

# The distribution of the invasive non-native gastropod *Crepidula fornicata* in the Milford Haven Waterway, its northernmost population along the west coast of Britain

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**Abstract** The invasive non-native gastropod *Crepidula fornicata* is well established in the Milford Haven Waterway (MHW) in south-west Wales, UK, since its first introduction to this ria in 1953. Whilst it reaches high densities within the MHW and has extended its range to the south of this ria, there has been very little northward expansion. Here, we report findings of a series of intertidal and subtidal surveys in 2009 and 2010 where we monitored the population density and the vertical distribution of *C. fornicata* at its northern range limit in Wales (the MHW). We also characterised the composition of the surface substrata of the seabed in the MHW to provide some insight into how the availability of certain settlement substrata may limit its distribution along the west coast of Britain. We found locally very dense aggregations (maximum  $2748 \pm 3859$  individuals  $m^{-2}$ , mean  $\pm$  SD) in the shallow subtidal and low intertidal of the MHW. Subtidally, highest densities were found in areas of high gravel content (grain sizes  $\sim 16$ –256 mm), suggesting that the availability of this substrata type is beneficial for its establishment at a site. In the intertidal, on the other hand, high gravel content was indicative of low *C. fornicata* abundance, possibly

because gravelly shores are an indicator of very exposed conditions that, at least in the intertidal, may result in high levels of early post-settlement mortality and low recruitment. *C. fornicata* was absent from the entrance of the MHW, possibly due to the lack of suitable settlement substrata. The presence of substantial populations in the MHW suggests that *C. fornicata*'s population growth and potential expansion in Welsh coastal waters is not fully limited by prevailing environmental conditions in the region, but that other processes may affect its local distribution.

**Keywords** *Crepidula fornicata* · Northern range limit · Milford Haven Waterway · Settlement substrata · Vertical zonation

## Introduction

The introduction of invasive non-native species (NNS) is ranked amongst one of the greatest threats to global biodiversity worldwide, owing to their severe ecological and economic impacts in the recipient environment (Grosholz 2002). Most commonly, a NNS is considered as invasive only once it has passed all stages of the invasion process, including the survival of transport and release into the recipient habitat, the successful uptake of the NNS in its new environment, its subsequent establishment, and its spread beyond its first location of introduction (Richardson et al. 2000; Kolar and Lodge 2001; Sakai et al. 2001; Colautti and MacIsaac 2004; Blackburn et al. 2011). A variety of biotic and abiotic factors may affect any one of these stages, thus determining the invasion success of the NNS. Whilst many studies have examined the processes and factors that facilitate the early invasion stages (Levine

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and D'Antonio 1999; Colautti and MacIsaac 2004), little is known about how NNS spread beyond the first site of introduction. It can be assumed, however, that similar ecological principles that determine the distributions of species in their native range will also limit the secondary spread of NNS through natural dispersal mechanisms (Davis et al. 2001). The availability of suitable habitats, geographical dispersal barriers, the species' dispersal potential, and abiotic and biotic environmental conditions, impairing growth, survival, and/or reproduction, are all potential determinants of species' range limits (see Holt et al. 2005; Gaston 2009a, b for summary).

The invasive non-native gastropod *Crepidula fornicata*, native to the coastal waters of the West Atlantic, was first introduced into European coastal waters in the 1880s/1890s, attached to the American oyster *Crassostrea virginica* that was imported into the UK for aquaculture at that time (Crouch 1893; McMillan 1938; Korringa 1942; Blanchard 1997). Initial establishment occurred rapidly: By the early 1950s, *C. fornicata* was distributed from Northumberland in the north-east to the south coast of Cornwall (Orton 1950; Cole 1952). Populations in the coastal waters of Central and Western Europe became established during the same time, followed by later records from more southern and more northern locations (Blanchard 1997). A variety of biological traits may explain its success during the early invasion stages throughout European shores. Its ability to colonise most natural and man-made hard substrata and structures (Loomis and Van Nieuwenhuyze 1985; McGee and Targett 1989; Mineur et al. 2012) has likely resulted in the repeated accidental introductions of adult *C. fornicata* attached to ships, wreckage, and especially, transported shellfish species (Korringa 1942, 1951; Cole and Baird 1953). Transport of the free-swimming larvae with ballast water may also occur during the relatively long pelagic larval phase of ~2–4 weeks (Pechenik 1980, 1984). The larvae, juveniles, and adults are relatively euryhaline and eurythermal (Pechenik and Lima 1984; Pechenik and Eyster 1989; Rigal 2009; Diederich et al. 2011; Schubert 2011), hence increasing the chances of survival when exposed to the changeable environmental conditions between the donor region, the transport vector, and release into the new environment. This also enables *C. fornicata* to thrive in a variety of environmental conditions and habitat types, predominantly shallow estuaries and bays (Loomis and Van Nieuwenhuyze 1985; Blanchard 1997), but also relatively deep high-energy environments (Hinz et al. 2011).

The success of *C. fornicata*'s secondary spread in a region following initial establishment has varied greatly between locations. For example, it spread quickly (within ~40 years) through the full east–west extent of the English Channel (Orton 1915; Cole 1952), and both its geographical

spread and local densities increased noticeably between the 1950s and 2006 (Holme 1961; Hinz et al. 2011). Today, densities in the coastal waters of the UK and France are often >1000 individuals m<sup>-2</sup> (FitzGerald 2007), with maximum densities of >4700 individuals m<sup>-2</sup> reported from the Bay of Marennes-Oléron, France (de Montaudouin and Sauriau 1999). In other areas, however, its spread and abundance at colonised sites were found to be restricted by limited habitat availability (de Montaudouin et al. 2001) or unsuitable air and seawater temperature (Thieltges et al. 2003, 2004; Richard et al. 2006). Temperature has been shown to affect the length of the reproductive season (Valdizan et al. 2011), larval growth, and survival (Rigal 2009) and may cause climate-induced mass mortality events of the adult population (Thieltges et al. 2003, 2004). High levels of early post-settlement mortality may restrict adult densities, at least intertidally (Bohn et al. 2013a, b). The role of natural larval dispersal in determining the secondary spread of *C. fornicata* has been debated (Orton 1915; Adam and Leloup 1934; Korringa 1942, 1951). Whilst its long larval phase certainly allows for dispersal over long distances, the need for gregarious attachment to ensure successful reproduction through internal fertilisation, in combination with such a long larval phase, could also impede the spread of self-sustaining populations. This will be the case especially when larval retention in the region is low (Rigal et al. 2010). Biotic factors such as predation or competition for food are unlikely causes for its limited population increase (Thieltges et al. 2004; Thieltges 2005; Beninger et al. 2007; Decotignies et al. 2007).

