


First records of *Ptilohyale littoralis* (Amphipoda: Hyalidae) and *Boccardia proboscidea* (Polychaeta: Spionidae) from the coast of the English Channel: habitat use and coexistence with other species

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Received: 12 May 2016 / Revised: 28 July 2016 / Accepted: 1 August 2016
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Abstract This paper presents the first record of *Ptilohyale littoralis* (Stimpson, 1853) and *Boccardia proboscidea* (Hartman, 1940) from the French coast of the eastern English Channel. This record is the second for *P. littoralis* in European waters following a record from the Netherlands, which is suspected as the site of initial introduction from the Atlantic coast of North America. The observed high densities (up to 270 ind. 0.25 m⁻²), together with the presence of ovigerous females, suggest that the species could be considered as naturalised in the area. *Ptilohyale littoralis* was consistently found in the same habitat (mussel beds) as *Apothyale prevostii* (Milne Edwards,

1830). There was an apparent spatial segregation between these two species and the melitid *Melita palmata* (Montagu, 1804), the latter being associated with boulders covered with mud. *Boccardia proboscidea*, native from the west coast of North America and Japan, has already been recorded in European waters (Spain, Ireland, North Sea and French coast of Bay of Biscay), but the present record is the first for the English Channel. The species was found inhabiting the same habitat as *M. palmata*, i.e. boulders covered with mud. Further investigations are, however, needed along the coast of the English Channel and the North Sea to clarify the pathways of introduction and the status (casual, naturalised or invasive) of *P. littoralis* and *B. proboscidea* in European waters.

Communicated by D. Fiege

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Keywords English Channel · Amphipoda · Polychaeta · Non-indigenous species · *Ptilohyale littoralis* · *Boccardia proboscidea*

Introduction

The introduction of invasive species is considered as one of the most important anthropogenically driven perturbations that disrupt coastal ecosystems (Jackson et al. 2001), since it represents, combined with the effect of climate change, a key driver of biodiversity loss (Occhipinti-Ambrogi 2007; Mainka and Howard 2010; Galil et al. 2014). European waters are particularly subject to exotic introductions: in 2012, 1369 marine alien species had been reported in the European seas (Katsanevakis et al. 2013), and this number has now increased to about 1400 (see the European Alien Species Information Network, EASIN: <http://easin.jrc.ec.europa.eu>, and the expert system AquaNIS: <http://www.corpi.ku.lt/databases/index.php/aquanis>). Arthropoda (especially Crustacea) and Annelida are,

respectively, the second and fourth most numerous phylum and represent ca. 18 % and 12 % of all alien species in European marine waters (Katsanevakis et al. 2013). Both Crustacea and Annelida are major groups of the macrofauna communities in coastal benthic habitats. Crustacean amphipods are common invertebrates in rocky intertidal habitats, where they are considered as mesograzers on seaweeds and their epiphytes (Little and Kitching 1996; Duffy and Hay 2000), but are also found in mussel beds, which provide habitat and trap organic particles; see, e.g. Arribas et al. (2014) and references therein. Amphipods are consumed by other crustaceans (Blasi and O'Connor 2016) and fish (Savaria and O'Connor 2013). As such, they occupy a key position within the trophic network, as an intermediate between primary producers and predators (including birds as top predators). Spionids are among the most common and abundant interface feeding polychaetes in shallow water benthic communities (Radashevsky 2012). The genus *Polydora* Bosc, 1802 and related genera (also known as 'Polydorins' or 'mud worms') are of particular interest because of their potential impact on commercially harvested molluscs via either their shell-boring behaviour (e.g. Sato-Okoshi and Okoshi 1997) or external colonisation of the shell (Simon et al. 2009). Furthermore, Polydorins are able to form dense tube mats that accumulate fine particles and can form massive intertidal reefs, particularly (but not exclusively) in deteriorated habitats (e.g. Elías et al. 2015). Reef-building organisms are considered as ecosystem engineers that affect local biodiversity either by facilitation or inhibition (Bouma et al. 2009). Therefore, changes in the species composition, abundance and distribution of amphipods or spionids on a rocky shore, which may occur when an exotic species is introduced, might have consequences on the functioning of the community via changes in the community composition and/or local physical modifications of the environment. An absolute prerequisite to the assessment of these potential impacts is the collection of basic information on the occurrence and spatial distribution of alien species (Katsanevakis et al. 2013).

In the present study, we report the first records of the amphipod *Ptilohyale littoralis* (Stimpson, 1853) and the Spionid *Boccardia proboscidea* Hartman, 1940 on the French coast of the eastern English Channel, France. The sampling strategy adopted allowed to identify the habitat of the species and to examine the coexistence of *P. littoralis* with other species in a spatial context.

Materials and methods

Study location and sampling strategy

Sampling was conducted on a longitudinally oblong intertidal rocky reef located at the 'Fort de Croy' in Wimereux, Opal Coast, France (50°45.766'N/1°35.962'E; Fig. 1). This site is

