latters. These two taxa, previously synonymized or placed as subspecies of *Neopanope texana* (see Rathbun, 1930) have been separated and considered as true species by Abele (1972). Subsequent molecular phylogeny studies placed *D. sayi* and *D. texana* closely together and *N. packardii* in their immediate vicinity (Schubart *et al.,* 2000; Thoma *et al.,* 2014).

Furthermore, Abele (1972) used three morphological characters to distinguish *D. sayi* from *D. texana* (table 1). They are illustrated by Abele & Kim (1986, p. 629) for each species and by Squires (1990, p. 490), Froglia & Speranza (1993, p. 164) and Mizzan (1995, p. 127-129) for *D. sayi*. The first character was suggested by Benedict & Rathbun (1891, p. 364) and is based on the relative length of the dactylus and propodus of each of the five pereiopods. Abele (1972) indicated that in *D. sayi* the dactylus of the fifth pereiopod is as long as or shorter than the propodus with a mean ratio of 1.02 (range of 1 to 1.12). The second character is based on the pubescence of the dorsal and ventral borders of the fifth pereiopod dactylus, thick in *D. sayi* and sparse in *D. texana* (Abele, 1972, p. 266 figs. 2a, b and c). The third one is based on the structure and shape of first male pleopods (Abele, 1972, p. 266 figs. 3b, c and d). In *D. sayi*, the mesial lobe of gonopods is low and broadly rounded while elongate and more narrow in *D. texana*.

Syntypes examined from the MNHN crustacean collections

The three following syntypes were examined on 13th June 2014 at Muséum National d'Histoire Naturelle, Paris (MNHN) with the support and advice of Dr. Paula Martin-Lefevre and Dr. Danièle Guinot: *Panopeus sayi* Smith (1869), MNHN-B10044, 1 male, 1 female (New Haven 5-99 Collection Smith); *Neopanope texana* (Stimpson, 1859) MNHN-B10042, 1 male and *Neopanope texana* (Stimpson, 1859) MNHN-B9933, 1 male (Alligator Harbour, Florida Franklin County, 28th January 1968, L. Abele).

Table 1: *Dyspanopeus sayi* - *Dyspanopeus texana*, distinctive morphological characters (Abele, 1972) and comparison with specimens from the Seudre estuary collected in 2007-2012.

Morphological character	*Dyspanopeus sayi*	*Dyspanopeus texana*	Specimens from this study = *Dyspanopeus sayi*
Propodus length / dactylus length of the fifth pereiopod	Dactylus as long as or shorter than propodus, mean P/D = 1.02 range P/D = 1 to 1.12	Dactylus longer than propodus, mean P/D = 0.859 range P/D = 0.787 to 0.920	Dactylus as long as or shorter than propodus, mean P/D = 1.02 range P/D = 0.99 to 1.11
Pubescence of the fifth pereiopod	Ventral and dorsal borders with a thick pubescence	Ventral and dorsal borders with a sparse pubescence	Ventral and dorsal borders with a thick pubescence
First male pleopod (gonopod)	Mesial lobe low and broadly rounded	Mesial lobe elongate and narrow	Mesial lobe low and broadly rounded