*Crepidula fornicata* was first recorded in 1953 from the Milford Haven Waterway (MHW, Fig. 1) (Cole and Baird 1953), a natural ria in south-west Wales that still seems to hold the northern-most population of the species along the west coast of Britain (Bohn 2012). *C. fornicata* was most likely introduced to the MHW attached to hulls of merchant and naval ships that were brought to Pennar in the MHW (Fig. 1) in the years following WWII for repairs and breaking up (Cole and Baird 1953). Within the following ~10 years, *C. fornicata* established along most of the MHW (Crothers 1966). Solitary individuals and 'small' stacks were first found in the low intertidal of Hazelbeach and Pwllcrochan in 1954 and in Lawrenny in 1959 (Fig. 1) (Crothers 1966). By 1962, populations here had already increased to >200 individuals m<sup>-2</sup>. The species was present almost everywhere between Hazelbeach and Landshipping Quay (Fig. 1) and was 'very abundant' at Beggars Reach (Crothers 1966). The first live specimen on Dale beach, located at the mouth of the estuary (Fig. 1), was found in April 1964 (Crothers 1966).

*Crepidula fornicata* is now well established in the MHW (see NBN Gateway at <http://www.nbn.org.uk>) and is considered a nuisance to commercial shellfish species,



**Fig. 1** Map of the Milford Haven Waterway (MHW, large image) in Wales, UK (inset). *Crepidula fornicata* was first recorded at Pennar in 1953 and soon after in Hazelbeach, Pwllcrochan, Lawrenny, and Beggars Reach. By 1964, it had spread between Dale and Landshipping Quay. A few individuals were found in the Skomer Marine

Conservation Zone (Skomer MCZ) just outside of the MHW in 2008 and in the Menai Strait in North Wales in 2006, but there is no indication that this leads to an establishment of a population at these locations

especially the native oyster *Ostrea edulis* that used to form natural beds in the MHW and was dredged in some areas of the MHW until very recently. A series of anthropogenic pressures (possibly this includes the spread of *C. fornicata*) are thought to have led to the decline of *O. edulis* (Woolmer et al. 2011). Colonisations of *C. fornicata* in other areas in South Wales have also been successful since its introduction (Mettam 1979, see NBN Gateway at <http://www.nbn.org.uk>), but its northward range extension has been limited to date. A few *C. fornicata* were found within the boundaries of the Skomer Marine Conservation Zone (Skomer MCZ, Fig. 1), located immediately adjacent to the MHW, in 2008 (and again in 2011 and 2012 after the surveys that are presented here were undertaken) (Newman et al. 2009, 2012). However, the presence of an established population could not be confirmed in studies surveying the same region (Bohn 2012; Sciberras 2012; Sciberras et al. 2013). In 2007, the establishment of *C. fornicata* into the Menai Strait in North Wales (Fig. 1), following its accidental introduction to this area with a consignment of mussel spat, was averted due to the quick response of the involved parties by mechanically removing all infected mussels (Sewell et al. 2008). Its northern-most self-sustaining population thus seems to reside within the MHW (Bohn 2012).

Some of the individuals that were found in the Skomer MCZ and the Menai Strait since 2008 were forming stacks and showed signs of reproductive activity (Sewell et al. 2008; Burton pers comm). The current lack of self-sustaining populations to the north of the MHW can therefore not be solely due to impaired adult survival and reproduction at its northern range edge. This is further supported by a study that found no indication of impaired reproductive success of *C. fornicata* within the MHW (Bohn et al. 2012). Other factors, such as limited availability of suitable

habitats, may be especially important in limiting the regional spread of sessile invertebrate species (Fenberg et al. 2014). Previous work indicates that the availability of certain hard substrata types, in particular the sediment class gravel (16–256 mm) as well as shells of conspecifics and the native shellfish species *Mytilus edulis*, may be particularly important in determining *C. fornicata*'s distribution (Driscoll 1967; Loomis and Van Nieuwenhuyze 1985; Thieltges et al. 2003; Bohn et al. 2013b). These substrata types were found to be frequently used for settlement by *C. fornicata* larvae and may significantly increase post-settlement survival (Loomis and Van Nieuwenhuyze 1985; Bohn et al. 2013a, b).

Here, we describe *C. fornicata*'s fine-scale distribution between substrata types and along the vertical shore gradient in the MHW, its northern-most population along the west coast of the UK. We suggest causes for the observed distributional patterns in areas where the species is successfully established and are aiming at giving some insight into reasons for the limited northward spread over more than 50 years. We hypothesise that *C. fornicata*'s distribution correlates with the availability of certain substrata types (the substrata class gravel and the native shellfish species *M. edulis* that forms natural beds in the MHW) that are of particular interest due to other observations from the same study area (Bohn et al. 2013a, b).

## Methods

### Study area

The MHW (Fig. 1) is a shallow ria (depth <20 m), characterised by very wave-sheltered conditions and has a maximum tidal range during spring tides of nearly 8 m,

resulting in extensive movements of water masses (Nelson-Smith 1965). Freshwater influx is relatively low, resulting in fully marine conditions (salinity >30) and almost complete vertical mixing until the middle reaches of the MHW. Estuarine conditions are confined to the east and the upper reaches of the ria with a more variable salinity regime, where, for example, surface salinity may vary between 18 and 34, depending on weather and tidal conditions. Vertical stratification of water masses here may result in salinity differences of up to 8 between surface and bottom waters (Nelson-Smith 1965; Bohn pers. obs.). The seabed varies from eroded rocky reefs interspersed with sandy beaches and muddy-gravelly banks at the mouth of the ria to mud flats interspersed with rocky shores in sheltered areas towards the east and the upper reaches (Nelson-Smith 1965). The various habitats support diverse marine assemblages, including macroalgal and filter-feeding communities, infaunal communities of mud and sand flats, *M. edulis* beds, seagrass beds, maerl beds, and salt marshes (Nelson-Smith 1967).

### Subtidal surveys

The subtidal distribution of *C. fornicata* in the MHW and its potential spread to areas adjacent to it were monitored in August 2010 from the survey vessel Pedryn (Countryside Council for Wales, now Natural Resources Wales). We used an underwater still images camera (model Canon EOS 400D Digital SLR, 10 megapixels) in waterproof housing that was mounted on a sled towed behind the survey vessel at a speed of 0.5–1.5 kn. The camera was mounted at a fixed height of 54 cm on the sled, pointing downwards. The area of the seabed on each photograph was therefore approximately constant ( $\sim 0.44 \text{ m} \times 0.30 \text{ m}$ ). Images were recorded every 10 s. Thus, when towed at an average speed of  $\sim 1 \text{ kn}$ , an area of  $\sim 0.13 \text{ m}^2$  of the seabed was photographed  $\sim$  every 5 m. The camera was deployed for  $\sim 10 \text{ min}$  at each station, resulting in  $\sim 60$  images that cover  $\sim 7.8 \text{ m}^2$  of the seabed in total during each deployment. All tows were 150–210 m in length.