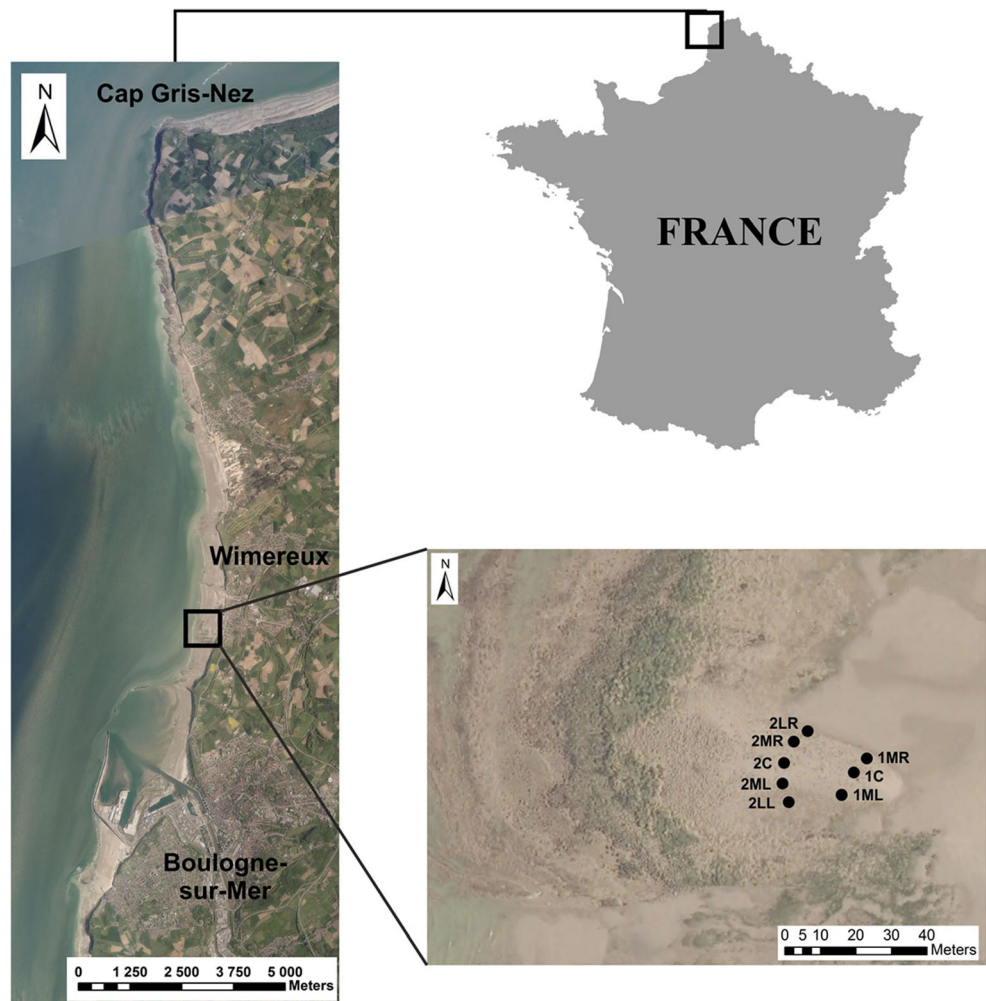
directly exposed (western exposition), submitted to a semi-diurnal megatidal regime (spring tidal range >8 m) and largely covered with mussel beds. This shore is among several rocky shores that have been surveyed for about 7 years to monitor the colonisation of the Opal Coast by the invasive Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835) (Dauvin et al. 2009; Dauvin and Dufossé 2011; Gothland et al. 2013). In this context, in April 2014, a sampling was conducted with the initial aim to investigate the distribution of *H. sanguineus*. Two transect lines were positioned parallel to the shoreline and separated ca. 30 m apart from each other in the mid-intertidal zone (Fig. 1). Along the two transects, sampling stations were positioned at different levels ranging from the top of the reef (iC) to the edges of the reef (iLR and iLL), where i refers to the transect number. Because of spatial constraints, the number of sampling stations varied between the two transects. Two levels were considered on the narrowest transect (Transect 1); one on the top of the reef (1C) and one on the left and right edges of the reef (1MR and 1ML). Three levels were considered on the longer transect (Transect 2); one on the top of the reef (2C), one on the middle of the left and right banks of the reef (2MR and 2ML) and one on the left and right edges of the reef (2LR and 2LL). At each of these eight stations, three 0.25-m² quadrats (i.e. a total of 24 quadrats) were haphazardly positioned within a 3-m radius. In each quadrat, macrofauna was collected by overturning the boulders and scraping the sediment to collect epifauna. Once back to the laboratory, samples were washed through a 1-mm mesh sieve and fixed and preserved in an 8 % formaldehyde-seawater solution until they were sorted and macrobenthic organisms were identified and counted (except cirripeds). Individuals of *P. littoralis* were determined using the species descriptions in Bousfield and Hendrycks (2002) and *B. proboscidea* after Martínez et al. (2006) and Kerckhof and Faasse (2014).

For both species, individuals were compared with specimens from the Netherlands (Faasse 2014; Kerckhof and Faasse 2014).

Data analyses

Benthic epifauna community composition was identified following Clarke (1993) and Clarke and Warwick (2001), using the Bray–Curtis similarity matrix of fourth root-transformed abundance data. The fourth root transformation is considered as an intermediate transformation that down-weights the effect of the most abundant species and allows contribution of the rarest species (Clarke 1993; Olgard et al. 1997). Analysis of similarities (one-way ANOSIM) was performed to test the significance of differences in epifauna assemblage composition between samples, using the reef level (C, M and L) as a factor. Data were explored further by applying the similarity percentages program (SIMPER) to determine the contribution of individual species to the average dissimilarity between

Fig. 1 Location of the study site along the French coast of the eastern English Channel, and sampling stations at the 'Fort de Croy' in Wimereux (C: top of the reef, M: middle of the reef banks, L: edges of the reef bank)



samples. Analyses were performed using the software package PRIMER® v6 (Clarke and Gorley 2006).

Correlations between abundances were examined using Spearman's rank coefficient (r_s) method, applying the correction for tied data when necessary (Zar 2010). Density distribution mapping was performed using aerial photographs (Ortholittorale© 2008) coupled with GIS (Geographic Information System) software (ArcGIS 10®).