Results

Morphology

Specimens from the Seudre estuary have a subhexagonal, slightly pubescent carapace with distinct protuberant dorsal regions and minute granulation. The colour of the dorsal side varies from greenish to brown-reddish with dots (figure 2A). The ventral side of the carapace is mainly white-cream (figure 2B). The front is very prominent and arcuate with a median notch. Five teeth are present on each anterolateral margin, the first two are coalescent and close to the margin of the ocular lobe, and the last three prominent but very different in shape. Walking pereiopods have long and slender dactylus; pereiopods 2 to 5 are shorter than pereiopod 1 (figure 2B). Propodus/dactylus ratios of the fifth pereiopod range from 0.99 to 1.11; mean value being 1.02 (table 1). The dactylus and propodus of major chelipeds are white, horn or black in colour with lighter tips (figures 2C, D, E). The shape and ornamentation of the male gonopods are species-specific and easily distinguishable from those of other Panopeidae (Guinot, 1978; Martin & Abele, 1986). Specifically, there is no stout lateral tooth, no lateral accessory, the apex is strongly deflected and the mesial lobe broadly rounded (Martin & Abele, 1986). The structure of the first male gonopods from the Seudre estuary agrees well with that of the male syntype *Panopeus sayi* Smith, 1869 MNHN-IU-2013-11309 (figures 3A, B). As previously noted by Abele (1972) and Mizzan (1995), a small variation occurred in the number of spines present on both the mesial and distal surfaces of first gonopods. In male specimens from the Seudre estuary, the number of spines on the mesial distal surface varies from 0 (unarmed) to 3, while 13 to 22 spines are present on its lateral surface.

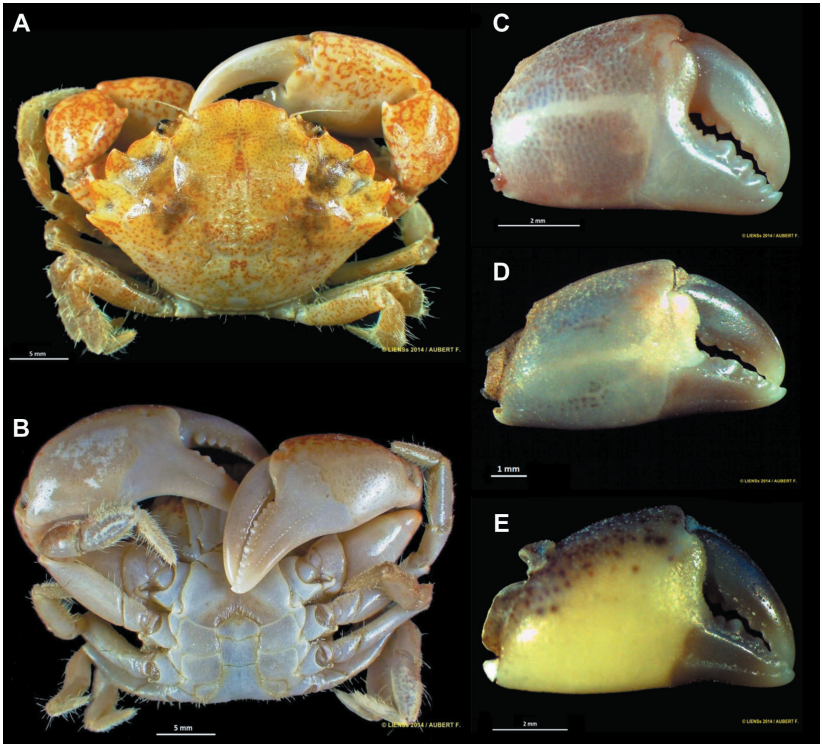

Figure 2: *Dyspanopeus sayi*, Seudre estuary. Dorsal (A) and ventral (B) view of a male collected in October 2012. Changes in colour of propodus and dactylus of cheliped from white ivory (C), horn (D) to black (E) from male crabs collected in 2007 and 2012.