Forty-two camera tows were placed in a grid formation  $\sim 1 \text{ km}$  apart between the mouth and the upper reaches of the MHW. An additional 26 tows were undertaken in the shallow subtidal parallel to 10 intertidal sites (these are described below) at varying distances from the shore (hereafter ‘distance to shore’, see Online Resource 1 for details). This aimed at studying the distribution of *C. fornicata* with increasing depth from the low intertidal to the middle of the channel in the subtidal zone. Also, nine tows were placed along a 1- to 2-km grid extending from the entrance to just outside the MHW, to assess the potential spread of *C. fornicata* outside its known distribution in the MHW.

All images were thoroughly checked for the presence of *C. fornicata*. For tows where *C. fornicata* was found to be present on any of the pictures, a subset of 30 pictures were randomly chosen for quantitative analysis, excluding all images with poor visibility and where surface canopy macroalgae (especially *Laminaria* spp., *Ulva* spp.) covered more than  $\sim 33 \%$  of the image area. All *C. fornicata* in the selected images were counted, and density estimates were derived by averaging values from all 30 images. If the field of view was obstructed by macroalgae or other objects, these areas were excluded from all analyses. All individuals in a stack could easily be distinguished, and we found it possible to reliably identify all individuals  $>5 \text{ mm}$  (provided they were visible on the surface of the seabed, i.e. not obstructed by other objects or biota including other *C. fornicata* individuals). The slipper limpet densities we estimated from the pictures may thus be underestimations of real densities.

The surface substrata composition of the seabed was described for each tow inside the MHW by analysing 20 of the previously selected pictures. A grid with 48 equidistant points was placed on the image using the software Adobe Photoshop v7 and the substratum type found underneath each point recorded. Grain sizes were estimated using the size of the grid cells ( $\sim 50 \text{ mm} \times 50 \text{ mm}$ ) as a reference scale. The fine grain sizes (mud, sand, fine, and medium gravel) were pooled owing to the difficulty of determining fine grain sizes accurately from the images. This resulted in five different substrata types: (1) *Fine sediment* (grain sizes up to  $\sim 16 \text{ mm}$ , i.e. mud, sand, fine, and medium gravel on the Wentworth scale); (2) *Gravel* (grain sizes  $\sim 16$ – $256 \text{ mm}$ , i.e. coarse gravel and cobble); (3) *Boulder* (grain size  $>256 \text{ mm}$ ); (4) *Shells* (all empty shells); and (5) *Live habitat-forming species* (live *M. edulis*, *Ostrea edulis* and scallops). The substrata composition of each of the surveyed sites was then classified into one of 11 habitat types (Table 1) depending on the percentage cover of each of the substrata classes, using the calculated averages from all 20 images per tow. If the field of view under the intercept point was obstructed, these points were excluded from all analyses. Similarly, if the intercept fell on live *Crepidula* shells, these points were also excluded, to avoid autocorrelation between *Crepidula* abundance and substrata composition.

### Intertidal surveys

Between February 2009 and October 2010, the low intertidal of 10 sites in the MHW was quantitatively surveyed for the presence/absence and, where present, *C. fornicata*’s population characteristics (density, stack sizes, substratum utilised for settlement). Sites were haphazardly chosen across a variety of habitat types within the full extent of the ria. Sites



**Table 1** Habitat types classified from percentage cover values of the five main substrata types derived from 20 still image pictures taken during the subtidal surveys or five still images taken during the intertidal surveys

Habitat types	Description
Sediment	>80 % sediment
Sediment with gravel	>70 % sediment and 10–30 % gravel
Sediment with shell	>70 % sediment and 10–30 % shell
Boulder	>80 % boulder
Boulder with sediment and gravel	>10 % each
Mix of sediment and gravel	30–70 % sediment and 30–70 % gravel
Mix of sediment and shell	30–70 % sediment and 30–70 % shell
Mix of sediment, gravel, and shell	>10 % each
Gravel*	>80 % gravel
Gravel with boulder*	>60 % gravel and 10–30 % boulder
Mussel bed mixed with sediment, gravel, and shell*	>10 % each

Substrata types were: (1) *Sediment* (grain sizes up to ~16 mm, i.e. mud, sand, fine, and medium gravel on the Wentworth scale); (2) *Gravel* (grain sizes ~16–256 mm, i.e. coarse gravel and cobble); (3) *Boulder* (grain size >256 mm); (4) *Shells* (all empty shells); and (5) *Live habitat-forming species* (live *Mytilus edulis*, *Ostrea edulis*, and scallops). Asterisks indicate habitat types that were only present at intertidal sites and are therefore not displayed on the map (Fig. 3)

in the upper stretches of the MHW could not be surveyed as accessibility was restricted. Three horizontal transects were sampled at each of the sites. Transects were ~100 m in length and ran parallel to the water line at a tidal height of 1.0–1.3 m above Chart Datum. In addition, the vertical distribution of *C. fornicata* was surveyed at four study sites (Pennar, Hazelbeach, Cosheston, Beggars Reach, Fig. 2, see Online Resource 1). For this, densities were additionally estimated at the tidal heights of 0.5–0.7 and 1.5–1.8 m above C.D. at one transect.