Results

A total of 35 taxa of epifauna was collected (Table 1). *Ptilohyale littoralis* (Fig. 2a) was found at all stations, in 18 of the 24 quadrats sampled and represented a total of 677 individuals. Oviparous females were observed, though not counted. Overall, *P. littoralis* was the third most abundant species, after the bivalve *Mytilus edulis* Linnaeus, 1758 (21,487 ind.) and the gastropod *Littorina littorea* (Linnaeus, 1758) (979 ind.). The highest density observed in a single quadrat was 270 individuals per 0.25 m⁻². The highest

abundances were recorded at stations 2C (177 ind. collected, i.e. 236 ind. m⁻²), 2ML (103 ind., i.e. 137 ind. m⁻²) and 2MR (313 ind., i.e. 417 ind. m⁻²; Table 1). In contrast, only one individual was collected at stations 2LL and 2LR (Fig. 3a and Table 1). *Ptilohyale littoralis* was consistently found in the same habitat as indigenous amphipods (Table 1). As for *P. littoralis*, *Apohyale prevostii* (Milne Edwards, 1830; previously *Hyale nilssoni* Rathke, 1843) was less abundant at stations 2LL and 2LR (Fig. 3b and Table 1), whereas *Melita palmata* (Montagu, 1804) was usually found at low densities, except for the two latter stations, where its highest abundances were recorded (36 and 31 ind. m⁻², respectively; Fig. 3c and Table 1).

Boccardia proboscidea (Fig. 2b, c) was the fifth most abundant species, with a total of 329 individuals collected and a presence in 15 of the 18 quadrats sampled. The highest density observed in a single 0.25-m² quadrat was at station 2LR, with 151 individuals collected; the highest abundance was observed at this station (197 individuals collected, i.e. 263 ind. m⁻²). At other sampling stations, the densities were <100 ind. m⁻², with no individual found at station 1C and only a

Table 1 Number of specimens of epifauna species collected at each sampling station within three 0.25-m² quadrats

Taxa	Stations							
	1ML	1C	1MR	2LL	2ML	2C	2MR	2LR
Anthozoa								
<i>Actinia equina</i> (Linnaeus, 1758)	18 (24)	0	23 (31)	9 (12)	18 (25)	1	38 (51)	18 (24)
<i>Sagartia troglodytes</i> (Price in Johnston, 1847)	21 (28)	0	59 (79)	17 (23)	3 (4)	0	5 (7)	48 (64)
<i>Urticina felina</i> (Linnaeus, 1761)	14 (19)	0	0	0	0	0	0	0
Annelida Polychaeta								
<i>Boccardia proboscidea</i> Hartman, 1940	6 (8)	0	57 (76)	33 (44)	15 (20)	2 (3)	19 (25)	197 (262)
<i>Eulalia clavigera</i> (Audouin & Milne Edwards, 1833)	8 (11)	3 (4)	6 (8)	2 (3)	1	10 (13)	10 (13)	5 (7)
<i>Malacoceros fuliginosus</i> (Claparède, 1870)	40 (53)	0	25 (33)	3 (5)	1	0	11 (15)	21 (28)
<i>Myxicola infundibulum</i> (Montagu, 1808)	0	0	1	6 (8)	5 (7)	1	1	24 (32)
<i>Phyllodoce mucosa</i> Örsted, 1843	0	1	0	14 (19)	1	0	0	57 (76)
<i>Polydora ciliata</i> (Johnston, 1838)	0	0	1	2 (3)	0	0	0	2 (3)
Crustacea								
Cirripedia								
<i>Balanus balanus</i> (Linnaeus, 1758)	+	+	+	+	+	+	+	+
<i>Semibalanus balanoides</i> (Linnaeus, 1767)	+	+	+	+	+	+	+	+
Decapoda								
<i>Carcinus maenas</i> (Linnaeus, 1758)	98 (131)	7 (9)	50 (67)	43 (57)	48 (64)	29 (39)	59 (79)	63 (84)
<i>Hemigrapsus sanguineus</i> (De Haan, 1835)	2 (3)	3 (4)	4 (5)	0	19 (25)	8 (11)	63 (84)	2 (3)
<i>Pinnotheres pisum</i> (Linnaeus, 1767)	1	0	1	0	0	0	0	0
<i>Porcellana platycheles</i> (Pennant, 1777)	1	0	1	0	0	0	0	1
Isopoda								
<i>Jaera (Jaera) albifrons</i> Leach, 1814	1	0	0	0	1	0	2 (3)	2 (3)
<i>Jaera (Jaera) praehirsuta</i> Forsman, 1949	0	0	0	0	1	0	0	0
<i>Lekanesphaera monodi</i> (Arcangeli, 1934)	8 (11)	11 (15)	95 (127)	5 (7)	11 (15)	16 (21)	20 (27)	63 (84)
<i>Sphaeroma serratum</i> (Fabricius, 1787)	0	3 (4)	0	0	8 (11)	1	2 (3)	1
Amphipoda								
<i>Abudomelita obtusata</i> (Montagu, 1813)	0	0	1	0	0	1	0	0
<i>Apohyale prevostii</i> (Milne Edwards, 1830)	14 (19)	78 (104)	9 (12)	3 (4)	57 (76)	54 (72)	34 (45)	4 (5)
<i>Calliopius laevisculus</i> (Krøyer, 1838)	0	0	0	0	0	0	0	2 (3)
<i>Crassikorophium bonellii</i> (Milne Edwards, 1830)	0	0	0	0	0	0	0	1
<i>Jassa marmorata</i> Holmes, 1905	0	0	0	0	0	0	0	1
<i>Melita palmata</i> (Montagu, 1804)	5 (7)	1	1	27 (36)	1	0	2 (3)	23 (31)
<i>Ptilohyale littoralis</i> (Stimpson, 1853)	19 (25)	50 (67)	13 (17)	1	103 (137)	177 (236)	313 (417)	1
<i>Photis longicaudata</i> (Bate & Westwood, 1862)	0	0	0	0	0	1	0	0
Collembola								
<i>Axelsonia littoralis</i> (Moniez, 1890)	0	1	0	0	0	0	0	0
Mollusca								
Gastropoda								
<i>Gibbula umbilicalis</i> (da Costa, 1778)	5 (7)	0	0	8 (11)	1	0	0	5 (7)
<i>Littorina littorea</i> (Linnaeus, 1758)	280 (373)	79 (105)	136 (181)	47 (63)	65 (87)	100 (133)	133 (177)	139 (185)
<i>Nucella lapillus</i> (Linnaeus, 1758)	55 (73)	1	27 (36)	17 (23)	49 (65)	15 (20)	30 (40)	9 (12)
<i>Patella vulgata</i> Linnaeus, 1758	5 (7)	9 (12)	1	6 (8)	8 (11)	9 (12)	12 (16)	5 (7)
Bivalvia								
<i>Mytilus edulis</i> Linnaeus, 1758	1268 (1687)	5369 (7141)	3609 (4800)	317 (422)	2204 (2931)	5307 (7058)	2249 (2991)	1164 (1548)
<i>Venerupis corrugata</i> (Gmelin, 1791)	1	0	1	1	1	0	0	11 (15)
Vertebrata								
<i>Lipophrys pholis</i> (Linnaeus, 1758)	0	0	0	0	0	0	1	0

