The distribution and potential northwards spread of the invasive slipper limpet *Crepidula fornicata* in Wales, UK

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Contents

List of Figures

1. Crynodeb Gweithredol

Y mae'r boldroediog ymledol *Crepidula fornicata* wedi ymledu'n eang yn nyfroedd glannau Cymru ers ei gofnodi gyntaf yn Nyfrffordd Aberdaugleddau (DA) ym 1953. Er iddo ymsefydlu'n eang yn ne a de-orllewin Cymru erbyn hyn, ni fu ond ychydig arwyddion i'r rhywogaeth ymledu tua'r gogledd trwy brosesau naturiol (ymwasgariad larfau, e.e.): ymddengys nas ceir i'r gogledd o DA. Bu i gyflwyno *C. fornicata* i ACA Afon Menai a Bae Conwy yng ngogledd Cymru, trwy ddamwain, yn 2006 ymysg grawn cregyn gleision beri pryder disymwth i Gyngor Cefn Gwlad Cymru (CCGC) a'r diwydiant acwafeithrin lleol, oherwydd gallu dichonol hysbys *C. fornicata* i beri niwed difrifol i fiota brodorol, gan gynnwys y gragen las feithrinedig, *Mytilus edulis*. Ysgogodd hyn ddechrau prosiect doethuriaeth, tan nawdd CCGC a Bangor Mussel Producers Ltd, gan Katrin Bohn tan oruchwyliaeth yr Athro Christopher A. Richardson a'r Dr Stuart R. Jenkins o'r Ysgol Gwyddorau Môr ym Mhrifysgol Bangor University yn 2008, er mwyn ymchwilio i allu'r rhywogaeth hon i ehangu ei thiriogaeth i ganolbarth a gogledd Cymru trwy ymwasgariad larfâu. Â chyfuniad o arsylliadau maes a labordy o gyflenwad larfaol, ymsefydliad larfaol a phrosesau ôl-ymsefydliadol, ynghyd â gwaith ar ffactorau cyfyngol megis tymheredd isel, ymchwiliais i ffactorau sy'n rheoli dosbarthiad presennol oedolion, a pha mor ddichonadwy yw y bydd poblogaeth fwyaf gogleddol Cymru, ar hyn o bryd, ymledu ymhellach tua'r gogledd. Dangosodd ganlyniadau'r prosiect ymchwil hwn fod *C. fornicata* wedi hen ymsefydlu yn DA, gydag ymgasgliadau helaeth iawn mewn mannau, a dim awgrym pall ar ei gallu i atgenhedlu. Fe'i ceir mewn sawl math o gynefin, a chanfuwyd fod argaeledd mathau neilltuol o is-haen yn fwyaf tebygol o hwyluso sefydliad poblogaethau. Awgryma hyn fod cyfyngu ar argaeledd cynefin, ac ataliad ar eu gallu i atgenhedlu oherwydd tymereddau dŵr môr is na'r hyn fyddai'n ddelfrydol, yn annhebygol o esbonio pam nad yw'n bresennol yn nyfroedd y canolbarth a'r gogledd. Roedd recriwtiad dyfnforol yn DA, ar y llaw arall, yn gyffredinol isel, ac yn digwydd yn ystod cyfnod llawer iawn byrrach na'r tymor larfaol hir, sy'n awgrymu y gall prosesau ymsefydliadol ac ôl-ymsefydliadol fod yn hynod bwysig wrth reoli patrymau dosbarthiad yr oedolion. Mae'r farwolaeth ôl-ymsefydliadol cynnar (MOSC) yn debyg o fod yn bwysig wrth benderfynu patrymau dosbarthiad yr oedolion, ond ymddengys nad yw'r cyflenwad larfaol ac ymddygiad ymsefydliadol y larfâu o bwys mawr. Mae a wnelo fy nghanlyniadau, fodd bynnag, â dosbarthiad yr oedolion yn y parth rhynglanwol yn unig, lle mae'n debyg bod agoredrwydd i'r amgylchiadau amgylcheddol garwach yn arwain at MOSC uwch. Yn olaf, canfûm y gallai argaeledd rhai meicrogynefinoedd neilltuol liniaru lefelau uwch MOSC yn y parth rhynglanwol, gan effeithio'n sylweddol, felly, batrymau graddfa-fechan dosbarthiad oedolion. Ymddengys, fodd bynnag, mai cyflenwad larfâu ar drothwy aeddfedrwydd, ynghyd â chyfuniad o amgylchiadau hydrodynamig ac ymddygiad ymsefydliadol larfâu, sydd fwyaf pwysig wrth gyfyngu ymlediad y boblogaeth ar raddfa ranbarthol, oherwydd presenoldeb tebygol poblogaethau islanwol. Dengys hyn bwysigrwydd cynnwys prosesau ymsefydliadol ac ôl-ymsefydliadol yn astudiaethau o lwyddiant recriwtio wrth anelu at ragfynegi ymlediad dichonol rhywogaeth oresgynnol a ddichon fod yn niweidiol.

Executive Summary

The invasive gastropod *Crepidula fornicata* spread rapidly within Welsh coastal waters since it was first recorded in the Milford Haven Waterway (MHW) in 1953. Although it is nowadays widely established in South and South West Wales, there has been only little indication of a northwards range extension of the species through natural processes (e.g. larval dispersal); it seems to remain absent from areas north of the Milford Haven Waterway (MHW). The accidental introduction of *C. fornicata* with a consignment of mussel spat to the Menai Strait and Conwy Bay SAC in North Wales, UK in 2006 raised immediate concern amongst the Countryside Council for Wales (CCW) and the local aquaculture industry due to *C. fornicata*'s known potentially very harmful impacts on native biota, including the cultured blue mussel *Mytilus edulis*. This prompted a Ph.D. project, funded by the CCW and the Bangor Mussel Producers Ltd, to be started by Katrin Bohn under the supervision of Prof Christopher A. Richardson and Dr Stuart R. Jenkins of the School of Ocean Sciences (SOS) at Bangor University in 2008, to investigate the potential of this species to expand its range to Mid and North Wales through natural larval dispersal. In a combination of field and laboratory observations of larval supply, larval settlement and post-settlement processes, combined with work on limiting factors such as low temperature, I investigated factors controlling its current adult distribution and potential for further northward colonisation from its current northernmost Welsh population. Results of this research project showed that *C. fornicata* is well established in the MHW, with locally superabundant aggregations and no indication for reduced reproductive success. It occurs across a variety of habitat types and the availability of certain hard substrata was found to facilitate population establishment. This indicates that limited habitat availability and decreased reproductive potential due to the exposure to sub-optimal seawater temperatures is unlikely to explain its absence from the coastal waters of Mid and North Wales. Benthic recruitment in the MHW, on the other hand, was generally low and occurred during a much shorter time period compared to the long larval season, indicating that settlement and post-settlement processes may be highly important in controlling adult distributional patterns. Early post-settlement mortality (EPSM) is likely important in determining patterns of adult distribution, whilst larval supply and larval settlement behaviour seem to be of minor importance. However, my results apply only to the distribution of adults in the intertidal, where exposure to harsher environmental conditions probably results in higher EPSM. Lastly, I found that the availability of certain microhabitats might attenuate the high levels of EPSM in the intertidal, thus having considerable impacts on fine-scale adult distributional patterns. The supply of late-stage larvae, in combination with hydrodynamic conditions and larval settlement behaviour, however, seems to be most important in limiting population spread at a regional scale, due to the likely presence of subtidal populations. This shows the importance of incorporating settlement and post-settlement processes into studies on recruitment success when aiming to predict the potential spread of a potentially harmful invader.

2. Background

The American slipper limpet *Crepidula fornicata* (Linnaeus 1758) is an invasive marine gastropod of the family Calyptraeidae that was first introduced from the North West Atlantic coast to European coastal waters in the late 19th Century. It received much attention and is widely studied because of its major impacts on the native fauna through modifications of soft and mixed sediment habitats, the resulting changes of the ecological balance of benthic communities, and its impacts on several commercial shellfish species by competition for space and food.

The accidental introduction of *C. fornicata* with a consignment of mussel spat to the Menai Strait and Conwy Bay SAC in North Wales, UK in 2006 raised immediate concern amongst the Countryside Council for Wales (CCW) and the local aquaculture industry due to *C. fornicata*'s known potentially very harmful impacts on native biota, including the cultured blue mussel Mytilus edulis. The successful mechanical removal of *C. fornicata* through the clearance of all infected mussel beds in 2007 and the manual removal of the few remaining *C. fornicata* specimens by 2008 prevented the introduction of the species to North Wales at that time. The northern-most self-sustaining population seemed to remain within the Milford Haven Waterway (MHW) in South West Wales, a natural ria with established populations of *C. fornicata* since its first occurrence in Welsh waters in the 1950s.

Previous work carried out in other parts of Europe suggest that the absence of the species from Mid and North Wales may be due to the exposure to low, sub-optimal seawater or air temperatures at its northern range limit, by causing high adult mortality during the winter months or hampering their reproductive success during the reproductive season (e.g. Pechenik 1984, Thieltges et al. 2003, 2004, Richard et al. 2006). However, the persistence of some individuals for ~2 years following their introduction to North Wales in 2006 suggests that prevailing seawater temperatures were not the prime reason for the absence of the species from Mid and North Wales, raising concern that the species may have the potential to establish self-sustaining populations to the north of its current distribution through either repeated introductions or natural larval dispersal in the near future.

In 2008 a research project, funded by the CCW and the Bangor Mussel Producers Ltd, was started by PhD student Katrin Bohn under the supervision of Prof. Christopher A. Richardson and Dr. Stuart R. Jenkins of the School of Ocean Sciences (SOS) at Bangor University, to investigate the potential of this species to expand its range to Mid and North Wales through natural larval dispersal. In a series of field and laboratory studies, we aimed at understanding the current adult distribution of *C. fornicata* at its northern-most self-sustaining population in Wales, the potential effects of low air or seawater temperatures on reproduction and recruitment success, as well as predicting the processes most important for controlling adult distributional patterns.

This report summarises the main findings of 4 years of research at SOS. A general review chapter outlines known introduction events and the current distribution of *C. fornicata* in its invasive range and discusses main vectors and processes aiding its spread. Three further chapters are summarising the main results from the research carried out during this PhD project.

3. The Distribution and Invasion Success of *Crepidula fornicata*

3.1. Native Range

Crepidula fornicata is native to the Atlantic coast of North America (Figure 1), where it is widely distributed between the Gulf of St. Lawrence in Canada to the Gulf of Mexico (Blanchard 1997; Fretter and Graham 1981; Rawlings et al. 2011; Walne 1956). Native populations are also reported from the Caribbean Islands of Puerto Rico, Cuba, Curacao and St. Thomas (Walne 1956).

3.2. Non-Native Range

The first introduction of *C. fornicata* to Europe happened approximately 135 years ago via movements of shellfish to Britain (Blanchard 1997). *C. fornicata* is now common in several parts of the world, and the steps of its global spread are summarised in Figure 1 (Blanchard 1997).

3.2.1. Early Introductions and Spread in Great Britain

The first record of *C. fornicata* in Europe is from Liverpool Bay in England and dates back to 1872 (McMillan 1938). Presumably, the species was introduced as adults attached to the American clam *Venus mercenaria* or the American oyster *Crassostrea virginica* that were transported to the coastal waters surrounding Liverpool Bay at that time. The same author also cites from The First Report upon the Fauna of Liverpool Bay (1886) where it is mentioned that *C. fornicata* was found in the Menai Strait close to Beaumaris in North Wales. The slipper limpets were associated with *C. virginica* that were imported to this area. Interestingly, although these are the first reports of the occurrence of *C. fornicata* in UK waters, no further records of its presence in these locations exist today (besides those reporting the accidental introduction of *C. fornicata* to commercial mussel beds in the Menai Strait in North Wales in 2006 that will be discussed later). It seems that these populations did not persist (Barnes et al. 1973), and *C. fornicata* was not recorded from the British west coast until the 1950s (Cole and Baird 1953; Robson 1929).