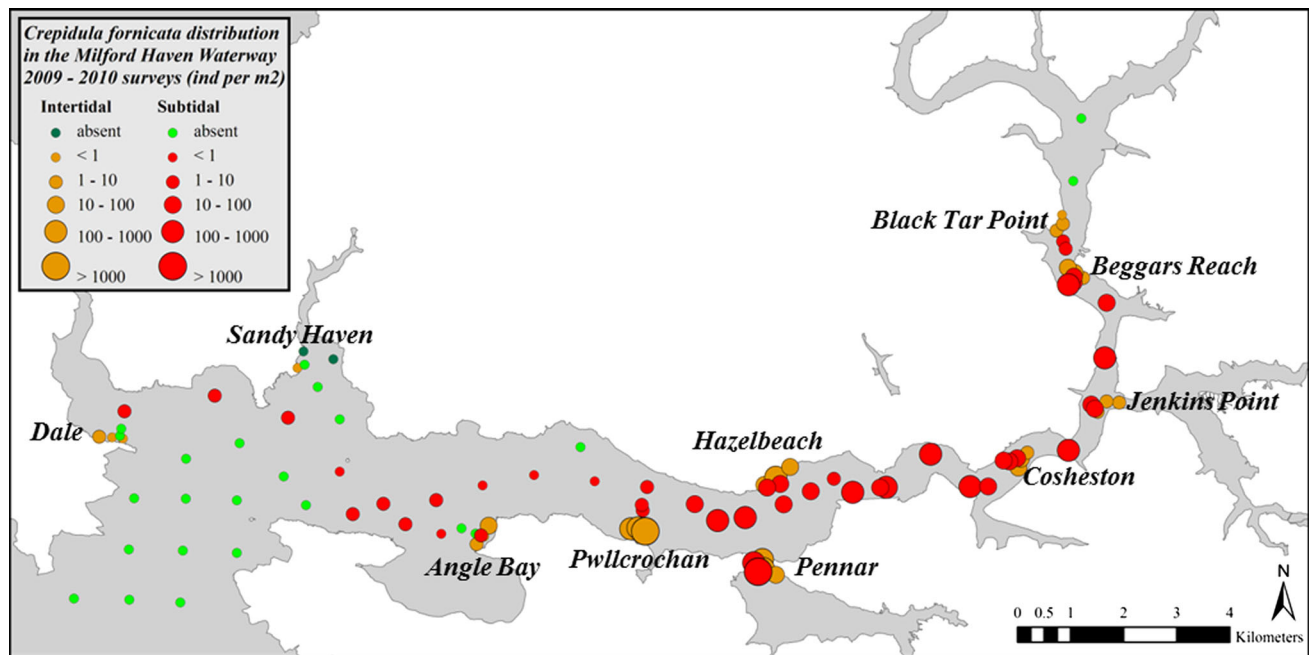
Densities along each transect were estimated by searching 10 randomly placed 1-m<sup>2</sup> quadrats for live individuals. In areas with very high densities of *C. fornicata*, random subsamples of the standard 1-m<sup>2</sup> quadrats were taken using a 0.25-, 0.1-, or 0.05-m<sup>2</sup> quadrat. When no or very few slipper limpets were found, 30-min timed searches beyond the vertical and horizontal extent of the transects were added to confirm the absence/rarity of *C. fornicata*. All individuals found inside the quadrats or during the timed search were counted, and the number of individuals per stack and the primary substratum used for attachment (i.e. used by the bottom-most individual) were noted. Due to the difficulty of spotting small individuals in the field, all *C. fornicata* <5 mm were excluded.

The substrata composition of the intertidal sites was determined from five digital images taken of 0.25-m<sup>2</sup> quadrats that were randomly placed along each transect. The area was cleared of macroalgae prior to taking the image to enable identification of the substrata underneath. Images were analysed in the same way as for the subtidal sites, but using a grid with 7 × 7 equidistant points.

## Statistical analysis

To determine the effects of substrata type on the density and distribution of adult *C. fornicata*, we tested for relationships between cover of different substrata classes and adult densities, stack sizes, and types of substrata used for primary attachment, using average values from each intertidal or subtidal transect where *C. fornicata* was present. Because of the different survey approaches used, separate analyses were run for the intertidal (1.0–1.3 m a. C.D. transects) and subtidal stations. For both intertidal and subtidal stations, regression analyses were run between percentage cover of gravel and recorded densities. For the intertidal stations only, regressions were also undertaken on the relationships between percentage cover of gravel to stack sizes, percentage cover of gravel, and the frequency with which gravel was recorded as the primary attachment substratum, and between the percentage cover of live *M. edulis* and the percentage of primary attachment substratum that were live *M. edulis*. All data were checked for normality, homogeneity of variances, and linearity before linear regressions were carried out. Percentage cover data were always arcsine square-root-transformed and density data log10-transformed to fulfil assumptions of linear regressions.

The effect of tidal height and distance from the shoreline on the distribution of *C. fornicata* were assessed at four sites (Pennar, Hazelbeach, Cosheston, Beggars Reach), using a two-factorial analysis (intertidal: site × tidal height; subtidal: site × distance to shore). The number of transects that could be placed in the subtidal varied between the four sites, so that subtidal densities were analysed only between two transects (subtidal I and



**Fig. 2** Distribution of *Crepidula fornicata* in the Milford Haven Waterway, its northern-most geographical location in Wales, UK. Each marker represents the start coordinates of a transect that was surveyed during the surveys of 2009 and 2010. Intertidal densities of *C. fornicata* were estimated at 10 sites (orange markers and place labels) from 10 1-m<sup>2</sup> quadrats per surveyed ~100 m transect

(1.0–1.3 m above C.D.). Subtidal densities (red markers) are averages of counts from 30 still images, each covering ~0.13 m<sup>2</sup> of the seabed, taken along ~150–210 m transects using an underwater camera mounted on a vessel-towed sled. Bright and dark green markers are stations where no *C. fornicata* were found subtidally or intertidally, respectively (colour figure online)

subtidal II). The nonparametric, two-factorial Scheirer–Ray–Hare test was chosen for this due to heterogeneity of variances that could not be removed with data transformations. Mann–Whitney pairwise comparisons were used when significant main effects were found.

## Results

### Spread and population status in the Milford Haven Waterway

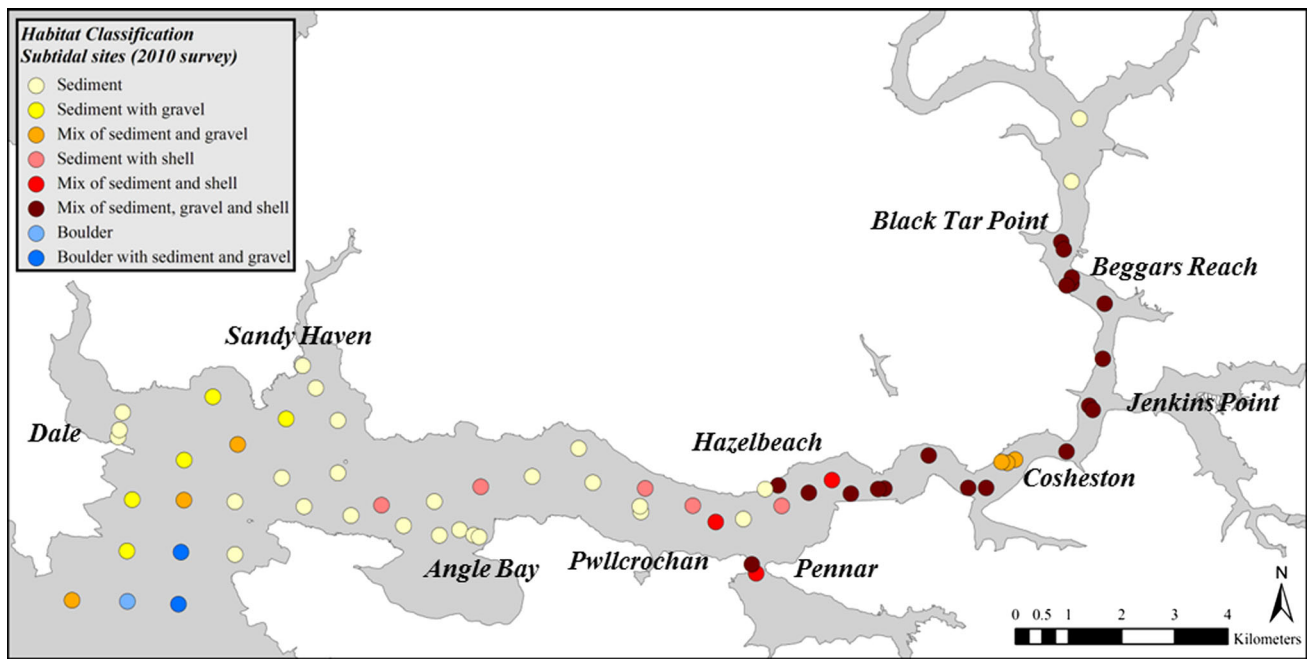
*Crepidula fornicata* was recorded over most of the extent of the MHW in the low intertidal and subtidal between Dale Fort close to the mouth and the upper reaches at Black Tar Point (Fig. 2). It was not recorded at the entrance and the upper-most reaches of the ria. No live individuals were found whilst surveying the areas just adjacent to the MHW (Fig. 2) which is in accordance with results from other surveys undertaken in the same area (Bohn 2012; Sciberras 2012; Sciberras et al. 2013).