Densities expressed as ind. m⁻² are given within brackets. For cirripeds, only the presence was reported (+)

few specimens at stations 1ML (6 ind., i.e. 8 ind. m⁻²) and 2C (2 ind., i.e. 3 ind. m⁻²; Fig. 3d).

The global *R* statistics from ANOSIM demonstrated that the overall difference between tidal levels was statistically significant (Global *R* = 0.612, *p* < 0.001). Pairwise comparisons demonstrated significant differences between all levels (*R* = 0.450, *p* < 0.001

for levels C and M; *R* = 0.561, *p* < 0.001 for levels M and L; *R* = 0.983 and *p* < 0.002 for levels C and L). A SIMPER analysis of epifaunal abundance data subsequently revealed that all levels were dominated by the bivalve *M. edulis*, the gastropod *L. littorea* and the decapod *Carcinus maenas* (Linnaeus, 1758) (Table 2). Amphipods and *B. proboscidea* were among the top ten species

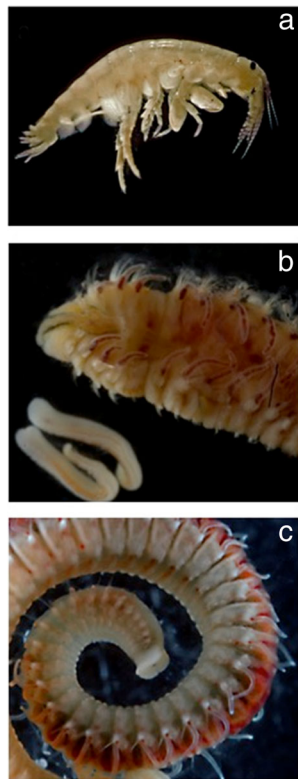


Fig. 2 **a** *Ptilohyale littoralis* (Stimpson, 1853) male, lateral view, Rotterdam (2010), and *Boccardia proboscidea* Hartman, 1940 from Borssele (2013). **b** Anterior end, dorsal view, palps separated. **c** Posterior end, lateral view

contributing to the intra-group similarity: *P. littoralis* and *A. prevostii* for levels M and C, and *M. palmata* and *B. proboscidea* for level L (Table 2). These species also contributed to the dissimilarity between groups. *Boccardia proboscidea* and *P. littoralis* accounted, respectively, for 7.5 and 7.0 % (Table 3) to the dissimilarity between levels M and C (average dissimilarity between groups = 32.6 %). *Ptilohyale littoralis* was the species that contributed the most (8.7 %) to the dissimilarity between levels M and L (average dissimilarity = 35.8 %) and *M. palmata* and *A. prevostii* were also found among the contributing species (Table 3). The dissimilarity between levels C and L (average dissimilarity = 48.4 %) was due to the contribution of *P. littoralis* and *B. proboscidea* for 8.0 % (second most contributing species), *A. prevostii* for 7.0 % and *M. palmata* for 6.5 %. *Ptilohyale littoralis* and *A. prevostii* hence appeared as the amphipod species characterising levels C and M, whereas *M. palmata* characterised level L, together with the spionid *B. proboscidea*.

No segregation between *P. littoralis* and *A. prevostii* was observed and their abundances were significantly correlated (Spearman rank coefficient $r_s = 0.827$, $n = 24$, $p < 0.001$). On the contrary, the abundances of *M. palmata* were significantly negatively correlated with those of both *P. littoralis* ($r_s = -0.526$, $n = 24$, $p < 0.01$) and *A. prevostii* ($r_s = -0.580$, $n = 24$, $p < 0.01$). Significant positive correlations were found between the abundances of *H. sanguineus* and those of both