Figure 1. World-wide distribution of the Crepidula fornicata and steps of spread: 1 Native range from Canadian border to Gulf of Mexico. 2 1880's - East coast of England. 3 1910's - Belgium, Germany, the Netherlands. 4 1930's - Northwest USA. 5 1940's - South England, France. 6 1950's - Denmark, Sweden, Norway. 8 1970's – Spain, Mediterranean Sea. 9 2000's - Northern Ireland. Its widely cited presence in Japan since the 1970s (7) has been a misidentification,

making the Northwest USA the only location with non-native populations. Adapted from Blanchard 1997

However, recurrent movements of shellfish such as *C. virginica* were undertaken between the 1870s and the 1920s, mainly to promote the British oyster trade after the collapse of stocks of the native oyster *Ostrea edulis* due to overfishing (Blanchard 1997; Korringa 1942). This resulted in a series of introductions of adult specimens of *C. fornicata* attached to the imported oysters to the east and south coasts of England. The earliest mentioning of *C. fornicata* in this region goes back to 1887-1888 when dead shells of *C. fornicata* were found at Grimsby in Lincolnshire (Adam and Leloup 1934; Crouch 1893). Further living and dead specimens of *C. fornicata* were found, in Lincolnshire and Essex, often attached to oysters (Crouch 1893). Cole (1952) later concludes that the source population of these specimens must have been in Essex where oysters had been re-laid. Also, he states that the distribution of the slipper limpet expanded north and south from there. *C. fornicata* became locally abundant on the east coast of England within a few years, but its range in England remained confined mainly to Essex and Lincolnshire at that time, although populations in Kent are mentioned elsewhere (Korringa 1942; Orton 1909; Orton 1912).

C. fornicata became a common component of the fauna of the south coast of England soon after and gradually extended its range westwards through the English Channel (Orton 1915). Between 1908-1909, some specimens were found close to Hastings in East Sussex, in 1911 in West Sussex, and only two years later in the harbour of Emsworth in Hampshire. In 1915, several shells were found on the shores of the Isle of Wright (Robson 1929). Orton (1915) mentions that there is no indication that any adult *C. fornicata* had been moved to these locations, and he therefore states that it “furnishes an excellent example of the efficacy of a free-swimming larva in extending the domain of a sea-dwelling animal“. Through natural larval dispersal and movements of adult specimen associated with oysters, *C. forniciata* had hence managed to extent its range from Mersea Island in Essex to the Isle of Wright by 1915 (Orton 1915; Robson 1929).

In the following three decades, *C. fornicata* expanded its range along the whole south coast of England. Slipper limpets first appeared in Weymouth Bay (Dorset) in 1939 (Minchin et al. 1995), in Lyme Bay in 1943 (Orton 1950), and in Salcombe (Devon) in 1950 (Cole 1952). The first confirmed record of *C. fornicata* along the coast of Cornwall dates back to November 1946 from the Helford River, followed by further findings in the River Fal and the Penryn River (Cole 1952). Cole (1952) argues that hull fouling was the most likely vector of introduction of *C. fornicata* to the south coast of England, disagreeing with Orton (1915) on the possibility that *C. fornicata* may have expanded its range through natural larval dispersal. Instead, Cole (1952) suggests that the slipper limpet was likely introduced to these locations on the bottom of merchant or war ships that had remained in infested areas on the east coast of England for several years and were towed from the east to the west coast of the UK for break up or repairs, passing the Cornish coast on the way (Cole 1952).

At about the same time of its spread along the south coast, *C. fornicata* had also spread further north from the Essex populations, and in 1936, *C. fornicata* was found seven miles offshore the Tyne Estuary (Minchin et al. 1995). In 1946, many individuals were found attached to a German ship that was broken up at Blyth in Northumberland and soon after, *C. fornicata* became successfully established here (Cole 1952). Hence, by the early 1950s, *C. fornicata's* distribution in England was already ranging from Blyth in Northumberland to the south coast of Cornwall (Cole 1952; Orton 1950).

The rapid extension of *C. fornicata* along the east and south coast of England was soon realized as problematic to the British oyster trade. As a consequence, the British Ministry of Fisheries paid a bounty for each shell. This management approach resulted in the collection of more than 2000 shells in 1953 (Minchin et al. 1995). This clearly shows that within six decades of its first appearance in English waters, *C. fornicata* became a common component of the fauna along the English coasts.

3.2.2. Current Distribution in England and Scotland

Today, *C. fornicata* is a very common component of the fauna of the coastal waters of the east, south and southwest coasts of Great Britain (Utting and Spencer 1992). Current database searches imply that slipper limpets can be found as far north as Yorkshire on the east coast of England (NBN Gateway, see Figure 2), despite the above mentioned individuals that were found in Northumberland. Highest densities can be found in the Essex estuaries with more than 2000 individuals m^{-2} in some areas (FitzGerald 2007). *C. fornicata* is also present nearly anywhere in the English Channel in the south of the England (Hinz et al. 2011). Highest abundances are still thought to lie within the Solent, with estimated densities between ~200 to 400 individuals m^{-2} (FitzGerald 2007). Other areas where C. *fornicata* has established stable populations include Poole Harbour, Portland Harbour, Weymouth, Lyme Bay, Plymouth Sound and estuaries adjacent to it (FitzGerald 2007). Very little is known about the presence and population status of *C. fornicata* on the English west coast, but a single record exists from Lee Bay close to Ilfracombe on the north coast of Devon (see Figure 2). *C. fornicata* seems to be absent from the north west of England.

C. fornicata seems to remain absent from Scotland, although Scottish records can be found on the NBN Gateway (Figure 2). *C. fornicata* is also mentioned in the Scottish Natural Heritage (SNH) report 'Conservation of the Native Oyster *Ostrea edulis* in Scotland'. However, these records could not be verified yet (Bohn 2012).

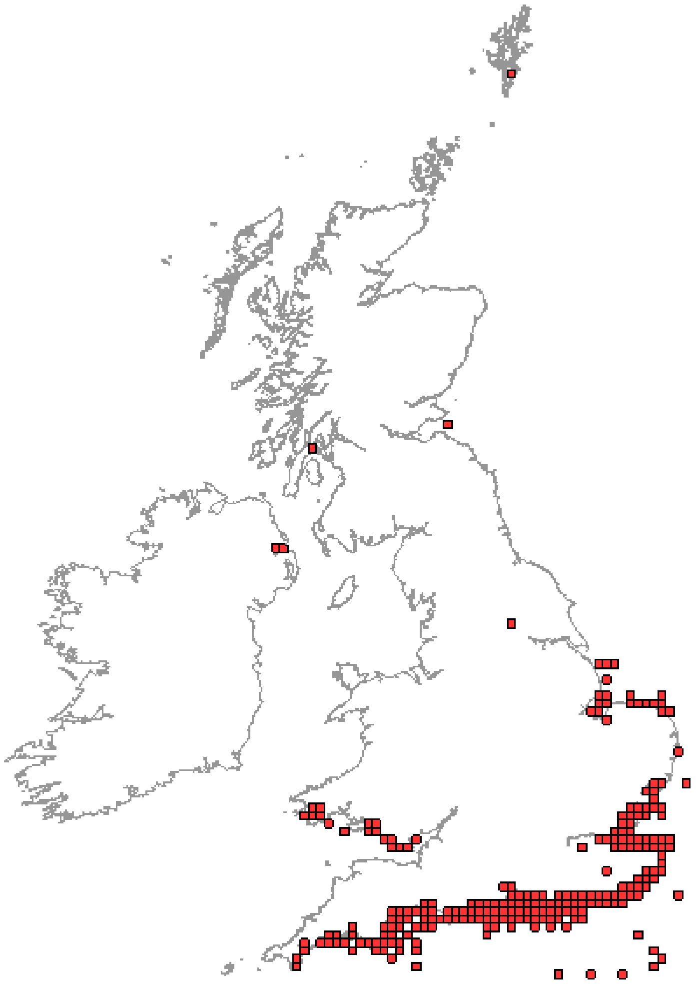

Figure 2. Map of the UK and the Republic of Ireland showing the distribution of *Crepidula fornicata* as available from records from the NBN-Gateway (available at http://data.nbn.org.uk, last accessed 09/09/2013)

3.2.3. Crepidula fornicata in Wales

Early Introduction and Spread

Besides the above mentioned records from Liverpool Bay and the Menai Strait from the 1880s, *C. fornicata* has not been reported from the west coast of Great Britain until six individuals were found in Pennar Gut in the MHW, Wales in 1953 (Cole and Baird 1953). Two of these slipper limpets were forming a stack and two of the single individuals were carrying spawn, which implies that, although few in numbers, these were already capable of reproduction. Most likely, these specimens have also been attached to the bottom of naval and merchant's ships. These were often brought to the MHW after remaining in *Crepidula*-infested areas on the east and south coast of England for many years, and often carried fouling communities (Cole 1952; Cole and Baird 1953). Only one year later, slipper limpets were also found as solitary individuals or in stacks of two in the low intertidal of Hazelbeach, Neyland and Pwllcrochan (Crothers 1966). Subtidal populations were confirmed from Lawrenny to Llangwrm and Landshipping Quay. Numbers of both intertidal and subtidal populations increased quickly thereafter. By 1960-1961 up to 150 stacks were brought up in an average dredge haul, and intertidal populations reached densities of up to 200 individuals m^{-2} at Lawrenny. Crothers (1966) writes that by October 1962, slipper limpets were present almost anywhere between Hazelbeach and Landshipping Quay, and that the first live specimen on Dale Beach, located at the mouth of the estuary, was found in April 1964.

Current Distribution and Recent Introduction Events

SOUTH AND SOUTH WEST WALES – *C. fornicata* has locally reached very high abundances in the MHW, its original location of introduction to Wales. It is also common along the Welsh south coast (Mettam 1979) (also see the NBN Gateway at http://www.nbn.org.uk), for example in Swansea Bay (pers. obs., Figure 2). However, little is known about the densities it may achieve and whether its introduction to the south is due to a range expansion from the MHW populations by natural larval dispersal, or through human-mediated introductions (e.g. hull fouling or aquaculture).

MID WALES - There is no conclusive evidence that *C. fornicata* has established self-sustaining populations anywhere to the north of the MHW (Figure 2; L. Allen, A. Bunker, B. Sampson and others pers. comm.). It is frequently stated that *C. fornicata* is present in South Cardigan Bay in South West Wales (Blanchard 1997; Rayment 2008). In fact it seems that these citations may be incorrect due to a misinterpretation of a single map in Blanchard (1997) (M. Blanchard pers. comm.). Enquiries to local fishermen and fisheries officers were made in 2009 to investigate the current range of *C. fornicata* along the Welsh coast line. It was reported that since 2006 *C. fornicata* is frequently found attached to scallops that are dredged in South Cardigan Bay, but in very low numbers. Also, some individuals of *C. fornicata* were found within the Skomer Marine Nature Reserve (SMNR) in 2008, 2011 and 2012, all of those attached to scallops (P. Newman and M. Burton pers. comm.). Attempts to confirm the presence of an established population were not successful during surveys undertaken in 2009 (see section 3), and most likely numbers of *C. fornicata* to the north of the MHW are extremely low.

NORTH WALES - In 2006, *C. fornicata* had been accidentally introduced into the Menai Strait and Conwy Bay Special Area of Conservation (SAC) in North Wales. This happened most likely with a consignment of mussel spat that had been imported from the English Channel to commercial mussel beds in the north east of Bangor Pier (Hewitt

2008; Morgan 2007). The presence of *C. fornicata* was confirmed in February 2007, and in March 2007 the affected area was dredged to remove all mussels with associated slipper limpets. Surveys were carried out the same month to investigate the success of the removal procedure. A few live *C. fornicata* were found in the affected area, possibly due to the onboard washing procedure during the removal which had allowed the re-introduction of small slipper limpets into the Menai Strait. It was decided to relay clean mussels onto the affected areas to smother any remaining slipper limpets (Morgan 2007). It seems that this procedure had been effective as no live or dead specimens of *C. fornicata* were found during intertidal surveys carried out in the Menai Strait in 2008 (Hewitt 2008) (K. Smith pers. comm.).