Highest densities were recorded in the middle stretches where *C. fornicata* occurs across a variety of habitat types (Figs. 2, 3). *C. fornicata* was most abundant in the low intertidal and shallow subtidal at Pennar with up to  $1152 \pm 881$

individuals m<sup>-2</sup> (mean  $\pm$  SD) and at Pwllcrochan (1.0–1.3 m tidal height) with  $2748 \pm 3859$  individuals m<sup>-2</sup> at transect 3 (Figs. 2, 4, 5). In particular, in the intertidal, a remarkable decline in densities from the middle stretches of the ria towards the mouth and towards the upper reaches is apparent: medium to high densities were found at Pennar and Hazelbeach, but densities at the intertidal sites of Cosheston, Jenkins Point, Beggars Reach, and Black Tar Point in the upper reaches were relatively low (Figs. 2, 4, see Online Resource 1). At the mouth of the ria, lowest intertidal densities were recorded at Sandy Haven, where individuals were only found during the timed search but not the quantitative survey, indicating average densities of  $<0.1$  individuals m<sup>-2</sup> (Figs. 2, 4).

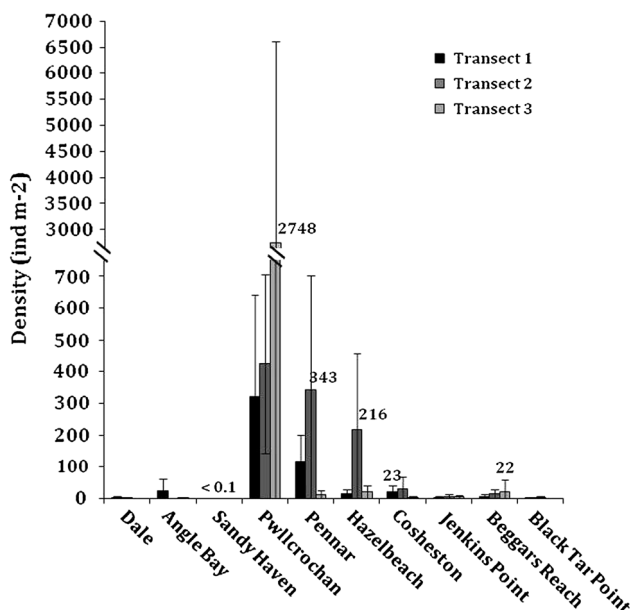
### Distribution across substrata types

*Crepidula fornicata* occurred in most substrata types, but was absent in areas with a high content of boulders (Figs. 2, 3). Densities remained low in homogenous substrata dominated by fine sediment ( $<16$  mm). Highest densities were found in areas where sediment had a high content of hard substrata (i.e. mix of fine sediment and shell; mix of fine sediment and gravel; or mix of fine sediment, gravel, and shell, Figs. 2, 3). This was supported by a highly significant positive relationship between gravel



**Fig. 3** Habitat distribution in the Milford Haven Waterway. Habitat types were classified by grouping average percentage surface cover of five different substrata classes (Fine Sediment, Gravel, Boulder, Shell, Live habitat-forming species) that were either determined from 20 randomly selected still images of the seabed taken during the subtidal

survey in August 2010 using a sled-mounted underwater still images camera, or from five digital images taken during intertidal surveys in 2009–2010. See “Methods” section for details on habitat classes (colour figure online)



**Fig. 4** Densities of *Crepidula fornicata* along three transects at each of 10 intertidal sites in the Milford Haven Waterway (1.0–1.3 m above C.D.). Data labels are mean densities of transects with highest (Pwllcrochan) and lowest densities (Sandy Haven) and the sites that were surveyed for *C. fornicata*’s vertical distribution. Note break and change in scale in y axis

percentage cover and densities of *C. fornicata* in the subtidal (Fig. 6c). However, this relationship was negative in the intertidal (Fig. 6b). Gravel surface cover was also

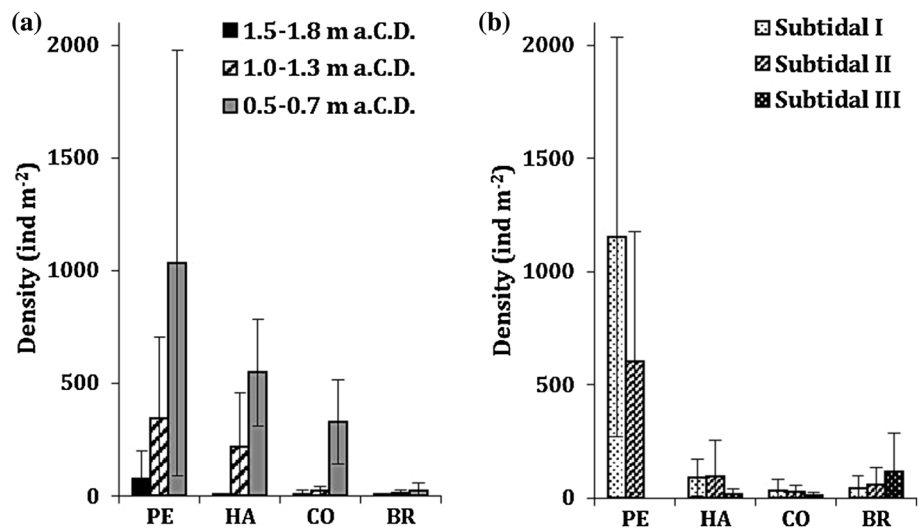
negatively related to the average number of individuals found in the stacks in the intertidal (Fig. 6d) and positively related to the frequency of primary attachment substrata that were gravel (Fig. 6e). Percentage cover of fine sediment and gravel was highly negatively correlated (Pearson product-moment correlation,  $r_{\text{intertidal}} = -0.878$ ,  $r_{\text{subtidal}} = -0.858$ ,  $p < 0.001$ , Fig. 6a).