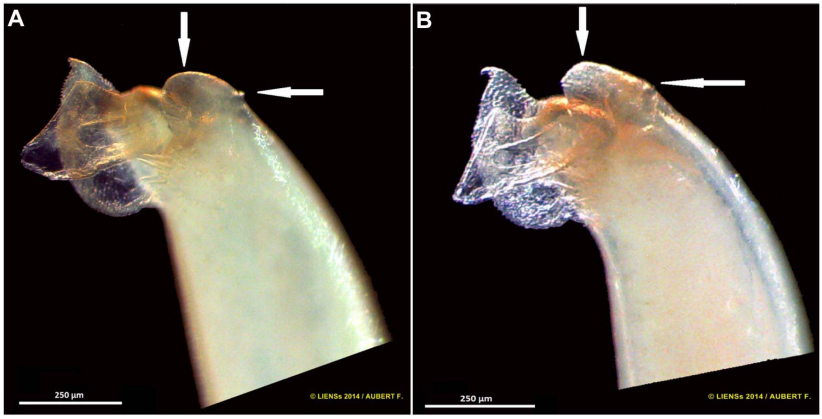

Figure 3: *Dyspanopeus sayi*, lateral view of apex of first male gonopod from a specimen collected from the Seudre estuary in October 2012 (A) and the syntype *Panopeus sayi* Smith, 1869 MNHN-IU-2013-11309 (B). Mesial lobe broadly rounded (vertical arrow) and distal spine (horizontal arrow).

Habitat, abundance, sex ratio and size

D. sayi was only recorded from the polyhaline middle estuary (Mornac-sur-Seudre) in subtidal bottoms characterised by shelly, sandy muds (Sauriau *et al.,* 2013). No specimens were collected from the intertidal mudflats. In all, 16, 5 and 3 crabs were collected in April 2007, October 2007 and October 2012, respectively. No specimens were sampled in 2008 and 2009. Abundance ranged from 0 to 5 crabs per grab sampler (0.1 m^2) and thus crabs densities (all dates combined) showed high variability and averaged 16 $\pm$ 19 crabs m^2 (mean $\pm$ SD, n = 15). The sex ratio (M:F) determined for all crabs (see Swartz, 1975) was 1.6:1 (i.e. 61 % of males and 39 % of females). No egg-bearing females as determined by visual examination were observed. Carapace width (CW) ranged from 3.5 to 25.7 mm; the largest crab being a male (figures 2A, B). In light of the carapace length (CL), CW/CL ratios varied between 1.19 (juvenile) to 1.37 (adult male). The regression slope of CW versus CL was 1.31 ($R^2 = 0.99$; $n = 24$, $p < 0.001$, highly significant relationship).

Specimens deposited at MNHN crustacean collections

Three specimens collected in October 2007 have been deposited at Muséum National d'Histoire Naturelle, Paris on 10th December 2014, and have been referenced as follows:

— MNHN-IU-2014-4031 France, Poitou-Charentes, Seudre estuary (middle), Latitude / Longitude (WGS84, decimal degree) 45.720299 N / 1.019004 W, van Veen grab sampler, October 2007, Sauriau. 1 male;

— MNHN-IU-2014-4047 France, Poitou-Charentes, Seudre estuary (middle), Latitude / Longitude (WGS84, decimal degree) 45.720299 N / 1.019004 W, van Veen grab sampler, October 2007, Sauriau. 1 male;

— MNHN-IU-2014-4051 France, Poitou-Charentes, Seudre estuary (middle), Latitude / Longitude (WGS84, decimal degree) 45.720299 N / 1.019004 W, van Veen grab, October 2007, Sauriau. 1 female.

Discussion

Relevant versus accessory characters in the distinction of the two *Dyspanopeus* species

Since Benedict & Rathbun (1891), Abele (1972) and Martin & Abele (1986) distinguished *D. sayi* from *D. texana* by several morphological characters (see table 1). Other morphological accessory characters, such as carapace shape (CW/CL ratio) and colour of major cheliped fingers (Rathbun, 1930; Ryan, 1956; Williams, 1965) have also been used in characterizing one of the two species (e.g. Mizzan, 1995). Our results support the view that these accessory characters are not relevant for distinguishing the two species.

Firstly, the regression slope of CW versus CL (1.31) for the Seudre estuary crabs fell well within the range (1.30 to 1.39) given by Abele (1972) for *D. sayi*. Although the carapace of *D. sayi* is relatively broader, the *D. texana* CW/CL ratio overlaps as it ranges from 1.28 to 1.36, the mean being 1.30 (Abele, 1972). Analysis of available data sets for carapace shape in *D. sayi* indicated that most of individual CW/CL ratios fell within the range of 1.30 to 1.39 (figure 4, grey dashed lines), however outliers are not uncommon due to ontogenic and/or

population variability. Some large crabs from Queen's Dock in Swansea (Naylor, 1960) and from the Venetian lagoon (Mizzan, 1995) are above the 1.39 regression line, while some small crabs from Ebro delta (Schubart *et al.,* 2012) and Seudre estuary are below the 1.30 regression line (figure 4).