Some of the females that were collected during the 2007 surveys were bearing eggs, indicating that between the introduction event in 2006 and their removal in 2007, the slipper limpets were reproducing and possibly also releasing larvae in the Menai Strait (Morgan 2007). Frequent monitoring of the intertidal and subtidal zone of the affected and adjacent areas should be carried out to fully exclude the possibility that established populations exist in North Wales. To our current knowledge, however, the most northern established self-sustaining populations of *C. fornicata* along the British coastline remain within the MHW.

3.3. The Invasion Success of *Crepidula fornicata* – Vectors, Species Traits and Environmental Tolerances

C. fornicata fulfils several characteristics of a successful invader, including its high dispersal potential through natural and human-mediated processes, its wide environmental tolerances, and a good reproductive potential. It has a relatively complex, well-studied life cycle that is summarised in Figure 3 in a simplified manner. *C. fornicata* begins its life as free swimming veliger larva directly after hatching. After spending approximately 2 to 4 weeks in the plankton, the larvae undergo metamorphosis which is associated with the loss of the swimming organ, the velum. The newly metamorphosed juveniles hence leave the pelagic and start their benthic life. Whilst being capable of slow crawling for some time following metamorphosis, the juveniles soon find a permanent substrate for attachment. This is ideally an already existing stack consisting of several adult *C. fornicata*. Settlement in isolation is possible and often initiates the formation of a new stack. Juveniles reach maturity just a few months after settlement, i.e. they usually reach the male stage fairly early in their lives. The arrival of new males in the stack and the resulting change of the sex ratio in the stack allows the bottom most male to gradually develop into a female. Internal fertilisation may occur as soon as both male and female animals are present in the same stack. If fertilisation was successful, the females will brood the eggs for several weeks, until the veliger larvae hatch (Fretter and Graham 1981).

The following key characteristics of the different life cycle stages were shown to have greatly contributed to its rapid spread along the European coasts:

- The high dispersal potential during a pelagic larval life lasting several weeks, and its capability of prolonging pelagic life even further when environmental conditions are unfavourable (Pechenik 1980; Pechenik 1984; Viard et al. 2006)
- The high potential to be transported to new locations through human-related activities, including discharge of ballast water (larvae), ship hull fouling (juvenile and adult form), and movements of shellfish for aquaculture purposes (juvenile and adult form) (McMillan 1938; Mineur et al. 2012)

- Its gregarious behaviour as an adult, securing reproductive success and ensuring appropriate environmental conditions, indicated by the presence of conspecifics in the environment
- A long reproductive season, enabling multiple spawnings per female in one year with more than 12,000 eggs released per spawning event (Richard et al. 2006)
- The protection of the offspring during brooding by the female until the fully developed free-swimming veliger larvae hatch
- A high tolerance towards environmental conditions, especially to low and high temperature, during all life stages (Diederich et al. 2011; Rigal 2009; Schubert 2011)
- The epibiotism of *C. fornicata*, i.e. its ability to colonise nearly any hard surface, including other organisms, and the resulting advantage of being a strong competitor for space and food (Mineur et al. 2012)

Biological traits of all life cycle stages may thus be important in facilitating the successful invasion of *C. fornicata* in its non-native range. Vector uptake and transport (the first stage in the invasion process, following (Colautti and MacIsaac 2004)) of *C. fornicata* are largely facilitated by the fact that *C. fornicata* is an epibiont to several commercially important shellfish species, including the American oyster *C. virginica*, the Pacific oyster *C. gigas*, the European oyster *O. edulis*, the blue mussel *M. edulis*, the king scallop *P. maximus* and the common whelk *B. undatum*. Transport of the larvae with ship ballast water most likely also aided its transoceanic movement. Survival of the transport and establishment in its non-native range in Europe require high environmental tolerances of all life cycle stages; studies are here partly lacking, especially on stress tolerances of the juveniles stage. Several studies have shown that *C. fornicata*'s further spread within its European range occurred through repeated introductions of adults on ship hulls and with consignments of aquaculture species. This was also the case in all three documented introduction events to Welsh waters: with aquaculture imports to Beaumaris in 1886 and the Menai Strait in 2006, and to the MHW attached to ships prior to 1953. Natural larval dispersal may have contributed to its spread in its non-native range, although this has been controversially discussed. Establishment and population increase are clearly also facilitated by the relatively high fecundity, resulting in high propagule pressure and good potential for high recruitment. Stack formation may also benefit population establishment, as it maximizes reproductive success and ensures larvae settle in suitable conditions for survival.

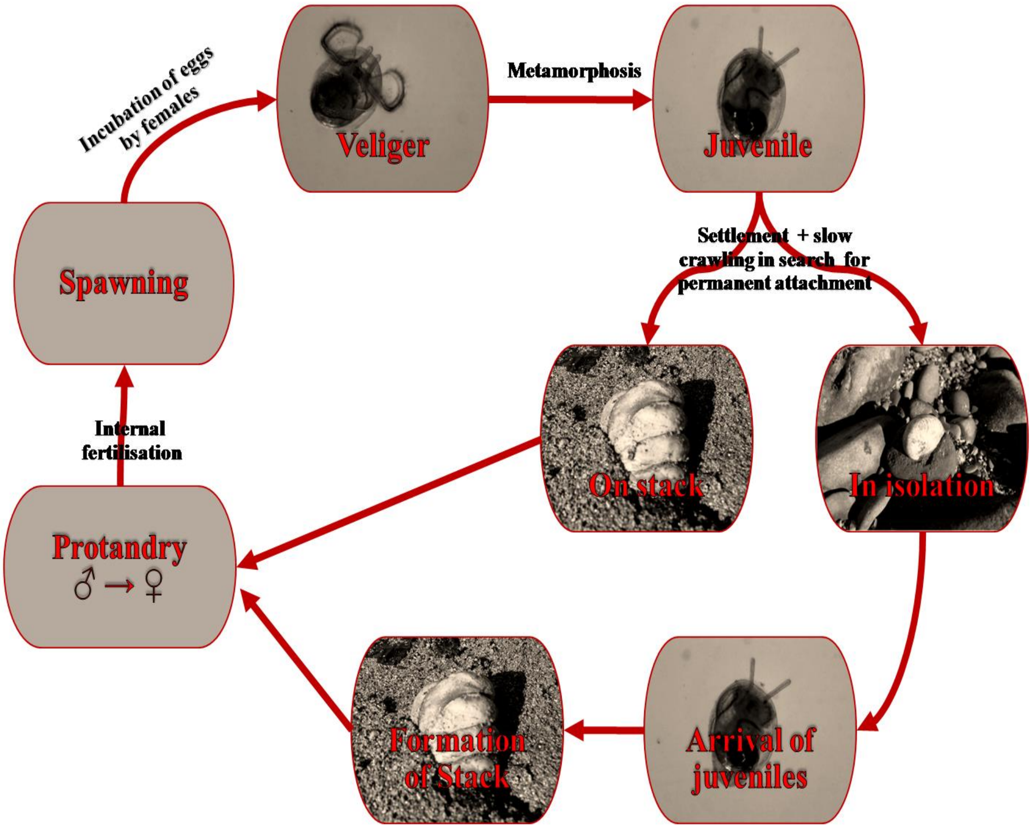

Figure 3. Summary of the life cycle of *Crepidula fornicata*. Details on the different stages will be discussed in the following pages. From Bohn 2012.

3.4. Research Aims and Objectives

Although clearly a very successful coloniser of new environments, *C. fornicata* does not always proliferate after introduction (i.e. remains at low population densities). High winter mortality of intertidal adult beds (Thieltges et al. 2003; Thieltges et al. 2004), limited habitat availability (de Montaudouin et al. 2001), restricted reproductive success due to low summer seawater temperatures (Richard et al. 2006) and low larval supply as a result of high larval export away from potential mates in adult beds (Rigal et al. 2010) have all been identified as potential limiting causes. None of these studies, however, incorporated settlement and post-settlement processes into their investigations, despite these processes being known to strongly affect adult distributional patterns of other marine invertebrates (Gosselin and Qian 1997; Hunt and Scheibling 1997; Jenkins 2005; Pawlik 1992). The failure of *C. fornicata* to expand northwards from the MHW, its original location of introduction to Wales, may be a consequence of any one of the above mentioned impediments on the larval or adult stage, or so far unknown effects on benthic recruitment via the transition to the juvenile stage and subsequent survival.

This PhD thesis dealt with the potential secondary spread of the American slipper limpet *C. fornicata* in Welsh coastal waters and investigated the potential limiting environmental conditions (seawater temperature, habitat composition and availability) and biological processes (larval supply, larval habitat selection, and post-settlement processes). This was done through i) confirmation of the northern-most established self-sustaining population in Welsh coastal waters and monitoring of its population status and habitat associations in this area, ii) investigations into the reproductive potential of *C. fornicata* at this northern range limit and iii) determination of the process of adult distributions in intertidal populations (larval supply, larval habitat selection or post-settlement mortality).

4. The Northern-Most Welsh Population of *Crepidula fornicata*

4.1. Background

Literature and database research has indicated that the current northern-most range of *C. fornicata* in Wales remains within the MHW (Cole and Baird 1953). However, as previously mentioned, the species is also repeatedly reported to be present in South Cardigan Bay in South West Wales (see Blanchard 1997, M. Burton and P. Newman pers. comm.). This PhD aimed to confirm whether a range expansion of *C. fornicata* to the outside and north of the MHW has occurred since its first record from the MHW in 1953 (Cole and Baird 1953). This was done through intertidal and subtidal surveys along the coasts of Pembrokeshire and Ceredigion in Wales to confirm the presence/ absence of *C. fornicata*, estimate densities and describe the habitats that support highest densities in its northern-most Welsh distribution.

4.2. Methods

We targeted three main survey areas to confirm the presence/ absence of *C. fornicata* to the north of its known distribution in Wales, UK: 1) the MHW, where a population is known to persist since 1953; 2) the SMNR, where individuals were found during routine surveys undertaken by CCW in 2008; and 3) Cardigan Bay, where its presence has been reported, but has not been confirmed so far (Fig 4, see Appendix I and Appendix II for full details on survey stations).

Subtidal work was undertaken during four surveys on vessels by SOS and CCW (Table 1) between August 2009 and 2010. Some surveys involved the deployment of a sled-mounted still image camera which recorded images of the seabed (image size 0.44m x 0.3m) along 150-200 m transects. All images were checked for the presence of *C. fornicata*, and when present, abundance estimates were achieved by averaging counts of live *C. fornicata* from 30 images per transect. The habitat was described from 20 images. When surveys involved beam trawls or dredges, samples were only checked for presence/ absence of *C. fornicata*. More details on survey design are described in Bohn (2012).

Between February 2009 and October 2010, the low intertidal of 24 sites along the Welsh coast line were quantitatively surveyed for the presence/ absence of *C. fornicata*. Ten of the 24 surveyed sites were located within the MHW (Appendix I). To ascertain the absence of *C. fornicata* outside and to the north of the MHW, 14 of the 24 survey sites were located within the SMNR and in Cardigan Bay, where there had been only anecdotal evidence of the rare occurrence of *C. fornicata*. Three horizontal transects were sampled at each of the 24 sites whenever possible. Densities were estimated by searching ten randomly placed 1 m^{-2} quadrats per transect for live and dead *C. fornicata*. 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*. The substrate composition of the intertidal sites was determined from five digital images taken of 0.25 m^{-2} quadrats that were randomly placed along each transect.

4.3. Main Findings and Conclusions

The results of our surveys could not confirm the presence of *C. fornicata* to the north of the MHW (the SMNR and Cardigan Bay, Figure 4). A single dead shell was found on a still image taken within the boundaries of the SMNR. Dead shells were also frequently abundant in the intertidal of New Quay, yet they likely stemmed from sources other than wild populations.