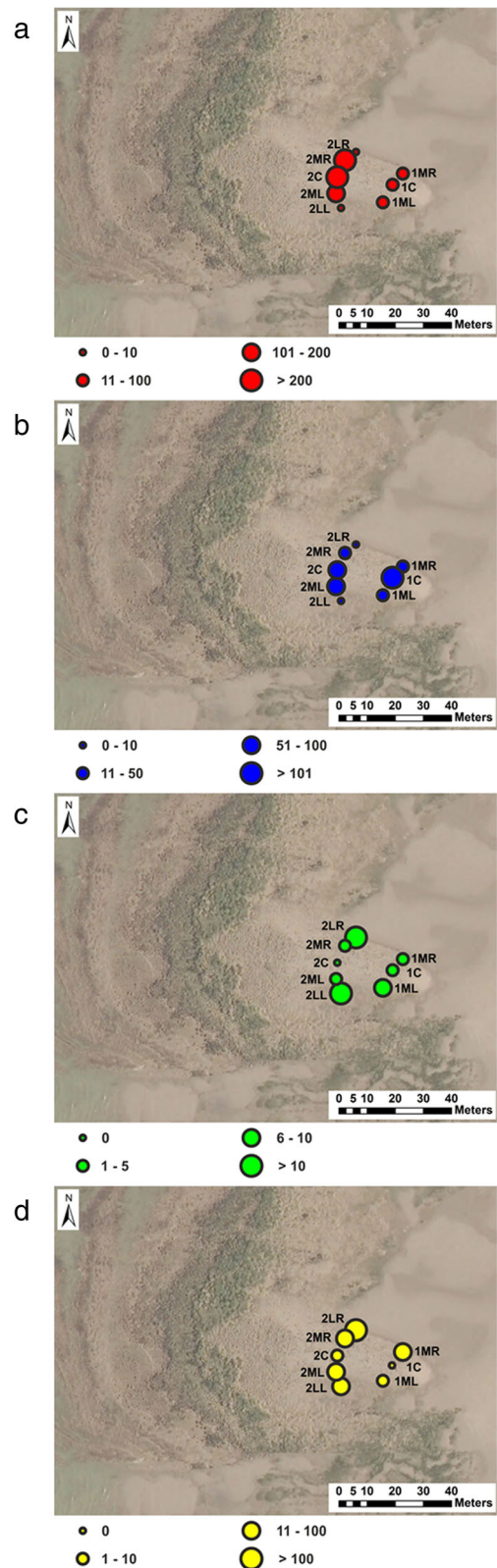


Fig. 3 Distribution maps (ind. m⁻²) of **a** *Ptilohyale littoralis*, **b** *Apohyale prevostii*, **c** *Melita palmata* and **d** *Boccardia proboscidea*

P. littoralis ($r_s = 0.741$, $n = 24$, $p < 0.01$) and *A. prevostii* ($r_s = 0.443$, $n = 24$, $p < 0.01$).

Table 2 Average density (ind. 0.25 m⁻²) and contribution to the intra-group similarity (%) of species (amphipods in **bold**) for each reef level

Level C (average similarity: 78.5 %)			Level M (average similarity: 73.0 %)			Level L (average similarity: 72.3 %)		
Species	Average abundance	Contribution to similarity	Species	Average abundance	Contribution to similarity	Species	Average abundance	Contribution to similarity
<i>Mytilus edulis</i>	1779	37.2	<i>Mytilus edulis</i>	778	23.5	<i>Mytilus edulis</i>	247	18.3
<i>Littorina littorea</i>	30	13.3	<i>Littorina littorea</i>	51	12.4	<i>Carcinus maenas</i>	18	10.5
<i>Apohyale prevostii</i>	22	11.8	<i>Carcinus maenas</i>	21	10.4	<i>Littorina littorea</i>	31	8.0
<i>Ptilohyale littoralis</i>	38	9.7	<i>Apohyale prevostii</i>	10	7.5	<i>Melita palmata</i>	8	7.5
<i>Carcinus maenas</i>	6	7.9	<i>Nucella lapillus</i>	13	6.7	<i>Sagartia troglodytes</i>	11	7.5
<i>Lekanesphaera monodi</i>	5	7.8	<i>Sagartia troglodytes</i>	7	6.3	<i>Phyllodoce mucosa</i>	12	7.4
<i>Patella vulgata</i>	3	5.4	<i>Ptilohyale littoralis</i>	37	6.2	<i>Boccardia proboscidea</i>	38	6.9
			<i>Actinia equina</i>	8	6.2	<i>Lekanesphaera monodi</i>	11	6.8
			<i>Lekanesphaera monodi</i>	11	6.0	<i>Actinia equina</i>	5	6.2
			<i>Boccardia proboscidea</i>	8	3.9	<i>Patella vulgata</i>	2	5.9
			<i>Patella vulgata</i>	2	3.1	<i>Gibbula umbilicalis</i>	2	5.9

Data are presented only for a cumulative contribution of 90 % for each reef level

Discussion

Introduction to the English Channel and distribution in European waters

This study presents the first records of *P. littoralis* and *B. proboscidea* on the French coast after an initial observation for the former on the same reef in December 2013 during the monitoring of *H. sanguineus* (Rolet pers. obs.) and of the latter on the French Atlantic coast at several rocky shores

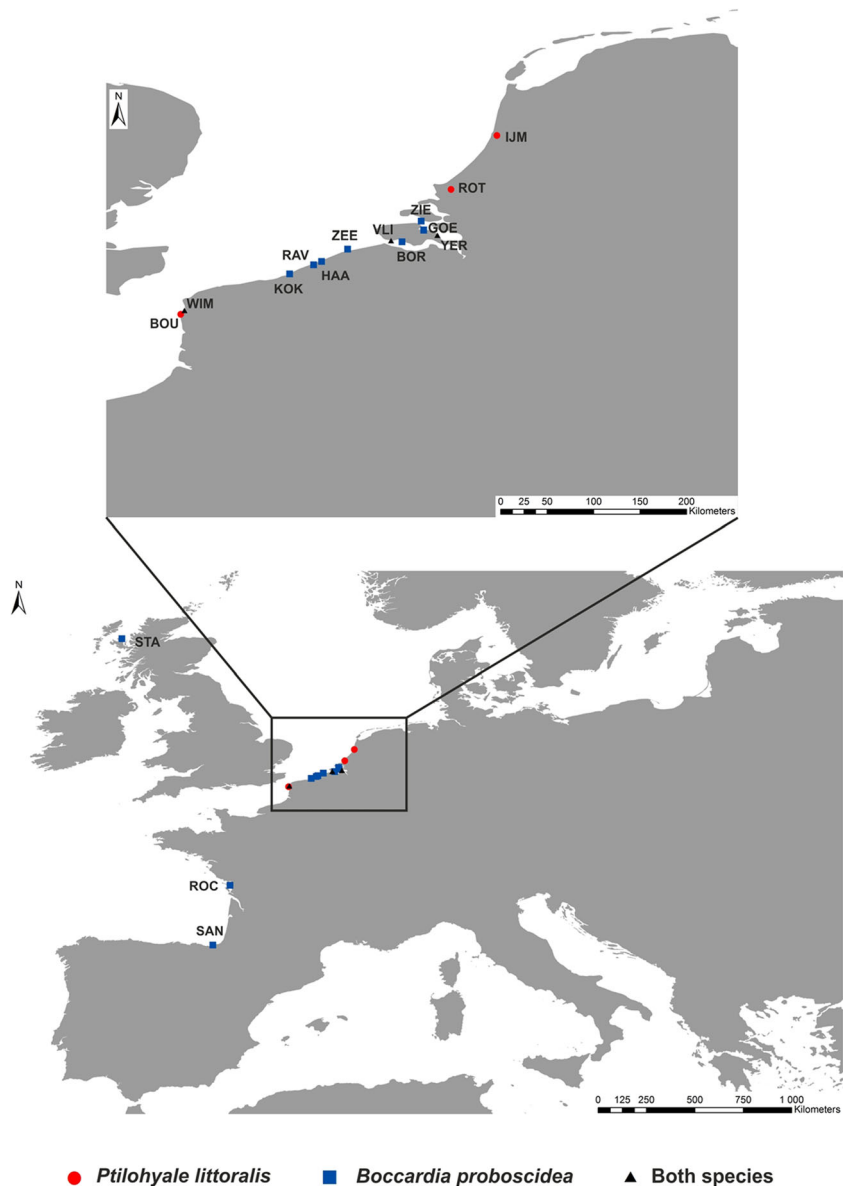
surrounding La Rochelle (Sauriau and Aubert pers. comm., Fig. 4). These species were not mentioned in the latest checklists of French benthic amphipods (Dauvin and Bellan-Santini 2002) and polychaetes (Dauvin et al. 2003), alien crustaceans of the European Atlantic coast (Noël 2011), marine alien species of France (Gouletquer 2016) or marine alien species in Northern France (Dewarumez et al. 2011). Both species have been recorded in the southern bight of the North Sea (Fig. 4) but not on the English side of the Channel (Minchin et al. 2013). However, *B. proboscidea* has been recorded on the