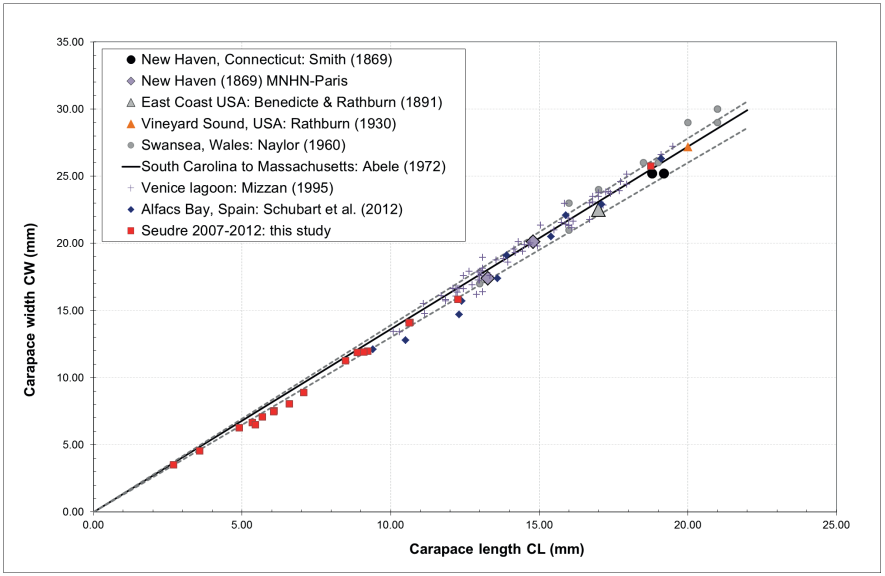

Figure 4: *Dyspanopeus sayi*, carapace width - carapace length relationship (mm). Data from Smith (1869), syntypes at MNHN-Paris from New Haven (MNHN-B10044, 1 male, 1 female), Benedict & Rathbun (1891), Rathbun (1930), Naylor (1960), Abele (1972), Mizzan (1995), Schubart *et al.* (2012) and this study (Seudre estuary 2007-2012). Abele (1972) data are given as regression lines with slopes of 1.36 (dark line, mean value), 1.30 and 1.39 (grey dashes, lower and higher value, respectively).

Secondly, cheliped finger colour was formerly used in several keys to xanthid and/or species of *Dyspanopeus* (Benedict & Rathbun, 1891, p. 357; Rathbun, 1930, p. 367; Ryan, 1956, p. 142; Williams, 1965, p. 190), with black fingers in the male *D. sayi* (Smith, 1869, p. 285) and white or pale brown in the male *D. texana* (Stimpson, 1859, p. 55). Variation from black to horn colour in the male *D. sayi* was already noted by Benedict & Rathbun (1891, p. 364). Similarly, Abele (1972, p. 265) reported white, horn and black fingers in *D. texana*. All these colour variations of cheliped fingers were observed in male *D. sayi* from the Seudre estuary (figures 2C, D and E). Published drawings and pictures of *D. sayi* (table 2) do not allow these colour changes to be fully assessed as all illustrated *D. sayi* have black or dark-coloured cheliped fingers (Ryan, 1956; Swartz, 1976; Ingle, 1980; Galil *et al.,* 2002; Ng *et al.,* 2008; Schubart *et al.,* 2012; Crocetta *et al.*, 2012 in Thessalou-Legaki *et al.,* 2012; Ungaro *et al.,* 2012). However, there are striking similarities between one of our crabs (figure 2A) and the one shown by Ng *et al.* (2008, fig. 145 p. 191) from Venice, in terms of the colour pattern of both the carapace and major chelipeds (palm, carpus and merus).