Within the MHW, we found that the abundance of *C. fornicata* is highly variable, occurring across a variety of habitat types (Figure 6 and 7). The highest intertidal and subtidal densities were reached in the middle stretches (Figure 6). Subtidally, *C. fornicata* was most abundant in the shallow waters at Pennar with 1152±881 individuals m^{-2} (mean±SD, Figure 6). Extremely high intertidal densities were recorded at Pwllcrochan with mean densities of 2748±3859 individuals m^{-2} at one transect (Figure 6). Especially in the intertidal, a remarkable decline in densities from the middle stretches of the ria towards the mouth and the upper reaches is apparent: whilst medium to high densities were still found at Pennar and Hazelbeach, densities at the intertidal sites of Cosheston, Jenkins Point, Beggars Reach and Black Tar Point in the upper reaches were relatively low in density (Figure 6, Appendix I). At the mouth of the ria, the lowest intertidal densities were recorded at Sandy Haven, where individuals were only found during the timed search but not the quantitative survey, indicating that average densities were <0.1 individuals m^{-2}.

Table 1. Boat surveys in 2009 and 2010 to study the Welsh distribution of *Crepidula fornicata.* CB – Cardigan Bay; SMNR – Skomer Marine Nature Reserve; MHW – Milford Haven Waterway; SOS – survey boat of School of Ocean Sciences; CCW – survey boat of Countryside Council for Wales.

Survey ID (area, date, location)	Area Surveyed	Vessel	Date	Methodology
CB, Aug09, Mya	Cardigan Bay (New Quay – Aberaeron)	RV Mya (SOS)	19th Aug 2009	17 samples, mussel dredge
CB, Aug09, Prince Madog	Cardigan Bay (New Quay – Aberaeron)	RV Prince Madog (SOS)	24th-25th Aug 2009	19 samples, beam trawl/ dredge
SMNR, May10, Skalmey	Skomer Marine Nature Reserve (Inside & Outside)	RV Skalmey (CCW)	5th-12th May 2010	30 samples, sled-mounted stills camera
MHW, Aug10, Pedryn	Milford Haven Waterway (Inside & Outside)	RV Pedryn (CCW)	2nd-6th Aug 2010	76 samples, sled-mounted stills camera

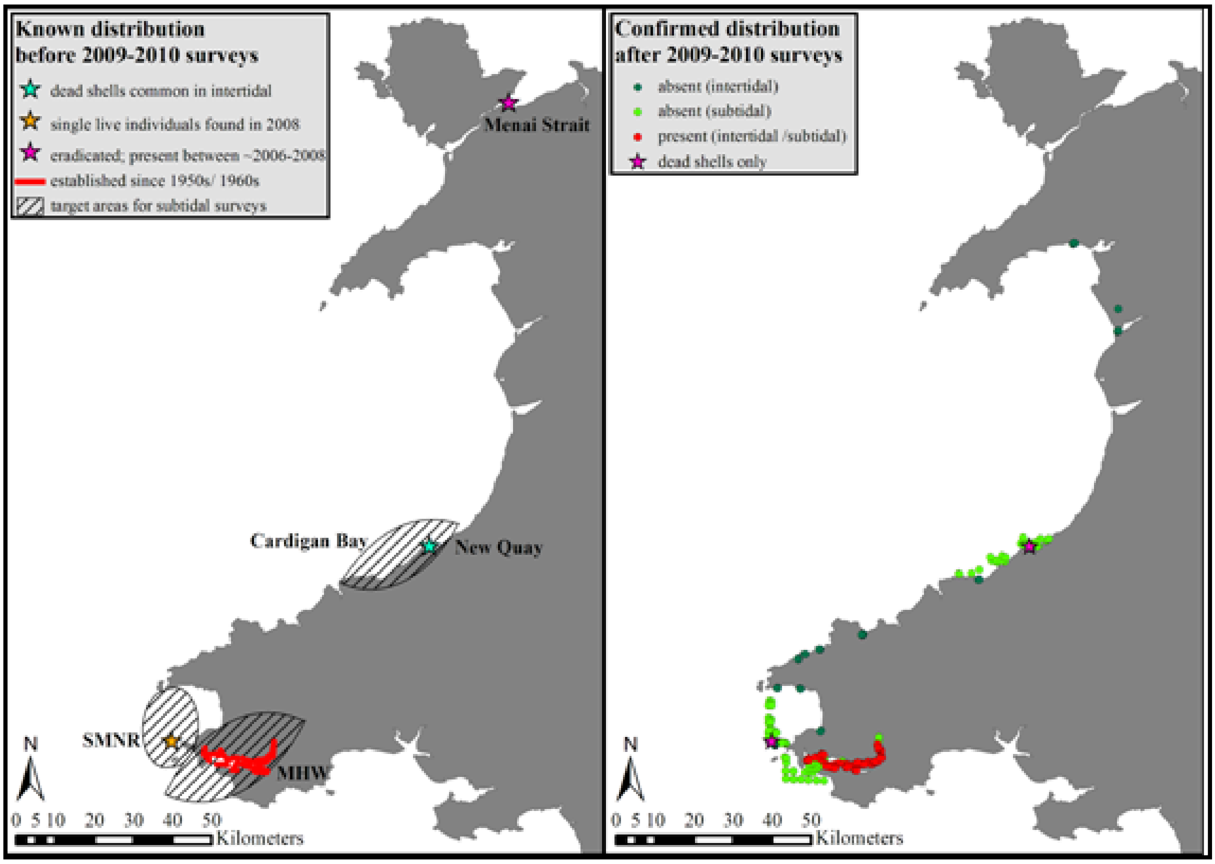

Figure 4. Left: Known distribution of *Crepidula fornicata* along the Welsh coast line before surveys were started in 2009 as part of the PhD project. Subtidal surveys were targeted at the Milford Haven Waterway (MHW), the Skomer Marine Nature Reserve (SMNR) and Cardigan Bay (hatched areas). Right: The presence and absence of *C. fornicata* as confirmed during the 2009/ 2010 surveys (intertidal as well as subtidal). From Bohn 2012.

C. fornicata occurred in most habitat types, but it was absent in areas with a high content of boulders (Figures 6 and 7). Densities remained low in homogenous habitats dominated by sediment (<16 mm). Highest densities were found in areas where sediment had a high content of hard substrata (i.e. mix of sediment and shell, mix of sediment and gravel, or mix of sediment, gravel and shell, Figures 6 and 7). Nine intertidal sites were found to support live *M. edulis*, with 0.7-23% of the total surface of the site (1.0-1.3 m above C.D.) covered in this substratum type. The higher availability of live mussels at a site did not result in the utilisation of live mussels as a primary attachment substratum for *C. fornicata* stacks (Figure 5).

The surveys from 2009 and 2010 found no indication of a spread of *C. fornicata* to the north of the MHW. The finding that *C. fornicata* may form locally superabundant aggregations, and that it occurs across various habitat types however suggest that its absence from the entrance and north of the MHW is unlikely due to unsuitable regional environmental conditions such as the absence of certain habitat types and favourable climatic conditions like seawater temperature. However, *C. fornicata* has been recorded from the SMNR. Most likely, the species is very rare in the SMNR and the sampling effort employed in our study could not detect its presence at such low densities. Also, *C. fornicata* may only have started expanding its range in recent years. Within the MHW, densities were highly variable and may be locally superabundant. Results from these surveys thus suggest little limitation through environmental conditions.

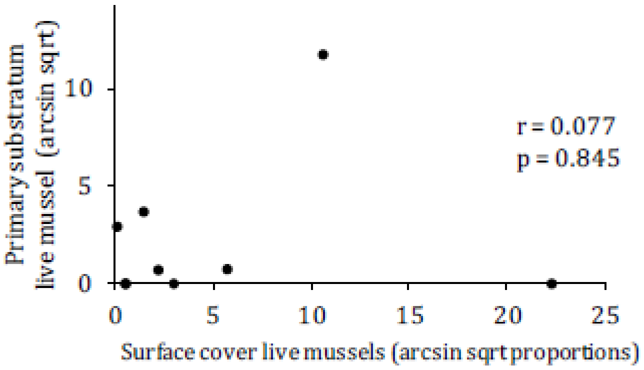

Figure 5. The relationship between the availability of live *Mytilus edulis* at the intertidal site (surface cover live mussels) and the utilization of mussels shells as attachment substratum for Crepidula fornicata stacks (primary substratum live mussels). The relationship is non-significant, suggesting that the higher availability of mussels does not necessarily lead to attachment of slipper limpets on the mussel shells. From Bohn 2012.

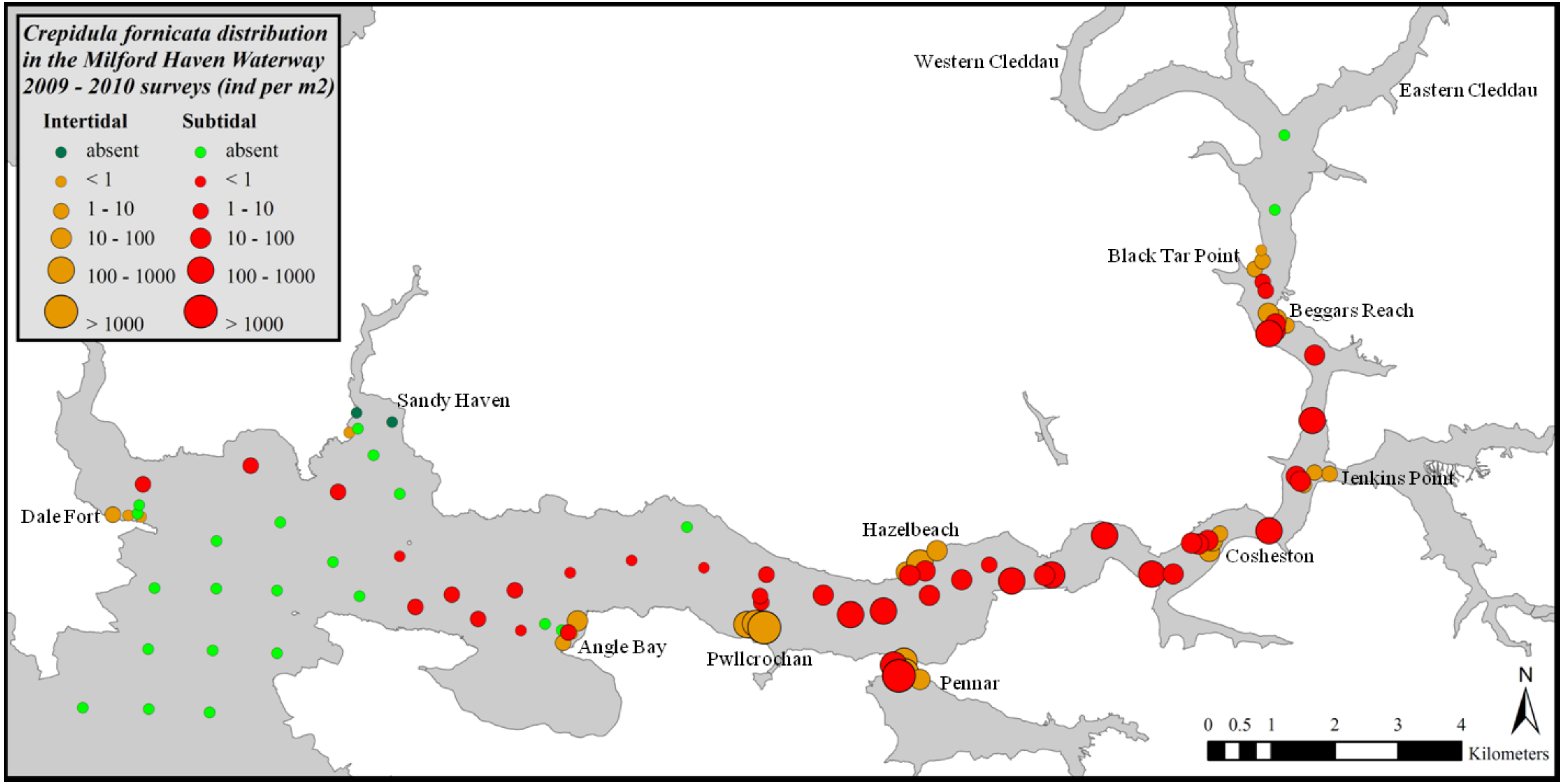

Figure 6. Densities of *Crepidula fornicata* in intertidal and subtidal sites in the Milford Haven Waterway (MHW). From Bohn 2012.