Table 3 Top ten most contributing species (amphipods in **bold**) to the dissimilarity between reef levels

Level M/level C (32.6 % dissimilarity)		Level M/level L (35.8 % dissimilarity)		Level C/level L (48.4 % dissimilarity)	
Species	Contribution to dissimilarity (%)	Species	Contribution to dissimilarity (%)	Species	Contribution to dissimilarity (%)
<i>Mytilus edulis</i>	9.7	<i>Ptilohyale littoralis</i>	8.7	<i>Mytilus edulis</i>	12.1
<i>Sagartia troglodytes</i>	9.6	<i>Phyllodoce mucosa</i>	8.5	<i>Ptilohyale littoralis</i>	8.0
<i>Actinia equina</i>	8.9	<i>Mytilus edulis</i>	8.1	<i>Boccardia proboscidea</i>	8.0
<i>Boccardia proboscidea</i>	7.5	<i>Boccardia polybranchia</i>	6.5	<i>Sagartia troglodytes</i>	7.4
<i>Ptilohyale littoralis</i>	7.0	<i>Melita palmata</i>	6.0	<i>Apohyale prevostii</i>	7.0
<i>Nucella lapillus</i>	6.7	<i>Apohyale prevostii</i>	5.9	<i>Phyllodoce mucosa</i>	6.6
<i>Hemigrapsus sanguineus</i>	5.9	<i>Gibbula umbilicalis</i>	5.6	<i>Melita palmata</i>	6.5
<i>Eulalia clavigera</i>	4.7	<i>Hemigrapsus sanguineus</i>	5.3	<i>Gibbula umbilicalis</i>	5.3
<i>Carcinus maenas</i>	4.2	<i>Littorina littorea</i>	4.4	<i>Actinia equina</i>	5.3
<i>Patella vulgata</i>	3.9	<i>Eulalia clavigera</i>	4.1	<i>Nucella lapillus</i>	3.5

Average dissimilarity between groups is given within brackets and contributions are expressed in %

Fig. 4 Distribution map of known records of *Ptilohyale littoralis* (circles) and *Boccardia proboscidea* (squares); locations where both species were recorded are symbolised with a triangle. (The Netherlands: *IJM* Ijmuiden, *ROT* Rotterdam, *ZIE* Zierikzee, *GOE* Goese Sas, *YER* Yerseke, *BOR* Borssele, *VLI* Vlissingen; Belgium: *ZEE* Zeebrugge, *HAA* De Haan, *RAV* Raversijde, *KOK* Koksijde; France: *WIM* Wimereux, *BOU* Boulogne-sur-Mer, *ROC* La Rochelle; Scotland: *STA* Staffin harbour; Spain: *SAN* San Sebastián)



coast of the Isle of Skye in UK waters (Hatton and Pearce 2013) and its southernmost record is San Sebastián in Spain (Martínez et al. 2006; Fig. 4).

No historical data on polychaete or amphipod abundances are available for the study area and the densities recorded here cannot be compared with a reference situation before the introduction of *B. proboscidea* and *P. littoralis*. Both species were previously recorded in intertidal mussel beds (Martínez et al. 2006; Faasse 2014; Elías et al. 2015) and observed densities of *A. prevostii* and *P. littoralis* (Table 1) are consistent with those usually observed for hyalids on exposed rocky shores covered with mussel beds (e.g. 153 ± 44 ind. m^{-2} , see Arribas et al. 2014). Densities of *B. proboscidea* are highly variable and can reach 1,500,000 ind. m^{-2} in organically impacted areas (Jaubet et al. 2015). Wimereux is considered a non-impacted site and the recorded densities (ca. 600 ind.

m^{-2}) are consistent with those observed in the North Sea ($100\text{--}1250$ ind. m^{-2} ; Kerckhof and Faasse 2014). A previous study recorded an isolated large population (about 50,000 ind. m^{-2} in spring) of the spionid *P. ciliata* (Johnston, 1838) at the ‘Fort de Croy’ (Lagadeuc and Brylinski 1987). Only a few individuals were collected in the present study (Table 1) and, since a confusion with *Boccardia* sp. is unlikely, it can be hypothesised that the *P. ciliata* population declined and has ultimately been replaced by *B. proboscidea*.