Table 2: *Dyspanopeus sayi*, synopsis of available drawings and photographs (* black and white, ** colour).

Taxa	Illustration	Sources
Panopeus sayi	Dorsal view, left and right chelipeds	Benedict & Rathbun (1891): plate 22 fig. 4, plate 23 figs. 7-8
Neopanope texana sayi	Male in dorsal view	Hay & Shore (1915): plate 34 fig. 8
Neopanope texana sayi	Male cheliped, male in dorsal view	Rathbun (1930): fig. 58 p. 370 and plate 168 figs. 3-4
Neopanope texana sayi	Dorsal view (*)	Ryan (1956): plate 1B p. 144
Neopanope texana sayi	Male in dorsal view, right cheliped, abdomen	Naylor (1960): fig. 1 p. 256
Neopanope texana	Dorsal view of carapace, cheliped	Smith (1964): figs. 23-24 plate 16 p. 123
Neopanope texana sayi	Male in dorsal view, cheliped, first male pleopod	Williams (1965): fig. 173 p. 191, fig. 183G p. 200
Neopanope texana sayi	Dorsal view	Allen (1967): p. 104
Neopanope sayi	Dactylus fifth pereiopod, first male gonopod	Abele (1972): figs. 2B, C and D, Fig.3D p. 266
Neopanope sayi	Dorsal views of males (*) and females (*), some crabs with barnacles on their carapace	Swartz (1976): figs. 1-2 p. 25 and figs. 4-7 p. 27-29
Neopanope sayi	Dorsal view (*)	Ingle (1980): plate 20 p. 166
Neopanope sayi	Male in dorsal view, major cheliped, mesial view of first male gonopod	Williams (1984): fig. 324 p. 410 from 1965, fig. 331k p. 418
Neopanope sayi	Male in dorsal view, major cheliped, dactylus and propodus of fifth pereiopod, mesial view of first male gonopod	Abele & Kim (1986): fig. h, i p. 629 from Williams (1984) and fig. j, k p. 629 from Abele (1972)
Dyspanopeus sayi	Dorsal view	Pohle (1990): p. 26 from Williams (1965)
Neopanope sayi	Dorsal view, female second pleopod, male first and second pleopod, female abdomen, male abdomen, antennule, antenna, mandible, maxillule, maxilla, first, second and third maxiliped	Squires (1990): fig. 262b, p, q, r, y, x p. 490 fig. 263c, d, e, f, g, h, i, k p. 491

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Table 2: *(Continued from previous page)*

Taxa	Illustration	Sources
Dyspanopeus sayi	Carapace of male in dorsal view, major cheliped, abdomen, first male gonopod	Froglia & Speranza (1993): fig. 1a, b, c, d p. 164
Dyspanopeus sayi	Male in dorsal and ventral views, female in ventral view, dactylus and propodus of fifth pereiopod, first male gonopod in dorsal, lateral and ventral views (5 views)	Mizzan (1995): figs. 1, 2, 3a,b, 4a, b, c, d p. 127-129
Dyspanopeus sayi	Dorsal view (*), carapace with one barnacle on it	Fabbri & Landi (1999): fig. 4 p. 16 photograph by L. Landi
Dyspanopeus sayi	Dorsal view (**) Dorsal view (**)	Galil *et al.* (2002): photograph C. Froglia p. 120 http://www.ciesm.org/atlas/Dyspanopeussayi.php
Dyspanopeus sayi	Dorsal view (**)	Ng *et al.* (2008): fig. 145 p. 191 photograph by A. De Angeli
Dyspanopeus sayi	Dorsal and ventral views of male, female and ovigerous female (**)	Micu *et al.* (2010): figs. 2a, b, c, d p. 3 photograph by D. Micu.
Dyspanopeus sayi	Dorsal view (*)	Martin (2011): p. 227 photograph credit Ingle (1980)
Dyspanopeus sayi	Male in dorsal view (*)	Schubart *et al.* (2012): fig. 2 p. 82
Dyspanopeus sayi	Dorsal and ventral views of two crabs (**)	Ungaro *et al.* (2012): fig. 2 p. 195
Dyspanopeus sayi	Dorsal view (*)	Crocetta *et al.* (2012) in Thessalou-Legaki *et al.* (2012): fig. 3 p. 315
Dyspanopeus sayi	Male in dorsal view, eggs, first zoea (**)	Pastore *et al.* (2014) in Katsanevakis *et al.* (2014): fig. 6 p. 679