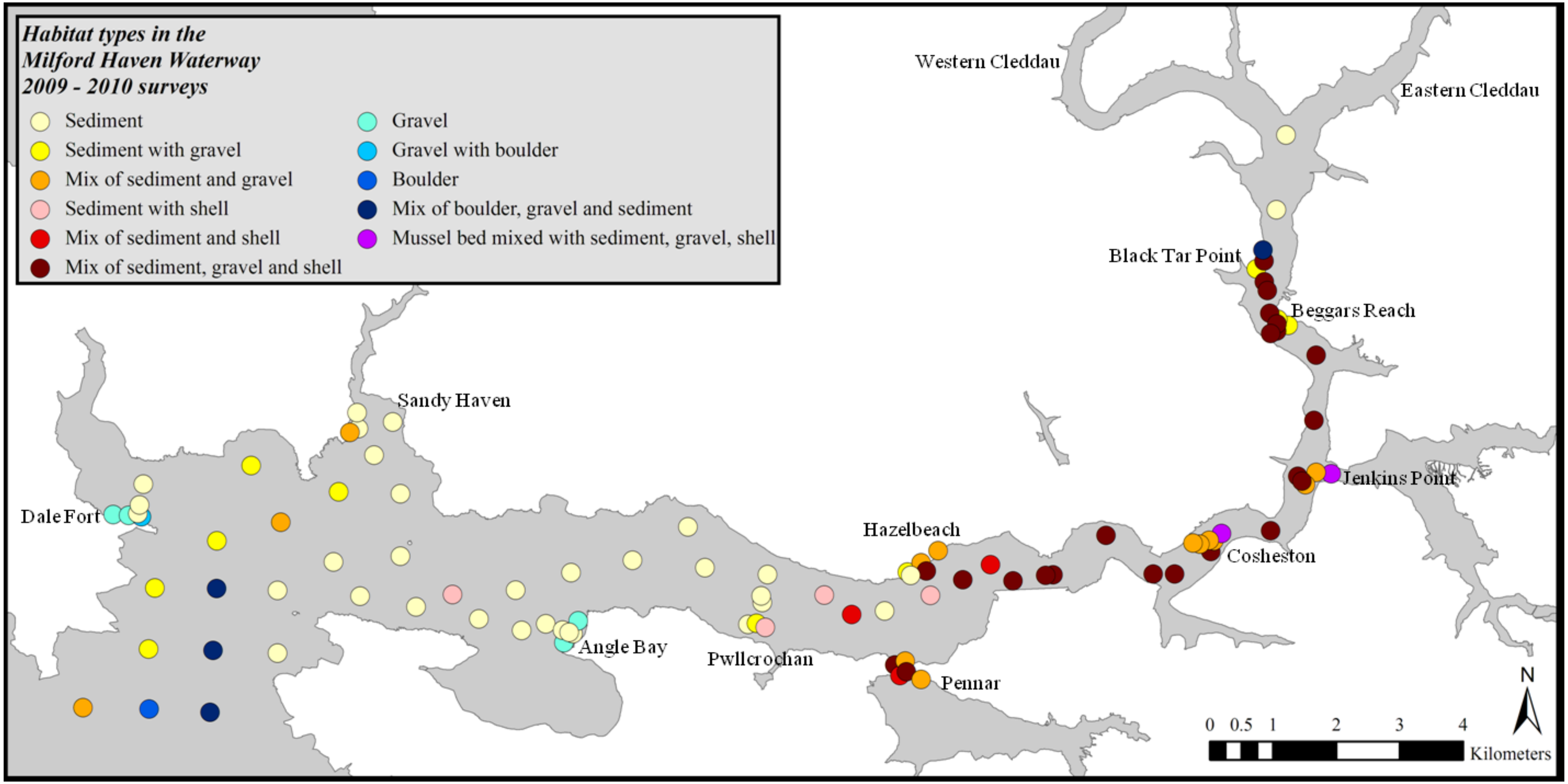

Figure 7. Habitat distribution in the Milford Haven Waterway. Habitat types were classified by grouping average percentage surface cover of 6 different substrata classes (*Sediment*, *Gravel*, *Boulder*, *Shell*, *Live habitat-forming species*, *Crepidula fornicata*). From Bohn 2012.

5. *Crepidula fornicata's* Reproductive Biology in the Milford Haven Waterway

5.1. Background

It is widely assumed that the limited proliferation and spread of *C. fornicata* in many study sites is due to the effects of low seawater temperatures during the summer months affecting reproductive potential of the adults (Richard et al. 2006), or low winter air temperatures resulting in high adult mortality (Thieltges et al. 2004). The previously reported absence of (detectable numbers of) *C. fornicata* from Mid and North Wales prompted the installation of an intensive monitoring programme of the reproductive season and various life cycle-stages of the slipper limpet at its northern-most established self-sustaining population, to investigate whether low summer or winter air- or seawater temperatures account for its limited spread in Welsh waters.

5.2. Methods

Between February 2010 and January 2011, we collected biological data and temperature data from up to 4 intertidal sites in the Milford Haven Waterway (MHW). The shores differed in their location along the estuary and the abundances of adult slipper limpets found (low adult abundance: Beggars Reach; moderate/ low: Cosheston Point; moderate: Hazelbeach; high: Pennar; see Figure 6 and Appendix I for details). During monthly visits, we recorded the following:

- the spawning period of females, by collecting a minimum of 100 slipper limpets and checking for the presence of laid egg capsules under the foot of each individual;
- the abundance of larvae and length of the larval period, by taking a plankton tow close to each of the intertidal sites;
- the abundance of settlers and length of the settlement season, by installing settlement panels in the low intertidal and recording the newly settled spat *C. fornicata*, and
- the air and sea water temperature from 2 study sites in the MHW and 2 sites to the north of the MHW for comparison (the SMNR and the Menai Strait).

More details on sampling design can be found in (Bohn 2012; Bohn et al. 2012).

5.3. Main Findings and Conclusions

The data suggests that neither low winter temperatures nor low summer temperatures are acting as a strong limiting factor for the northward spread of *Crepidula* by negatively impacting its reproductive success. Instead, we have observed a long reproductive season similar to those reported from areas elsewhere in Europe where there are lower adult densities and cooler temperatures (Figures 8 and 9). Egg-brooding females were found between March and September, similar to reports from the French (Richard et al. 2006) and German (Thieltges et al. 2004) coasts. Larvae were even found during the winter of 2010/ 2011 (Figures 8 and 9), when seawater temperatures were much lower than those previously reported to be necessary to elicit spawning (this study: <6°C, compared to ~10°C as reported in (Chipperfield 1951; Hoagland 1979; Richard et al. 2006; Valdizan et al. 2011).

Another indicator of the lack of restricted reproductive success is the very high larval densities that we recorded during the peak reproductive season in summer (maximum larval densities >1200 larvae m^{-3}, Figure 8). Furthermore, females were capable of spawning multiple times, as estimated from the recorded percentage of egg brooding females and assuming a length of embryonic development of ~20-30 days (Bohn 2012; Bohn et al. 2012; Brante et al. 2009).

Whilst the reproductive season (estimated through the length of the spawning and larval period) showed no indication of restrictions due to low summer seawater temperatures, we have found some evidence that settlement and recruitment may be limited in the MHW, at least in the intertidal populations. Settlement occurred much later in the summer and during a much shorter time period (July-September) at seawater temperatures >16°C (Figures 8 and 9). This is ~10°C higher than the minimum temperature at which larvae were observed in the water column. Settlement was highly variable between sites and months with highest densities recorded at Pennar in July and lowest recorded at Cosheston and Hazelbeach throughout most months (Figure 8).

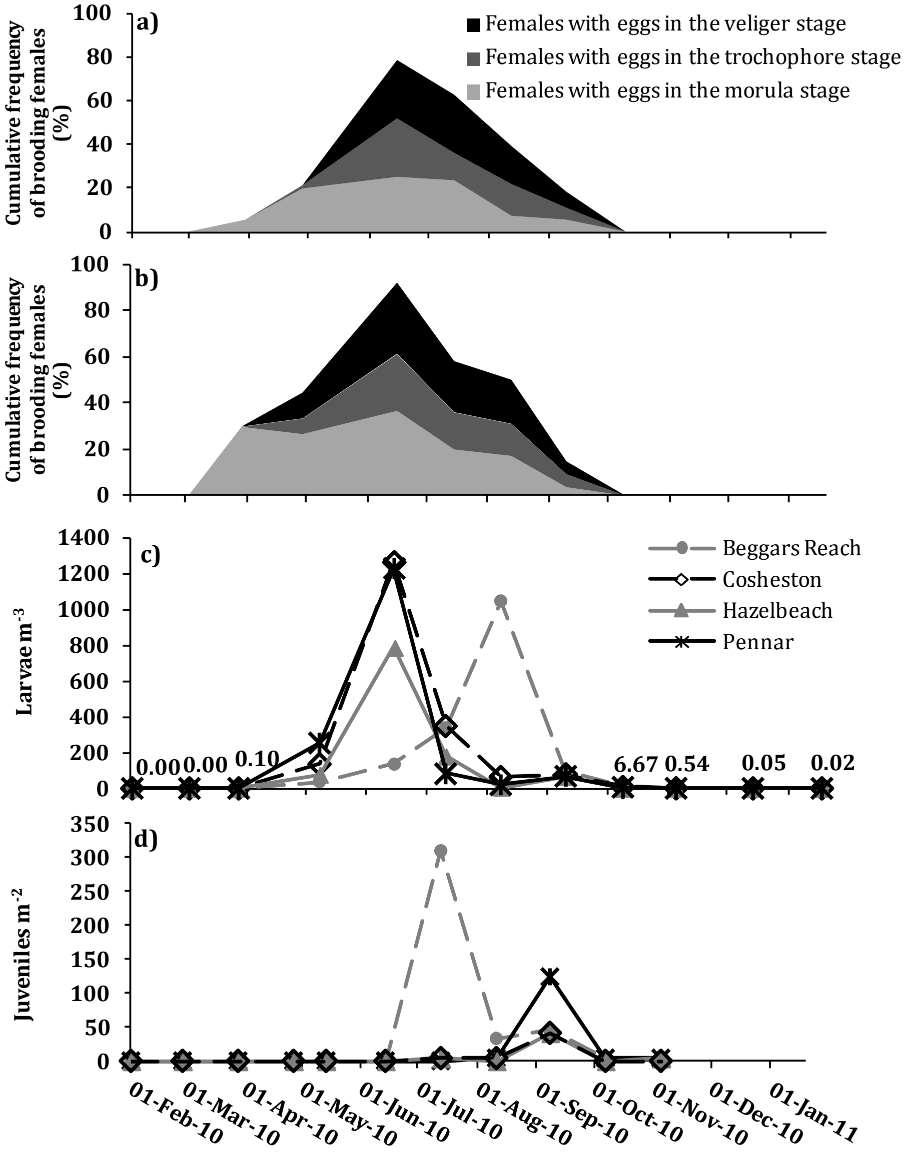

Figure 8. Seasonal reproduction of *Crepidula fornicata* in the Milford Haven Waterway between February 2010 and January 2011. a) and b) Percentage of females found with broods of eggs in the different embryonic development at (a) Cosheston and (b) Hazelbeach. c) Densities of *C. fornicata* larvae in monthly plankton samples. Numbers above the Pennar data series are data

labels to visualize very low densities. d) Mean densities of juvenile *C. fornicata* <4 mm on artificial settlement substrata (slate panels) at all four study sites. From Bohn 2012, Bohn et al. 2012.