Live *M. edulis* was found at nine intertidal sites, with 0.7–23 % of the total surface of the site (1.0–1.3 m above C.D.) covered in this substratum type. In contrast to what was observed for the substratum class gravel, the availability of live mussels at a site did not result in the increased utilisation of live mussels as primary attachment substrata for *C. fornicata* stacks (Fig. 6f). For example, 23 % of the surface of Coshaston transect 3 consisted of live *M. edulis*, but no *C. fornicata* was found attached to mussels.

### Distribution across the vertical shore gradient

Intertidal densities differed significantly between the three intertidal heights and the four sites that were surveyed for the vertical distribution of *C. fornicata* (both main effects:  $p < 0.001$ , Table 2). The lowest intertidal height always contained highest densities (e.g. mean  $\pm$  SD:  $1031 \pm 943$  individuals  $\text{m}^{-2}$  at  $\sim 0.5$ – $0.7$  m above C.D. compared to  $76 \pm 124$  individuals  $\text{m}^{-2}$  at  $\sim 1.5$ – $1.8$  m above

**Fig. 5** Vertical distribution of *Crepidula fornicata* at Pennar (PE), Hazelbeach (HA), Cosheston (CO), and Beggars Reach (BR) in the Milford Haven Waterway. Bars are means ( $\pm$ SD) from 10 1-m<sup>2</sup> quadrats taken in the intertidal (a) or 30 still images taken using a sled-mounted underwater still camera in the subtidal (b). Subtidal I 50 m distance from  $\sim$ 0 m above C.D. Subtidal II 150 m distance, Subtidal III middle of the channel and  $\sim$ 250–500 m distance (n.a. for PE due to narrow width of channel at this site)



C.D. at Pennar; Table 2; Fig. 5a). Differences between the tidal heights were consistent between sites (interaction site  $\times$  tidal height:  $p > 0.05$ , Table 2).

Subtidally, densities did not differ between the parallel transects surveyed with varying distance from 0 m above C.D. (factor distance from shore:  $p = 0.50$ , Table 3). This was despite there being large differences in *C. fornicata* densities between the four study sites (factor site:  $p < 0.001$ , Table 3). The effect of distance to shore was consistent between study sites (interaction site  $\times$  distance from shore:  $p = 0.58$ , Table 3). No clear relationship between intertidal and subtidal densities was apparent, as revealed by visual inspection of the data (Fig. 5a, b). For example, whilst densities were high at Pennar in the intertidal as well as the subtidal, this was not the case for Hazelbeach or Cosheston, where densities were highest in the lowest intertidal height, but relatively low in the subtidal transects.

## Discussion

We found that *C. fornicata* occurred at very high densities ( $>1000$  individuals m<sup>-2</sup>) in the MHW, the location of its northern-most self-sustaining population along the west coast of Britain since its first introduction into Wales in the 1950s (Cole and Baird 1953; Bohn 2012). The apparent lack of a northward range extension despite its healthy population status within the MHW is surprising. Our study was not designed to investigate the potential causes for *C. fornicata*'s limited northward spread; yet, we think that our observations from the population that resides within the MHW may give us some useful insight into causes for its limited expansion. The secondary spread of NNS following initial introduction and establishment in a region may be

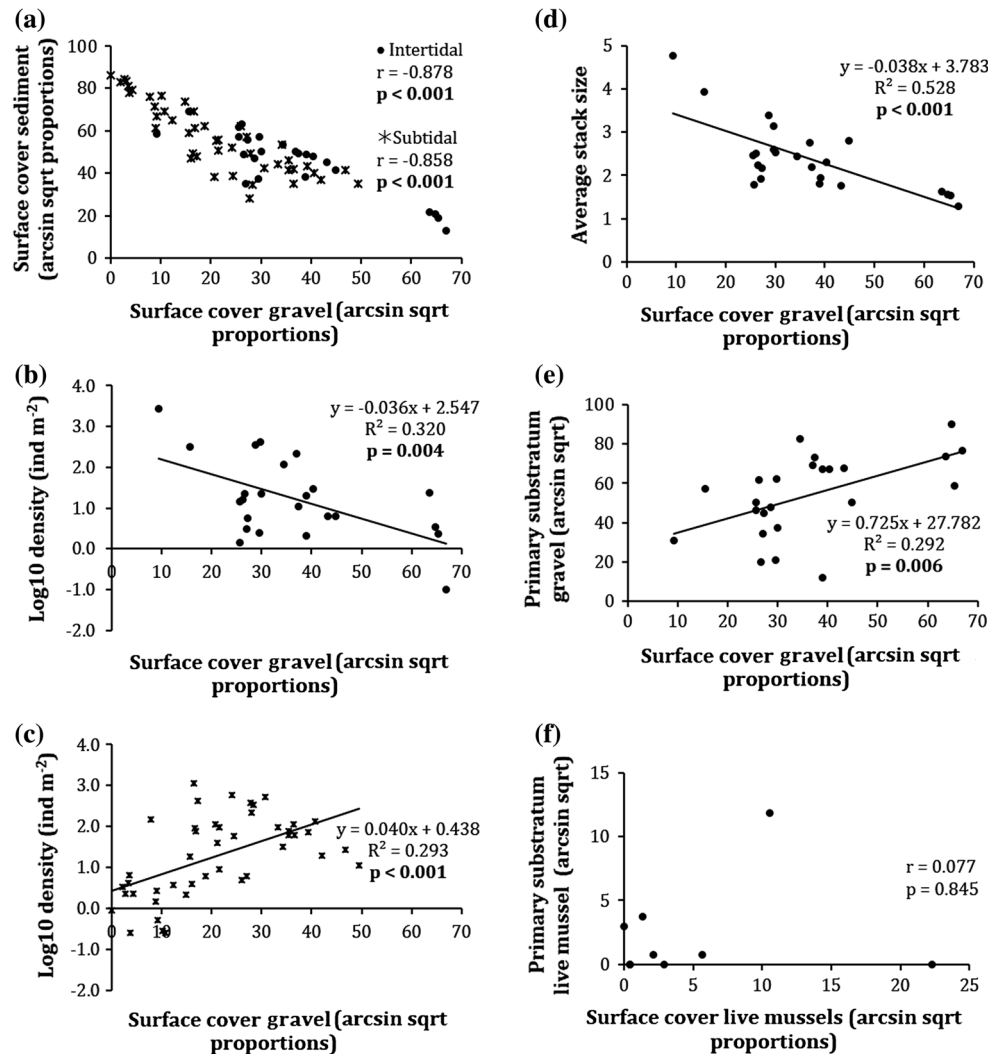
limited by the availability of suitable habitats (Colautti and MacIsaac 2004). Inside the MHW, *C. fornicata* occurs across a variety of substrata types, making it unlikely that *C. fornicata*'s absence to the north of the MHW is solely due to the absence of suitable habitat types. We also found that *C. fornicata* occurs in greatest abundances in mixed-substrata habitat types with high content of hard substrata; these are abundant in areas to the north of the MHW (e.g. the Cardigan Bay SAC, Sciberras et al. 2013). However, we observed that *C. fornicata* only occurs in very low densities or is fully absent in certain homogeneous habitats such as boulder and fine sediment-dominated areas. These were primarily located at the entrance of the MHW, possibly forming a dispersal barrier and hampering a rapid expansion of the species along the Welsh coast. Similar processes were found to restrict the range of other gastropod molluscs for very long time periods, even if this dispersal barrier may eventually be overcome (Fenberg and Rivadeneira 2011; Fenberg et al. 2014). We think that the presence of a dispersal barrier, in combination with high larval export and certain life history traits, is the most likely explanation for the absent, or very slow, northward spread of *C. fornicata* along the Welsh coast line.