Dyspanopeus sayi from the Seudre estuary

Similar to the native populations, the size (carapace width) of *D. sayi* from the Seudre estuary ranged from 3.5 to 25.7 mm (Swartz, 1976; Strieb *et al.,* 1995). *D. sayi* is a small species with an adult reaching up to 30 mm CW (Naylor, 1960; Williams, 1984; Strieb *et al.,* 1995). The largest crab observed in this study was a male (25.7 mm CW, figures 2A, B).

D. sayi occurred in low densities in shelly, muddy subtidal bottoms of the Seudre estuary with maximum of 50 crabs m^2 and mean value of 16 $\pm$ 19 crabs m^2. Lower densities were observed in bare sand or non-vegetated muddy sediments while similar or much higher densities were observed in *Zostera marina* habitats (Strieb *et al.,* 1995). The presence of biogenic structures, such as bivalve shells and shell debris, favors juveniles and adults *D. sayi* by serving as both a refuge and food source (Lindsey *et al.,* 2006). Other habitats such as wooden and concrete piles among algae and other fouling organisms were however described as suitable for *D. sayi* (Ryan, 1956; Naylor, 1960).

The absence of ovigerous females in this study may be explained by unsuitable sampling dates (early April and mid-October) with regard to their reproductive season. Along the east coast of North America, the reproductive season extends from March/April to September/October (Williams, 1965; Swartz, 1976; Strieb *et al.,* 1995). In view of the thermic regime of the Seudre estuary, it would be better to sample in summer to confirm the occurrence of egg-bearing females. Their presence would support the view of a self-sustaining population but their absence would suggest multiple introductions of crabs (larvae, juveniles and/or young adults) into the Seudre estuary. The main vectors for the introduction and/or spread of *D. sayi* are ballast waters and hull fouling associated with commercial shipping (Naylor, 1960; Mizzan, 1995) together with accidental release through shellfish aquaculture (Florio *et al.,* 2008). These vectors, separately or as a whole, are likely to occur at the scale of the Marennes-Oléron Bay (Goulletquer *et al.,* 2002).

Geographic distribution of *Dyspanopeus sayi* along the north-eastern Atlantic coast

The geographic distribution of *D. sayi* along the north-eastern Atlantic coast during the period 1950-1980 was summarized by the map of Clark (1986). There was only one occurrence at Queen's Dock, Swansea (Naylor, 1960; Naylor, 1965; Bullimore *et al.,* 1978). Since then, and to the best of our knowledge, there are no new records for the British coast (d'Udekem d'Acoz, 1999; Minchin *et al.,* 2013). However, four citations of the species have arisen in the French literature (Noël, 1992; Noël, 1993; Vaz *et al.,* 2007; Martin, 2011). In particular, Vaz *et al.* (2007) was totally misinterpreted resulting in inaccuracies throughout the European literature about the geographical distribution of *D. sayi* along the north-eastern Atlantic coast. Details about these four citations are given below:

Noël (1992) included the genus *Dyspanopeus* in his preliminary key of French crustaceans decapods and main European species (Noël, 1992, p. 116). The species *D. sayi* was also included in the French atlas of crustacean decapods (Noël, 1993, p. 31) but was quoted as absent from France (cf. the minus symbol) and seen once in Europe (cf. the number 1). Referring to the atlas map (Noël, 1993, carte 1, p. 19), this is indeed the record of Naylor (1960) at Swansea. These two synopses are properly cited by the "Inventaire National du Patrimoine Naturel" web site (http://inpn.mnhn.fr/accueil/index), in which *D. sayi* is still quoted as absent from France (Inventaire National du Patrimoine Naturel, 2015).