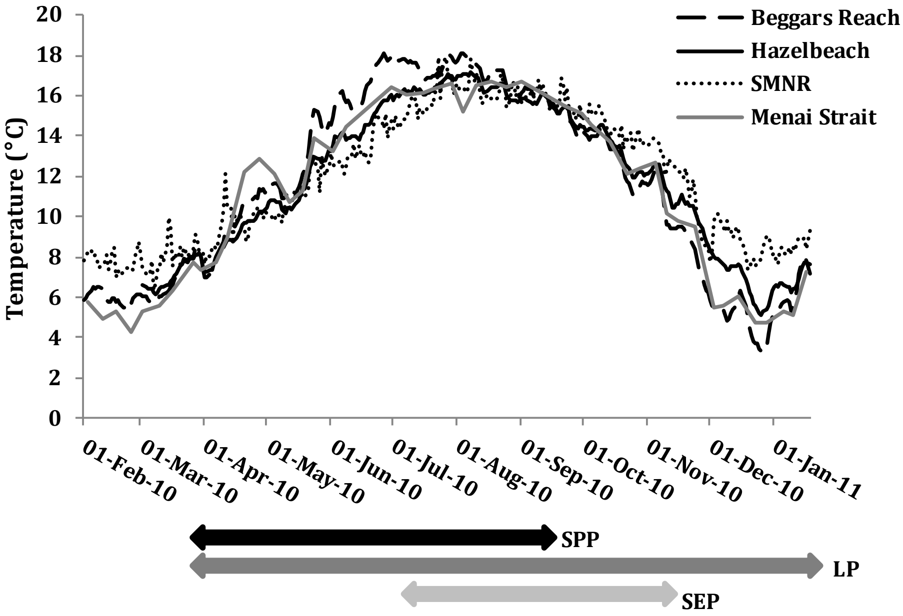

Figure 9. Average daily seawater temperatures at Beggars Reach and Hazelbeach in the Milford Haven Waterway (MHW), South West Wales. For comparison, temperature data from the Skomer Marine Nature Reserve (SMNR, South West Wales) and the Menai Strait (North Wales) outside the Milford Haven Waterway are shown. Data loggers were installed ~1.0-1.3 m above C.D. Arrows indicate approximate length of spawning (SPP), larval (LP) and settlement period (SEP). From Bohn 2012, Bohn et al. 2012.

The spatial and temporal variations in settlement densities are likely the result of varying environmental conditions causing high early post-settlement mortality (EPSM). This is expected in intertidal locations due to repeated exposures to heat, cold and/ or desiccation stress. The recorded patterns may therefore differ largely to those observed subtidally.

Whilst our data suggests that recruitment might have been low as a result of low settlement in the year the study was undertaken, it is important to note that our findings likely only apply to intertidal populations. Settlement may have occurred over a longer time period in the subtidal, requiring further investigations. However, our findings suggest that *C. fornicata*'s reproductive success (larval release, egg brooding) is not impacted at its northern-most population in Wales (the MHW).

A restricted recruitment season could explain its failed northwards spread to date at least partly, but is unlikely the sole cause as the species may form subtidal populations as in the MHW (see previous section). It is likely that other factors may contribute to *C. fornicata*'s limited spread in Wales, e.g. larval supply and the effects of hydrodynamic conditions in the region, larval settlement behaviour and microhabitat choice and its effects on recruitment success. Some of these factors were the subject of experimental work during this PhD study, and will be summarised in the following section.

6. Processes Explaining Recruitment Patterns: Larval Supply, Larval Habitat Selection and Post-Settlement Mortality

6.1. Background

The data that was summarized in the previous two sections demonstrated that the abundance and spread of *C. fornicata* along the Welsh coast line is unlikely limited through restricted reproductive success as a consequence of the prevalent environmental conditions – adult densities, larval densities and the occurrence of egg-brooding females can be very high, at least locally. However, despite its successful reproduction in the MHW, there is little indication for a northwards spread. Another aspect of this PhD project were studies into which biological processes may drive the recruitment of *C. fornicata* in intertidal habitats and potentially limit its colonization of previously unoccupied habitats – the roles of larval supply, larval habitat selection and early post-settlement mortality (EPSM). Of particular interest was the potential use of shells of the blue mussel *M. edulis* as settlement substrata by *C. fornicata* larvae, and how this may affect the recruitment success of the slipper limpet in the intertidal.

6.2. Methods

Several laboratory and field experiments were undertaken between March and September 2011:

i. A field experiment was designed at PE and BR to monitor larval supply as well as biweekly, monthly and seasonal settlement densities (see Bohn et al. (2013a) for details);
ii. Settlement rates and recruitment were also compared on various substrata types (Bohn et al. 2013b);
iii. Juvenile survival was monitored in the intertidal after transplanting plates with known numbers of *C. fornicata* juveniles attached to them (Bohn et al. 2013a);
iv. In laboratory assays, ready-to-settle larvae were offered various settlement substrata to establish whether the distribution of juveniles may be due to active larval choice (Bohn et al. 2013b);

6.3. Main Findings and Conclusions

The results of this part of the study indicated that the recruitment success of *C. fornicata* in intertidal populations is primarily determined by EPSM and the effects of the availability of certain microhabitats on recruitment success, by increasing or decreasing EPSM. Other processes (larval supply, larval habitat selection) are likely less important in determining recruitment and structuring adult densities.

Monitoring of late-stage larval densities (experiment i.) showed that larval supply does not correlate with settlement densities; it does not differ between sites with low (Beggars Reach) and high adult densities (Pennar, Figure 10), thus unlikely being the main factor determining recruitment and adult distribution patterns (Bohn et al. 2012; Bohn et al. 2013a). EPSM was very likely very high: biweekly settlement rates were always moderate only (Figure 10). Also, when comparing settlement densities after various durations on different substrata types (experiment ii., Bohn et al. (2013b)), it becomes apparent that the long-term settlement rates do not equal the sum of biweekly settlement rates: most likely the substrata were ‘wiped clean’ repeatedly (Figure 11).

Similar results were found during the transplanting experiment (iii): mortality was nearing 100% when the juveniles were not in cages that offered protection from various physical and biological stressors (Figure 12).

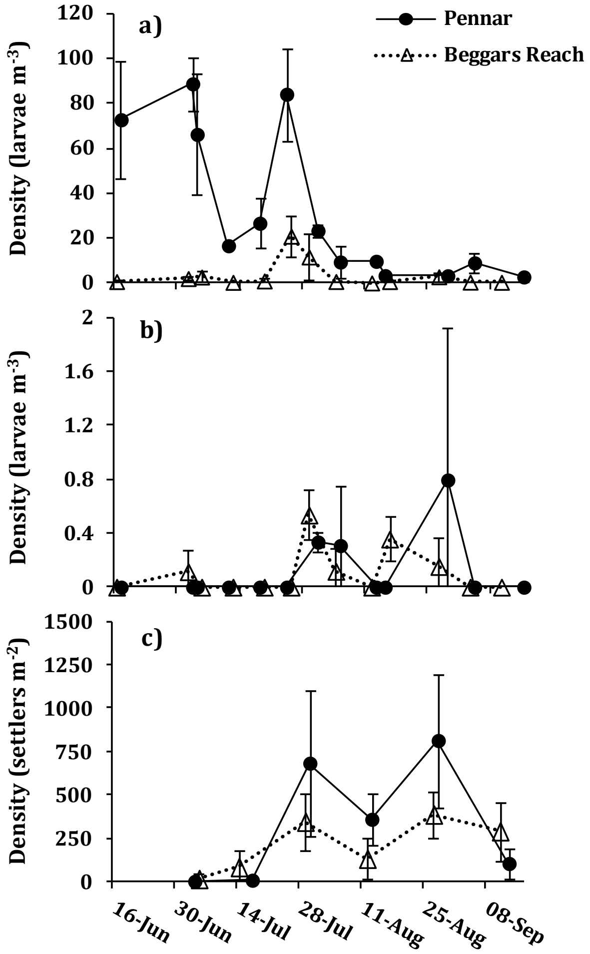

Figure 10(a). *Crepidula fornicata* total larval densities, estimated from duplicate plankton samples, (b) larval supply, i.e. densities of late-stage larvae, and (c) biweekly settlement rates, estimated from the deployment of 12 slate settlement panels in the intertidal zone (~1.2 m above C.D.) at Beggars Reach, a site with low abundance of adult *C. fornicata*, and Pennar, a site with high adult abundance. Mean±SD. From Bohn 2012, Bohn et al. 2013a.

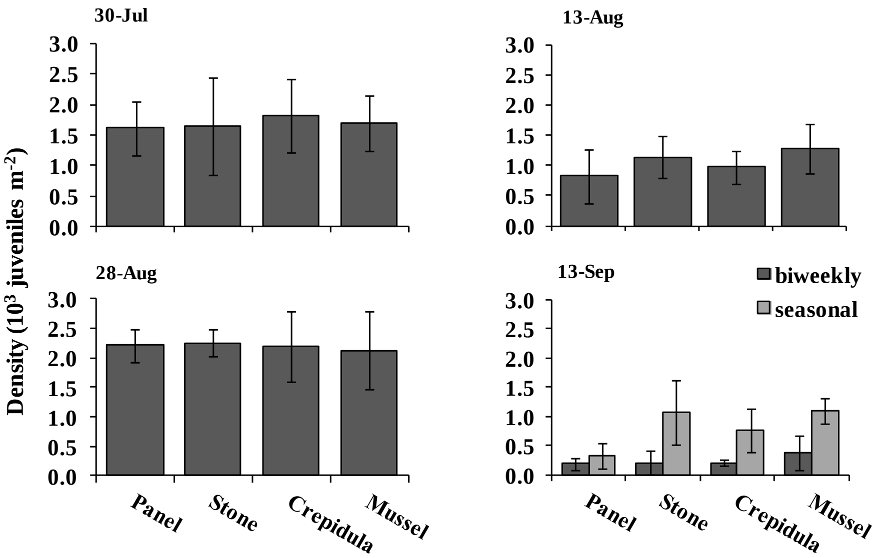

Figure 11. Settlement densities on the different substrata types after two weeks (biweekly) or eight weeks (seasonal) at Pennar. Ordinary roofing slates were used as a base and either left bare ('Panel'), or covered in flat stones ('Stone'), empty *Crepidula fornicata* shells ('Crepidula') or empty *Mytilus edulis* shells ('Mussel'). Mean±SD. From Bohn 2012, Bohn et al. 2013b.

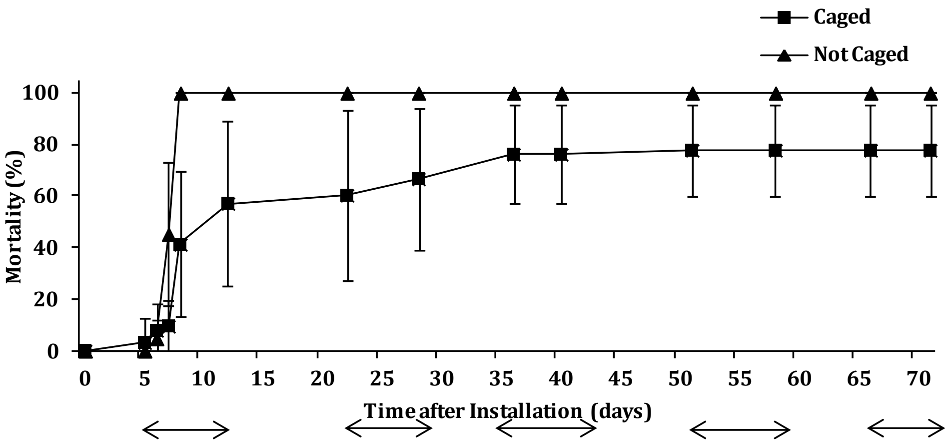

Figure 12. Mortality (%) of juvenile *Crepidula fornicata* at Beggars Reach. Fifteen slate panels with 7 laboratory-reared juveniles attached were transplanted into the low intertidal in July 2011. Panels were caged (n=9) or uncaged (n=6). Data points are average mortality (%) calculated for each sampling event and treatment (mean±SD). Arrows show the periods of spring tides when juveniles were emersed twice a day. From Bohn 2012, Bohn et al. 2013a.