*Crepidula fornicata*'s larval phase lasts  $\sim$ 2–4 weeks (Pechenik 1980, 1984) which certainly aids its long-distance dispersal from a source population to surrounding areas under the prevailing regional hydrodynamic conditions. For this reason, it has been suggested that *C. fornicata*'s spread from the UK to the Netherlands in the 1920s was a result of larval dispersal (Orton 1915; Adam and Leloup 1934). Similarly, larval transport from the MHW to Mid-Wales is likely due to the prevailing northward direction of the water masses across the Irish Sea (Evans 1995). *C. fornicata*'s reproductive mode through internal fertilisation requires the formation of permanent



**Fig. 6** Effect of substrata type composition on adult *Crepidula fornicata* densities and dispersal in the Milford Haven Waterway.

**a** Correlation between two dominant substrata classes (fine sediment, grain size <16 mm, and gravel, grain size 16–256 mm) in the intertidal and subtidal transects. **b** Intertidal percentage cover of gravel versus average *C. fornicata* density of each intertidal transect. **c** Subtidal percentage cover of gravel versus average density of each subtidal transect. **d** Intertidal percentage cover of gravel versus average stack sizes. **e** Intertidal percentage cover of gravel versus the percentage of primary substrata that were gravel. **f** Intertidal percentage cover of live mussels *Mytilus edulis* versus the percentage of primary attachment substrata that were live mussels. *Markers* are means of all transects with densities >0.1 individuals m<sup>-2</sup>. All percentage data were arcsine square-root-transformed and densities log<sub>10</sub>-transformed to fulfil assumptions of homoscedasticity and normality



associations ('stacks'). Long-distance dispersal of the larvae however may result in the transport of larvae away from conspecifics (Rigal et al. 2010), reducing the likelihood of successful attachment to conspecifics, reproduction and the chances for the establishment of self-sustaining populations in the open ocean, thus limiting its regional spread (Korringa 1942, 1951). This may also explain the slow or lacking establishment of a breeding population beyond its original location of introduction in Mid and North Wales.

In its native range, *C. fornicata* is known to reach highest densities in shell-rich areas (Driscoll 1967) and areas with high surface cover of hard substrata (Loomis and Van Nieuwenhuyze 1985). This seems self-evident, considering that *C. fornicata* needs hard substrata for settlement. The results of our study partly support this. Highest abundances were observed in habitats with a mixture of substrata types with high content of gravel and shell. We found a significant positive relationship between

the percentage cover of gravel (grain size ~16–256 mm) and *C. fornicata* densities in the subtidal, indicating that this substratum type may provide suitable conditions for settlement and subsequent juvenile and adult survival. Surprisingly, however, this relationship was negative in the intertidal. We can only speculate on the causes for these opposing patterns. High *C. fornicata* densities are also often associated with sediments containing a high content of silt and clay (Driscoll 1967; Barnes et al. 1973), probably because a high proportion of fine sediments is a good indicator of sheltered conditions that are suitable habitats for *C. fornicata*. Our methodology for substratum classification resulted in a highly negative correlation between the percentage surface cover of the two most dominant substrata classes (fine sediment and gravel), as both had been recorded from the same images. The occurrence of high numbers of *C. fornicata* in areas with low content of gravel may thus be an indication of a positive correlation with content of fine sediment. In the

**Table 2** Distribution of *Crepidula fornicata* in the intertidal zone of the Milford Haven Waterway in South Wales, UK

	SS	SS/MS <sub>total</sub>	df	p
Site	17,540.0	33.8	3	<b>&lt;0.001</b>
Tidal height	24,980.6	48.2	2	<b>&lt;0.001</b>
Site × tidal height	5525.9	10.7	6	0.100
		BR	CO	HA
Mann–Whitney, factor site	PE	<b>&lt;0.001</b>	<b>0.002</b>	0.162
	HA	<b>&lt;0.001</b>	0.110	
	CO	<b>0.005</b>		
			1.8 m	1.2 m
Mann–Whitney, factor tidal height		0.6 m	<b>&lt;0.001</b>	<b>0.001</b>
		1.2 m	<b>&lt;0.001</b>	

Results of nonparametric two-way crossed Scheirer–Ray–Hare test and Mann–Whitney pairwise comparisons to test for differences in *C. fornicata* densities between three tidal heights (0.6 m—0.5–0.7 m above Chart Datum; 1.2 m—1.0–1.3 m a. C.D. and 1.8 m—1.5–1.8 m a. C.D.) at four study sites (*BR* Beggars Reach, *CO* Cosheston, *HA* Hazelbeach, *PE* Pennar). Nonparametric tests were chosen due to heterogeneity in variances that could not be removed with data transformations. Significant differences are shown in bold

intertidal zone, where environmental conditions are more stressful compared to in the subtidal, sheltered conditions may be more important to support survival and establishment of *C. fornicata*. Thus, it is possible that the establishment of large numbers of *C. fornicata* in high-energy environments is possible in the subtidal but not in the intertidal.