The first north-east Atlantic location where *P. littoralis* was recorded is the Netherlands (Faasse 2014), which is suspected as the first introduction of this species to European waters (EASIN: <http://easin.jrc.ec.europa.eu>). In the Netherlands, this species was first found in the port of Rotterdam in 2009 and later recorded at the mouth of the Westerschelde estuary and in Yerseke in 2013. The sibling species *P. explorator*

Arresti, 1989 has been described from the French Atlantic coast in Arcachon Bay (as *Parhyale explorator*). *Ptilohyale explorator* has been considered as a separate species due to slight morphological differences (i.e. spines on uropods 1 and 3, length of rami on uropod 2: Bousfield and Hendrycks 2002), but its taxonomic status still needs to be clarified (Faasse 2014). Given that amphipods lack pelagic larvae, their long-distance spreading is limited. They are easily transportable by human-mediated vectors (Carlton 2011), mainly ships' ballast and hull fouling (Hänfling et al. 2011; Noël 2011), and their introduction is, thus, expected to occur in areas where maritime activities are intense. More specifically, the suspected route of introduction of *P. littoralis* to the Netherlands is, therefore, ballast water and/or hull fouling in the port of Rotterdam (Faasse 2014). However, transfer of mussels from the Irish and Celtic Seas to the Netherlands should also be considered as initial or secondary sources of introduction (Wijsman and Smaal 2006). In the present study, the area where *P. littoralis* was found is located ca. 5 km north of the port of Boulogne-sur-Mer (Fig. 1), where *P. littoralis* was also observed (50°43.507'N/1°33.943'E), though inappropriate sampling did not allow density estimation (Rolet and Spilmont pers. obs.). Since there is neither commercial or leisure harbour, nor shellfish transport from/to Wimereux, the *P. littoralis* population encountered at the 'Fort de Croy' most likely originated from Boulogne-sur-Mer. Individuals may either have been transported directly from Boulogne to Wimereux (e.g. via recreational boating or floating debris) or progressively colonised in a stepping stone fashion (MacArthur and Wilson 1967), the discontinuous rocky substrate occurring from Boulogne-sur-Mer to Wimereux.

Boccardia proboscidea is native from the west coast of North America and Japan (e.g. Hatton and Pearce 2013) and is now considered to have dispersed to almost all the world's ocean due to its opportunistic traits (Jaubet et al. 2015). These traits include tolerance to varying temperatures and salinities (Hartman 1940) and a poecilogonous development (Gibson and Smith 2004), which confer strong advantages when colonising new areas. The spread of the species is attributed to human-mediated transport, mainly through shellfish transportation, as demonstrated for its introduction to, e.g. Hawaiï (Bailey-Brock 2000). However, the species can also be transported via ballast water and it is sometimes impossible to determine the vector of transportation where both mariculture and ship traffic are intense, such as, e.g. in Australia (Hewitt et al. 2004), South Africa (Simon et al. 2009) and the Netherlands (Kerckhof and Faasse 2014). As for *P. littoralis*, the *B. proboscidea* population encountered in Wimereux most probably originated from Boulogne-sur-Mer, where it could have been introduced via ballast water. To date, the species has not been recorded in the port of Boulogne-sur-Mer; the species may, however, still be unnoticed in the area or may have been confused with

B. polybranchia (Haswell, 1885), previously recorded in the English Channel (Dauvin et al. 2003), but also considered as non-indigenous (Gouletquer 2016).

As mentioned by Faasse (2014) and Kerckhof and Faasse (2014), the determination of the introduction pattern (i.e. multiple primary introductions vs. secondary introductions) of *P. littoralis* and *B. proboscidea* remains difficult, since the presence of these species might have gone unnoticed in different parts of Europe. This is particularly the case for intertidal rocky shore species, as their habitat is still rarely monitored per se on the coast of the English Channel. The discovery of introduced species often relies on opportunistic observations (e.g. Dauvin et al. 2009; Seeley et al. 2015) or on surveys targeting other species, which is the case in the present study. Even if the origin of the introduction of *P. littoralis* to Europe is undoubtedly the Atlantic coast of North America (Faasse 2014), it remains impossible to determine with certainty the initial introduction area(s) (where the species may still be currently unnoticed) and track the subsequent dispersal routes (including possible multiple introductions) within Europe. Deciphering the interplay between the presence and the dispersal routes of *P. littoralis* and *B. proboscidea* along the coast of north-western Europe would, hence, require a coordinated and systematic sampling scheme combined with a risk-analysis approach (Wijsman and Smaal 2006). More specifically, unravelling the question of the introduction process of *P. littoralis* and *B. proboscidea* would require an intensive sampling along the English Channel and North Sea coast, with a particular focus on harbours (in particular, Boulogne-sur-Mer, Calais and Dunkirk) and nearby rocky reefs. This task may be facilitated by the use of genetic markers (Comtet et al. 2015), as already used for *B. proboscidea* and some invasive amphipods (e.g. *Caprella mutica* Schurin, 1935; Simon et al. 2009; Ashton et al. 2008) and would help in tracking down invasive spread and the most likely sources of introduction.

Ecology: habitat and interactions with other species

Though still being discussed, the accepted definition of an invasive species does not include any connotation of impact (Richardson et al. 2011), but most invasive species actually have ecological impacts that can range from genetic to regional (even global; Lockwood et al. 2007). Impacts at the population level are the easiest and most commonly studied (Parker et al. 1999; Lockwood et al. 2007) and are mostly due to biological interactions (competition and predation) between the non-native and indigenous species, although an in-depth evaluation of the impact that *B. proboscidea* and *P. littoralis* may have on the structure and function of the local ecosystem would require further investigations, including experimental ones. A first approach would be to look at potential exclusions of indigenous species. In Wimereux, several indigenous

amphipods partly share the same habitat as *P. littoralis*, the most abundant being the mytilid *M. palmata* and the hyalid *A. prevostii*. The main features of both the left and right edges of the reef (2LL and 2LR) were: (i) the occurrence of large boulders covered with mud that retained water (Fig. 5a), (ii) the low abundances of *M. edulis* (Table 2) and (iii) the presence of species typical of mud covered rocky substrates such as the polychaetes *B. proboscidea* (found at high densities at these stations; Fig. 3d) and *P. mucosa*, Örsted 1843 (found only at these stations). In contrast, stations sampled on the top of the reef (iC) and in the middle of the reef banks (iM) were characterised by smaller stones and drier sediment essentially covered by mussels *M. edulis* (Fig. 5b, c) and the macrofauna community was typical of mussel beds (e.g. the gastropods *L. littorea*, *Nucella lapillus* (Linnaeus, 1758) and *Patella vulgata* Linnaeus, 1758, the decapod *C. maenas*; Table 2). The examination of their distribution along the two transects considered in the present work thus suggests a spatial segregation between *M. palmata* and both *P. littoralis* and *A. prevostii*.