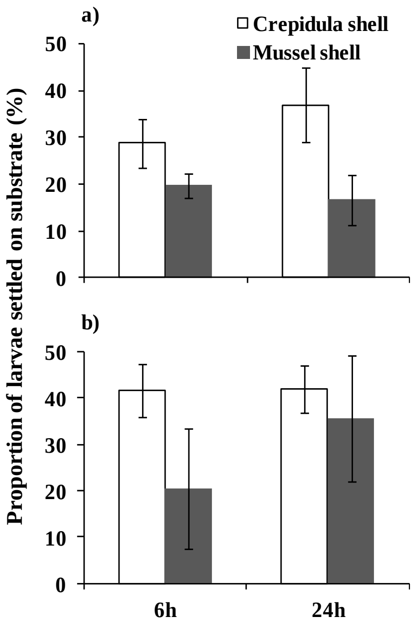

Figure 13. Proportions of newly metamorphosed juveniles settled on the empty *Crepidula* and mussel shells, of the total number of metamorphosed juveniles, during two runs (a and b) of the choice settlement assays. Larvae were offered both substratum types for 6 h or 24 h. Mean±SD. From Bohn 2012, Bohn et al. 2013b.

7. General Discussion and Conclusions

7.1. *Crepidula fornicata's* Broad Scale Distribution and Potential Northwards Spread in Wales

I found no evidence of a northwards spread of *C. fornicata* from its first location of introduction in Welsh coastal waters, the MHW, during the intertidal and subtidal surveys undertaken between 2009 and 2010. The northernmost, established self-sustaining Welsh population still seems to reside within the MHW. However, some individuals were found in the SMNR just outside the MHW between 2008 and 2012 attached to great scallops *Pecten maximus* (Newman et al. 2009; Newman et al. 2012). Mobility of *P. maximus* is highly restricted and its movement by humans is prohibited within the boundaries of the SMNR. This suggests that the *C. fornicata* individuals had settled as larvae after natural dispersal into the SMNR. Some of the stacks that were found in 2012 included egg-brooding females. Females begin to lay eggs in their third year (Deslous-Paoli and Heral 1986); therefore, first settlement in the SMNR must have already occurred prior to 2010. I found that females in South West Wales spawn multiple times. It is thus possible that the females in the SMNR had already released larvae prior to their removal by CCW, increasing the likelihood that larvae have already dispersed even further.

Total numbers of *C. fornicata* reported outside the MHW remain extremely low, despite the high monitoring effort undertaken by CCW and during the survey work of this research project in the last four years. It is likely that I did not cover its full potential non-native range in Mid and North Wales and that sampling effort was not large enough to detect a population at such low densities. Also, most records appeared after the survey work was undertaken, indicating that the northwards range extension beyond the MHW may only have occurred very recently, lowering the chances for its detection. Thus given that *C. fornicata* was recorded in this ria as early as 1953 (Cole and Baird 1953), natural expansion from the area has been extremely slow and limited in extent, a surprising observation in the light of my observations of effective reproductive output in these populations. Limited and slow dispersal is not necessarily a feature of *C. fornicata* in other parts of its introduced range. For example, natural dispersal along and possibly across the English Channel has occurred rapidly (Cole 1952; Orton 1950; Robson 1929).

A combination of factors including prevailing environmental conditions (especially temperature, habitat availability and hydrodynamic conditions), the species' physiological tolerances and biotic interactions determines the geographic range of marine invertebrates. Northern range limits in particular are usually set by sub-optimal prevailing seawater temperatures and sometimes geographic dispersal barriers. Similar processes may restrict the secondary spread of NNS after successful introduction to a novel region (Colautti and MacIsaac 2004; Davis et al. 2001). Restricted reproductive success as a result of low summer seawater temperatures or an insufficient availability of suitable habitat types are unlikely the main reasons for *C. fornicata*'s limited northwards spread, as shown by results from this research project. In particular reproduction and larval release are not limited in the MHW and would likely also not be in areas with similar seawater temperatures (the SMNR and the Menai Strait). However, I found that spatfall in the MHW is restricted to a relatively short time period. This implies that benthic recruitment only occurs at warmer seawater temperatures which could limit its northwards spread if larvae were introduced to areas with cooler seawater temperatures.

7.2. Fine-Scale Distribution and Processes Limiting Intertidal Recruitment

Factors other than environmental conditions or physiological tolerances of the species tend to affect species distributions at a much finer scale. For example, selective larval settlement behaviour, differential larval supply and differential post-settlement mortality or migration can determine the distribution of species among microhabitat types. Although these processes usually operate at a scale of meters, the rejection of certain substrata types by the larvae during settlement or the microhabitat's insufficiency to support juvenile survival may in some cases also explain the absence or limited proliferation of a species in a larger area (Hunt and Scheibling 1997; O'Riordan et al. 2010; Strathmann et al. 1981). In the case of *C. fornicata*, gregarious settlement behaviour is thought to result in the aggregated distribution of adults, enabling reproduction after stack formation (McGee and Targett 1989). I found that levels of seasonal recruitment as well as biweekly and monthly settlement rates were similar at several intertidal shores despite variation in adult abundances. Also, I showed that survival may differ between various substrata types. This suggests that processes after settlement are most important in determining the intertidal distribution of *C. fornicata*. EPSM seems to be high due to repeated exposure of the newly settled individuals to intertidal conditions during spring tide emersion which also may be the reason for the low intertidal recruitment observed in both settlement seasons of 2010 and 2011. If gregarious settlement takes place intertidally, any aggregation of juveniles that may be established during settlement by the larvae is most likely re-distributed by EPSM.

7.3. Intertidal versus Subtidal Processes

Subtidally, adult patterns are likely determined through other processes, as EPSM is likely to be less intense. This is supported by the fact that adult densities between subtidal transects were found to be less variable compared to densities between the different intertidal heights, suggesting that subtidal recruitment is less variable. Work on settlement and post-settlement processes in the subtidal zone was not possible during this research project. Previous work however suggests that larval supply, influenced by local hydrodynamic conditions and the location of adult spawning grounds, may strongly limit the proliferation of *C. fornicata* in the open coast, due to transport of the larvae away from conspecifics (Rigal et al. 2010). It is likely that this also applies to the distribution of *C. fornicata* in the MHW. I found that larval supply (i.e. old, ready to settle larvae) generally did not differ between the intertidal study sites, irrespective of total numbers released at the location (i.e. including the small, newly released larvae). This indicates that strong mixing of the larval pool takes place after release, resulting in homogenous supply between locations, a result matching the observations of Jenkins (2005) on intertidal barnacles over similar spatial scales. Strong tidal currents may result in high dispersal of the larvae and minimise the chances for gregarious attachment, thus slowing down the establishment of self-sustaining populations outside the MHW. The very recent recurrent findings of *C. fornicata* in the SMNR suggest that establishment outside the MHW only occurs now after a long lag-phase of ~50 years, possibly due to high larval dispersal that resulted in low supply of ready-to-settle larvae. The combination of supply of late-stage larvae, hydrodynamic conditions, larval settlement behaviour and the necessity for reproduction through internal fertilization are therefore likely affecting successful stack formation and population spread. EPSM on the other hand, whilst surely important in structuring the vertical distribution and its distribution between microhabitat types, probably is less important in restricting *C. fornicata*'s geographic spread in Wales, as subtidal populations that are unaffected by high levels of EPSM are likely to form.

The roles of habitat availability and composition are also likely to differ between intertidal and subtidal conditions. For example, subtidal densities were positively related to a higher content of the substrata class gravel, most likely as it provides a suitable surface for settlement and aids the creation of new stacks. In the intertidal, on the other hand, I found that high gravel content was indicative of low *C. fornicata* abundance. This may be because gravelly intertidal shores are an indicator of more exposed conditions which is a less suitable environment for *C. fornicata* establishment. The negative effect of high energy environments on *C. fornicata* abundance is likely more pronounced in the intertidal, where environmental conditions are more stressful, due to high levels of EPSM. The importance of microhabitat availability is therefore likely more important in determining recruitment success intertidally than subtidally.

7.4. On its Way North? The Potential Northwards Spread of *Crepidula fornicata* and Advice for Future Work

Ultimately, this research project was designed to understand *C.fornicata*'s absence from certain areas. This is particularly challenging as evidence on whether a NNS could potentially establish and spread outside its current range would ultimately require research based in so far uninvaded areas. This, of course, is impossible due to obvious associated risks of an introduction of the NNS to that area and only leaves the possibility of excluding potential causative factors through investigations undertaken at other study areas. In this research project, I provide evidence that the population inside the MHW is not negatively affected by two of the main processes that usually set the northern range of marine invertebrates: sub-optimal seawater temperatures and habitat availability. Other dispersal barriers may exist, for example hydrodynamic conditions that restrict the potential for stack formation through high larval dispersal. However, it is likely that this will only delay its establishment to the north of the MHW, until propagule pressure is large enough after repeated inoculations with larvae so that successful gregarious settlement can occur. From the result of this PhD research I thus infer that population establishment to the north of the MHW is not unlikely, if transport of larvae or adults through repeated human-mediated introductions or natural larval dispersal occurred repeatedly. If population establishment of *C. fornicata* in Mid and North Wales in fact is possible, it is crucial to use results from studies such as this one to derive advice for future monitoring practices and research work:

Firstly, much of the monitoring and research that was undertaken in the past, including the studies presented in this thesis, have been undertaken in the intertidal. However, in this thesis I showed that the intertidal zone represents a particularly stressful environment for *C. fornicata* and may thus not be suitable to sustain high levels of recruitment. Future monitoring work should focus on subtidal areas in particular, as these are the most likely areas occupied by *C. fornicata*. Also, research is needed on processes that are determining the subtidal distribution of *C. fornicata* and whether these differ to those in the intertidal.

Secondly, the role of larval supply and how this is influenced by hydrodynamic conditions is not fully understood. This would require detailed knowledge on larval swimming behaviour in relation to prevailing hydrodynamic patterns. This information is currently lacking for the case study of *C. fornicata* in South West Wales, UK and research on this topic was beyond the scope of the present study. Future research however would benefit if this was incorporated into studies.

Thirdly, I presented the importance of microhabitat structures and availability of certain habitat types for *C. fornicata* establishment. Although generally ubiquitous in its distribution, it is likely to occur in higher densities in gravel-rich areas subtidally, but not intertidally. Also, I found that different microhabitat types may differ in their suitability to support recruitment. These differences should be kept in mind when targeting specific sites for routine monitoring.

This thesis provided some first insights into environmental conditions, processes and species traits that could explain the limited spread of the potentially harmful non-native gastropod *C. fornicata* in Wales, UK. Work carried out in an area with well-established populations (the MHW) showed little indication for environmental limitations of its spread. Future work should be directed at investigations into the differential recruitment patterns in intertidal and subtidal areas and how larval transport, swimming and settlement behaviour determines settlement patterns.

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10. Appendices

10.1. Appendix 1: List of Ten Survey Stations in the Milford Haven Waterway that were Surveyed for the Vertical Distribution from the Intertidal to the Shallow Subtidal

All stations in the Milford Haven Waterway in South West Wales, UK, in which a minimum of three intertidal and two subtidal transects were surveyed for the presence and abundance of *Crepidula fornicata*. Start and end coordinates are in decimal degrees. Study sites of this project are highlighted in grey.