In the intertidal, we found a highly positive relationship between the percentage cover of gravel and the utilisation of gravel as the attachment substratum of the bottom-most individual. This may be interpreted as a trend that the availability of gravel results in dispersed, less clustered distribution of adults, resulting in the more frequent creation of ‘new’ stacks when such settlement space is freely available. In contrast, in areas dominated by fine sediments, attachment might be ‘forced’ to take place on top of conspecifics, as other substrata are scarce. This is in accordance with our observation that average stack size decreases with higher surface cover of gravel. It is possible that the availability of the substratum-type gravel does not only affect the local, clumped distribution of *C. fornicata*, but also increases the success with which the species disperses into previously un-colonised areas through the formation of ‘pioneer stacks’. However, gravel availability may also significantly decrease the reproductive potential of *C. fornicata* in the area—stack formation (i.e. the formation of permanent aggregations with at least two individuals) is essential to ensure reproductive success and thus recruitment success,

**Table 3** Distribution of *Crepidula fornicata* in the subtidal zone of the Milford Haven Waterway in South Wales, UK

	SS	SS/MS <sub>total</sub>	df	p
Site	99,977.3	95.4	3	<b>&lt;0.001</b>
Distance to 0 m a. C.D.	476.0	0.5	1	0.500
Site × distance	2048.0	2.0	3	0.582
		BR	CO	HA
Mann–Whitney factor site	PE	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
	HA	0.060	<b>&lt;0.001</b>	
	CO	0.133		

Results of nonparametric two-way crossed Scheirer–Ray–Hare test and Mann–Whitney pairwise comparisons to test for differences in *C. fornicata* densities between two parallel transect with varying distance to 0 m above C.D. at four study sites (*BR* Beggars Reach, *CO* Cosheston, *HA* Hazelbeach, *PE* Pennar). Nonparametric tests were chosen due to heterogeneity in variances that could not be removed with data transformations. Significant differences are shown in bold

whilst solitary individuals will remain unable to reproduce until the arrival of the second member of the stack.

We found no indication that the availability of the substratum-type ‘live *M. edulis*’ affects the frequency with which live *M. edulis* are utilised as primary attachment substratum. This is in contrast to what has been found in the German Wadden Sea. *C. fornicata* is clearly well established in that area, but abundances remain relatively low at  $\sim 141$  individuals  $m^{-2}$   $\sim 70$  years after its first introduction into the area (Thieltges et al. 2003). This is likely due to a combination of climate-induced mortality events and the limited availability of hard substrata for attachment. *C. fornicata* mainly occurs on *M. edulis* and *C. gigas* beds that are distributed in the intertidal–subtidal transition zone in the otherwise primarily muddy–sandy sediments of the Wadden Sea. This results in the frequent exposure to freezing air temperatures during spring tide emersion, possibly causing the limited increase in the population since establishment (Thieltges et al. 2004). Similarly, limited habitat availability due to the extensive coverage of the bay by *Zostera marina* beds is thought to be a main cause for *C. fornicata*’s modest densities in Arcachon Bay, France, even  $\sim 30$  years after the first introduction (de Montaudouin et al. 2001). Our results similarly show that habitat availability can affect *C. fornicata*’s distribution: the availability of gravel may determine the distribution and potentially even facilitate the spread of *C. fornicata*, but is not necessarily the case for other hard substrata such as shellfish species. Interestingly, *C. fornicata* was fully absent in boulder-dominated areas. This observation is consistent with that of other studies (Loomis and Van Nieuwenhuyze 1985).

Post-settlement movement and mortality have been found to be highly important in restructuring the distribution of *C.*

*fornicata* established during settlement (Shenk and Karlson 1986; McGee and Targett 1989; Bohn et al. 2013a, b). Early post-settlement mortality (EPSM) in particular may be crucial in determining adult distributional patterns, particularly in the intertidal zone where environmental conditions tend to be particularly stressful (Gosselin and Qian 1997; Hunt and Scheibling 1997). The data on *C. fornicata*'s vertical distribution suggest that EPSM may restrict the distribution of *C. fornicata* in the intertidal zone. Highest densities were always attained in the low intertidal (below ~0.7 m above C.D.), and the species was almost absent at the highest tidal height (above ~1.8 m above C.D.), irrespective of overall nearby abundances. Densities between neighbouring transects in the subtidal zone never varied as strongly as densities between the different intertidal heights, which suggests that processes typical to the intertidal (e.g. EPSM as a result of tidal elevation) cause the observed differential adult distributional patterns. Results from other studies undertaken in the same study area implied the same (Bohn et al. 2013a, b). The failing northward expansion, however, cannot be attributed to this process, due to the presence of dense, subtidal *C. fornicata* beds.

In our study, we could not confirm the presence of *C. fornicata* outside the MHW: no live individuals were found in the samples taken from areas just adjacent to the MHW, suggesting a lack of a northward range expansion. Unsuitable environmental conditions were suggested to cause *C. fornicata*'s limited population expansion elsewhere. Low summer seawater temperatures impair reproductive activity of the adults (Richard et al. 2006), and low winter air temperatures can cause adult mass mortality events (Thieltges et al. 2003, 2004). Similar patterns have been observed for other NNS (e.g. Firth et al. 2011). Limited food availability may also restrict the abundance and distribution of marine invertebrates, in particular of filter-feeding organisms if phytoplankton availability is limited. We think it is unlikely that any of these factors is limiting the population in the MHW and adjacent areas, given the very high population densities we reported and the strong mixing of water masses reported in the area. Also, a long reproductive season, high larval densities, and multiple spawning events by the females have been observed in the MHW (Bohn et al. 2012)—further indicators for a healthy population status. A few individuals were found within the boundaries of the Skomer MCZ in 2008, and in 2011 and 2012 after the completion of the survey work that is presented here (Newman et al. 2009, 2012; M. Burton pers comm). All individuals were found during only three occasions despite the very frequent monitoring work that is carried out in this area by Skomer MCZ staff. This suggests that no dense population was established until fairly recently. Our survey methodology had some limitations: only those individuals could be

quantified from the images that were clearly visible on the seabed surface. Small individuals (<5 mm) and those that were obstructed by other organisms, in particular macroalgae, were difficult to spot. This will have inevitably resulted in the underestimation of slipper limpet densities. The use of cameras has however proven the preferred survey methodology for subtidal habitats in many studies (e.g. Lambert et al. 2011; Sciberras et al. 2013), as it enables to survey large areas which would not be achievable using other methodologies (dive surveys, grab sampling, dredges, and trawls). Due to the high quality of the images and the large size of adult *C. fornicata*, we think that this was a reliable method to estimate densities of adult *C. fornicata*, even if subtidal densities should be considered as 'minimum' estimates of real densities. Most likely, *C. fornicata* is very rare outside the MHW and our sampling effort not large enough to detect its presence at such low densities. The expansion of the species into areas north of the MHW may be at its start now; this would explain the increased frequency of its occurrence in the Skomer MCZ between 2008 and 2012. This would be surprisingly late as its initial introduction occurred prior to 1953 (Cole and Baird 1953). In comparison, *C. fornicata* spread very rapidly through the full extent of the English Channel. The availability of settlement substrata, in combination with high larval dispersal and post-settlement processes, may be crucial processes in explaining the limited secondary spread of this potentially harmful NNS.

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