Vaz *et al.* (2007) reported the list of benthic invertebrates caught during the French and Dutch contribution to the first quarter IBTS (International Bottom Trawl Survey 2002-2007) in the southern North Sea and north-eastern English Channel. Surveys were conducted by both Imares and Ifremer, with the latter research institute utilizing a standard list of species potentially present in bottom trawls (Vaz *et al.,* 2007, Table 1: Community composition). *D. sayi* is included in this list under the reference "DYSPSAY" but there are no records since the "taxon occurrence" cell of the table is actually empty. As any ICES communication should not be cited without prior reference to the author, S. Vaz was consulted on this matter. She confirmed the absence of *D. sayi* from IBTS 2002-2007 results and subsequent IBTS surveys (Vaz, pers. com., 3rd December 2013). However, this table was misinterpreted by Micu *et al.* (2010) who first claimed that *D. sayi* was recorded from the Dutch and French North Sea coasts. Unfortunately, this erroneous opinion was used again (Schubart *et al.,* 2012; Thessalou-Legaki *et al.,* 2012; Kapiris *et al.,* 2014) leading to great confusion and inaccuracies in the current geographic range of *D. sayi* along the north-eastern Atlantic coasts (Marco-Herrero *et al.,* 2013).

Martin (2011) included *D. sayi* in her handbook aimed at facilitating the identification of more than 500 invertebrates sampled by bottom trawls within the Bay of Biscay, Celtic Sea, eastern English Channel and southern North Sea for the period 1993-2010. It was listed as a potentially observable species in reference to the exhaustive account of European Decapoda by d'Udekem d'Acoz (1999). The small book symbol placed beside the picture of *D. sayi* clearly indicated, together with the explanation text, that *D. sayi* was not sampled from the studied area (Martin, 2011, p. 227). The black and white picture of *D. sayi* was credited Ingle (1980) (see Martin, 2011, p. 297) and actually matched the *D. sayi* picture of Ingle (1980, p. 166 plate 20a), providing indirect evidence of absence of record. Since then, *D. sayi* has not yet been recorded from the studied area (Martin, pers. com., 1st September 2014).

Dyspanopeus sayi as a novel allochthonous species along the French Atlantic coasts

D. sayi, as a novel allochthonous species recorded from the Seudre estuary, is also new to the Pertuis Charentais Sea marine fauna (de Montaudouin & Sauriau, 2000), as well as for the French Atlantic coast considering autochthonous Decapoda (Bouvier, 1940; Noël, 1992; Noël, 1993; d'Udekem d'Acoz, 1999; Vaz *et al.,* 2007; Martin, 2011) and marine alien checklists (Goulletquer *et al.,* 2002). Regarding the French Mediterranean coast, the available synopsis (Galil *et al.,* 2002) and related CIESM atlas (http://www.ciesm.org/atlas/) support the view that *D. sayi* is not as yet recorded there. However, *D. sayi* has been reported in the western Adriatic Sea since the 1990's (Froglia & Speranza, 1993; Mizzan, 1995) and is currently spreading northwards and southwards along Adriatic coasts (Mistri, 2004; Florio *et al.,* 2008; Tiralongo & Baldacconi, 2014 in Kapiris *et al.,* 2014). The species has also been reported in the Spanish Mediterranean coast near the Ebro Delta (Schubart *et al.,* 2012). Finally, it is likely that *D. sayi* will be detected in the French Mediterranean coast in the near future, as well as in other bays and estuaries along the French Atlantic coast.

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