The invasive decapod *H. sanguineus* was found mainly on transect 2, with low abundances at the edges of the reef (Table 1). No segregation was found between this species and non-native (i.e. *P. littoralis*) and indigenous amphipods (i.e. *A. prevostii* and *M. palmata*), since they were found in the same habitat. A recent study (Blasi and O'Connor 2016) demonstrated that indigenous *P. littoralis* (as *H. plumulosa* (Stimpson, 1857)) were a potential prey for the invasive Asian shore crab *H. sanguineus*, which suggests a potential interaction between these two species being non-native in Wimereux. Since amphipod densities are regulated by biological interaction, including predation, it is emphasised that, although the study of the interactions between *H. sanguineus* and amphipods is a very complex task (Blasi and O'Connor 2016), the two-alien species predator–prey relationship that may be occurring in our study is uncommon and might represent a unique opportunity to decipher the complexity of interspecific interactions from an alien perspective. These investigations could provide a major contribution to the understanding of ecological assembly rules in community ecology (Weiher and Keddy 1999) and, therefore, help to clarify the relationships among community saturation, diversity and ecosystem functioning (Stachowicz and Tilman 2005).

The specificity of the study site in Wimereux is the presence of mussel beds and areas covered with mud. Gregarious mytilids are considered as ecosystem engineers (e.g. Borthagaray and Carranza 2007; Buschbaum et al. 2009; Arribas et al. 2014) and intertidal mussel beds provide habitat for numerous adult crustaceans, including amphipods (e.g. Saier 2002; O'Connor and Crowe 2007; Arribas et al. 2014), as well as for decapod juveniles (Thiel and Darnedde 1994; Pezy and Dauvin 2015). The observed spatial segregation in Wimereux is suspected to be due to a selectivity in the habitat,

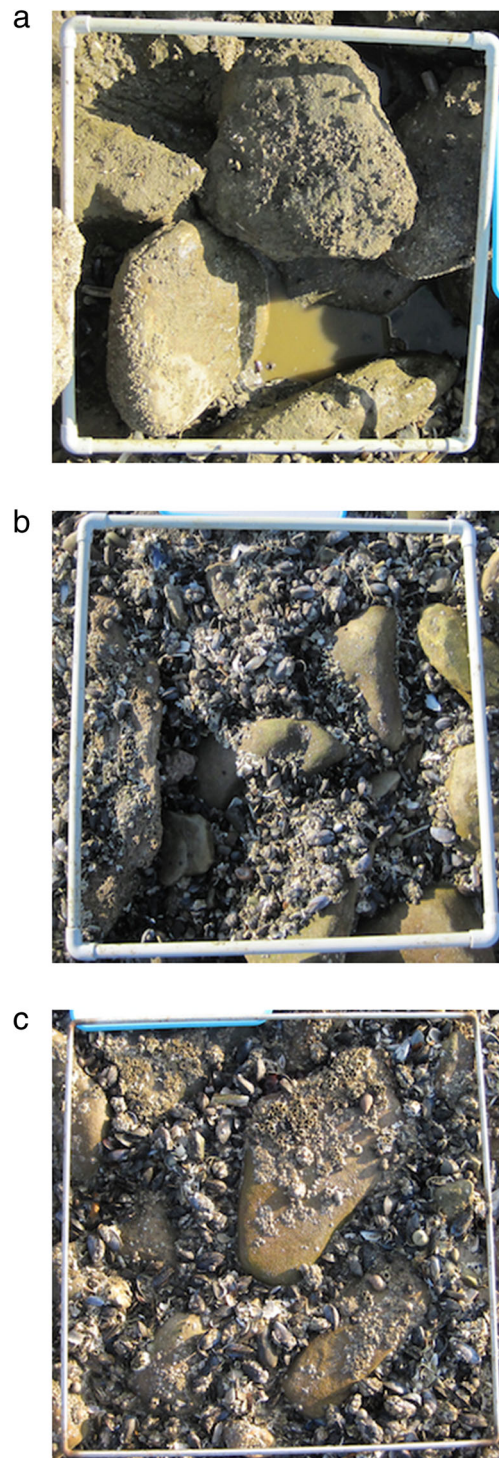


Fig. 5 Example of archetypical quadrats sampled along transect 2 at different reef levels: **a** reef edge (station 2LL), **b** mid-reef bank (station 2MR) and **c** reef-top (station 2C)

M. palmata preferring sandy or muddy sediments with stones and cobbles (Lincoln 1979). Although Hyalidae are usually described as intertidal species associated with algae (Lincoln 1979; Little and Kitching 1996; Bousfield and Hendrycks 2002), *P. littoralis* and *A. prevostii* were preferentially found

in mussel beds lacking macroalgae in Wimereux. However, amphipods choose their habitat to get protection from predators and/or wave mechanical disturbance (Fenchel and Kolding 1979), which is locally provided by mussel beds for hyalids. These field observations are, however, not sufficient to conclude on a selection behaviour which can be validated only if tested in laboratory experiments (Gestoso et al. 2014).

Acknowledgements The authors thank S. Reubrecht, B. Doucet and V. Serreau for their help in the field, K. Butelle and V. Serreau for sorting macrofauna samples, and P.-G. Sauriau and F. Aubert for providing data from La Rochelle. We also thank the two anonymous referees and the associate editor who helped improve the manuscript. J.J. identified the specimens of *P. littoralis* in the framework of activities founded by the RESOMAR network.

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