Site	Intertidal Height/ Distance from Shore+Depth	*Crepidula fornicata* density (mean±SD)	Habitat type	Start Coordinate		End Coordinate		Survey Method + Date
				Long	Lat	Long	Lat	
Dale Intertidal 1	1.0–1.3 m a. C.D.	3.4±3.6	Gravel	51.70430	-5.15901	51.70448	-5.15642	Intertidal, quadrat, 26/02/2009
Dale Intertidal 2	1.0–1.3 m a. C.D.	0.1±0.3	Gravel	51.70426	-5.15550	51.70411	-5.15288	Intertidal, quadrat, 26/02/2009
Dale Intertidal 3	1.0–1.3 m a. C.D.	0	Gravel with boulder	51.70350	-5.15107	51.70414	-5.15256	Intertidal, quadrat, 26/02/2009
Dale Subtidal I	50 m distance, 2 m below C.D.	0	Sediment	51.70462	-5.15337	51.7042	-5.15132	Subtidal, underwater stills camera
Dale Subtidal II	150 m distance, 3 m below C.D	0	Sediment	51.70575	-5.15308	51.70515	-5.15108	Subtidal, underwater stills camera
Dale Subtidal III	500 m distance, 4 m below C.D.	2.2±6.0	Sediment	51.70882	-5.15235	51.70758	-5.15052	Subtidal, underwater stills camera
Sandy Haven Intertidal 1	1.0–1.3 m a. C.D.	0	Sediment	51.72412	-5.10683	51.72023	-5.10436	Intertidal, quadrat, 09/03/2009
Sandy Haven Intertidal 2	1.0–1.3 m a. C.D.	present	Mix of sediment and gravel	51.71737	-5.10583	51.71787	-5.10645	Intertidal, quadrat, 09/03/2009
Sandy Haven Intertidal 3	1.0–1.3 m a. C.D.	0	Sediment	51.71787	-5.10645	51.71911	-5.09612	Intertidal, quadrat, 09/03/2009
Sandy Haven Subtidal I	50 m distance, 2 m below C.D.	0	Sediment	51.71798	-5.10393	51.71653	-5.10433	Subtidal, underwater stills camera

Site	Intertidal Height/ Distance from Shore+Depth	*Crepidula fornicata* density (mean±SD)	Habitat type	Start Coordinate		End Coordinate		Survey Method + Date
				Long	Lat	Long	Lat	
Sandy Haven Subtidal II	n.a. (obstructed by rocks)	---	---	---	---	---	---	---
Sandy Haven Subtidal III	500 m distance, 5 m below C.D.	0	Sediment	51.71433	-5.10012	51.71302	-5.10105	Subtidal, underwater stills camera
Angle Bay Intertidal 1	1.0–1.3 m a. C.D.	23.6±38.1	Gravel	51.69339	-5.05150	51.69202	-5.05190	Intertidal, quadrat, 25/02/2009
Angle Bay Intertidal 2	1.0–1.3 m a. C.D.	0	Sediment	51.69168	-5.05203	51.69014	-5.05297	Intertidal, quadrat, 25/02/2009
Angle Bay Intertidal 3	1.0–1.3 m a. C.D.	2.3±2.6	Gravel	51.68985	-5.05329	51.68882	-5.05494	Intertidal, quadrat, 25/02/2009
Angle Bay Subtidal I	50 m distance, 1 m below C.D.	2.2±7.0	Sediment	51.69033	-5.05393	51.69323	-5.05327	Subtidal, underwater stills camera
Angle Bay Subtidal II	150 m distance, 1 m below C.D.	0	Sediment	51.69062	-5.05535	51.69188	-5.05445	Subtidal, underwater stills camera
Angle Bay Subtidal III	500 m distance, 1 m below C.D.	0	Sediment	51.69137	-5.05932	51.68998	-5.06108	Subtidal, underwater stills camera
Pwllcrochan Intertidal I	1.0–1.3 m a. C.D.	321.0±320.7	Sediment	51.41549	-5.00791	51.41563	-5.00713	Intertidal, quadrat, 11/04/2009
Pwllcrochan Intertidal II	1.0–1.3 m a. C.D.	424.8±281.9	Sediment with gravel	51.41562	-5.00674	51.41553	-5.00613	Intertidal, quadrat, 11/04/2009
Pwllcrochan Intertidal III	1.0–1.3 m a. C.D.	2747.8±3859.3	Sediment with shell	51.41538	-5.00391	51.41518	-5.00550	Intertidal, quadrat, 11/04/2009
Pwllcrochan Subtidal I	50 m distance, 1 m below C.D.	3.3±12.4	Sediment	51.69573	-5.01007	51.6958	-5.01255	Subtidal, underwater stills camera
Pwllcrochan Subtidal II	150 m distance, 1 m below C.D.	4.3±15.6	Sediment	51.69662	-5.01043	51.69692	-5.01270	Subtidal, underwater stills camera

Site	Intertidal Height/ Distance from Shore+Depth	*Crepidula fornicata* density (mean±SD)	Habitat type	Start Coordinate		End Coordinate		Survey Method + Date
				Long	Lat	Long	Lat	
Pwllcrochan Subtidal III	500 m distance, 15 m below C.D.	3.8±10.3	Sediment	51.69965	-5.00918	51.70005	-5.01168	Subtidal, underwater stills camera
Pennar Intertidal 1	1.0–1.3. m a. C.D.	115.6±85.8	Mix of sediment and gravel	51.68890	-4.97481	51.68819	-4.97695	Intertidal, quadrat, 10/03/2009
Pennar Intertidal 3	1.0–1.3 m a. C.D.	10.8±16.3	Mix of sediment and gravel	51.68601	-4.97467	51.68567	-4.97316	Intertidal, quadrat, 10/03/2009
Pennar Intertidal 2 (high)	**1.5-1.8 m a. C.D.**	**76±124.7**	**Mix of sediment, gravel and shell**	**n.a.**	**n.a.**	**n.a.**	**n.a.**	**Intertidal, quadrat, 19/09/2009**
Pennar Intertidal 2 (mid)	**1.0–1.3 m a. C.D.**	**343.0±359.7**	**Mix of sediment, gravel and shell**	**51.68795**	**-4.97707**	**51.68671**	**-4.97661**	**Intertidal, quadrat, 10/03/2009**
Pennar Intertidal 2 (low)	**0.5-0.7 m a. C.D.**	**1031.4±943.4**	**Mix of sediment, gravel and shell**	**n.a.**	**n.a.**	**n.a.**	**n.a.**	**Intertidal, quadrat, 19/09/2009**
Pennar Subtidal I	50 m distance, 5 m below C.D.	1151.8±881.1	Mix of sediment and shell	51.68612	-4.97803	51.68743	-4.97832	Subtidal, underwater stills camera
Pennar Subtidal II	150 m distance, 5 m below C.D.	601.2±576.3	Mix of sediment, gravel and shell	51.68757	-4.9793	51.68943	-4.97983	Subtidal, underwater stills camera
Pennar Subtidal III	n.a. channel too narrow	---	---	---	---	---	---	---
Hazelbeach Intertidal 1	1.0–1.3 m a. C.D.	15.8±13.8	Sediment with gravel	51.70025	-4.97946	51.70087	-4.97731	Intertidal, quadrat, 11/03/2009
Hazelbeach Intertidal 3	1.0–1.3 m a. C.D.	19.7±20.7	Mix of sediment and gravel	51.70336	-4.97144	51.70405	-4.97045	Intertidal, quadrat, 11/03/2009
Hazelbeach Intertidal 2 (high)	**1.5-1.8 m a. C.D.**	**4.4±6.5**	**Mix of sediment and gravel**	**n.a.**	**n.a.**	**n.a.**	**n.a.**	**Intertidal, quadrat, 10/10/2010**
Hazelbeach Intertidal 2 (mid)	**1.0–1.3 m a. C.D.**	**216.3±239.7**	**Mix of sediment and gravel**	**51.70124**	**-4.97610**	**51.70224**	**-4.97422**	**Intertidal, quadrat, 11/03/2009**
Hazelbeach Intertidal 2 (low)	**0.5-0.7 m a. C.D.**	**546.8±238.4**	**Mix of sediment, gravel and shell**	**n.a.**	**n.a.**	**n.a.**	**n.a.**	**Intertidal, quadrat, 10/10/2010**
Hazelbeach Subtidal I	50 m distance, 2 m below C.D.	91.0±80.0	Sediment	51.70043	-4.97645	51.70183	-4.9741	Subtidal, underwater stills camera
Hazelbeach Subtidal II	150 m distance, 5 m below C.D.	97.5±158.6	Mix of sediment, gravel and shell	51.70107	-4.97303	51.70002	-4.97463	Subtidal, underwater stills camera

Site	Intertidal Height/ Distance from Shore+Depth	*Crepidula fornicata* density (mean±SD)	Habitat type	Start Coordinate		End Coordinate		Survey Method + Date
				Long	Lat	Long	Lat	
Hazelbeach Subtidal III	500 m distance, 10 m below C.D.	18.3±24.4	Sediment with shell	51.69773	-4.97178	51.69697	-4.97388	Subtidal, underwater stills camera
Cosheston Intertidal 2	1.0–1.3 m a. C.D.	29.4±39.3	Mix of sediment and gravel	51.70622	-4.90802	51.70703	-4.90763	Intertidal, quadrat, 09/04/2009
Cosheston Intertidal 3	1.0–1.3 m a. C.D.	2.5±5.4	Mussel bed mixed with sediment, gravel, shell	51.70775	-4.90702	51.70812	-4.90597	Intertidal, quadrat, 09/04/2009
Cosheston Intertidal 1 (high)	**1.5-1.8 m a. C.D.**	**8.8±14.8**	**Mix of sediment, gravel and shell**	**n.a.**	**n.a.**	**n.a.**	**n.a.**	**Intertidal, quadrat, 20/09/2009**
Cosheston Intertidal 1 (mid)	**1.0–1.3 m a. C.D.**	**22.5±17.5**	**Mix of sediment, gravel and shell**	**51.70465**	**-4.90882**	**51.70550**	**-4.90825**	**Intertidal, quadrat, 09/04/2009**
Cosheston Intertidal 1 (low)	**0.5-0.7 m a. C.D.**	**328.8±188.0**	**Mix of sediment, gravel and shell**	**n.a.**	**n.a.**	**n.a.**	**n.a.**	**Intertidal, quadrat, 20/09/2009**
Cosheston Subtidal I	50 m distance, 1 m below C.D.	32.2±48.4	Mix of sediment and gravel	51.7071	-4.90873	51.7059	-4.91007	Subtidal, underwater stills camera
Cosheston Subtidal II	150 m distance, 2 m below C.D.	26.9±30.6	Mix of sediment and gravel	51.70645	-4.91082	51.70772	-4.90867	Subtidal, underwater stills camera
Cosheston Subtidal III	250 m distance, 6 m below C.D.	11.4±15.4	Mix of sediment and gravel	51.70658	-4.91237	51.70798	-4.91043	Subtidal, underwater stills camera
Jenkins Point Intertidal 1	1.0–1.3 m a. C.D.	3.10±4.79	Mussel bed mixed with sediment, gravel, shell	51.71698	-4.87970	51.71722	-4.88150	Intertidal, quadrat, 10/04/2009
Jenkins Point Intertidal 2	1.0–1.3 m a. C.D.	6.2±6.3	Mix of sediment and gravel	51.71740	-4.88310	51.71735	-4.88493	Intertidal, quadrat, 10/04/2009
Jenkins Point Intertidal 3	1.0–1.3 m a. C.D.	6.1±5.1	Mix of sediment and gravel	51.71653	-4.88678	51.71552	-4.88727	Intertidal, quadrat, 10/04/2009
Jenkins Point Subtidal I	50 m distance, 5 m below C.D.	63.3±40.3	Mix of sediment, gravel and shell	51.71595	-4.8881	51.71777	-4.88708	Subtidal, underwater stills camera
Jenkins Point Subtidal II	150 m distance, 10 m below C.D.	61.1±70.9	Mix of sediment, gravel and shell	51.71665	-4.88912	51.71833	-4.88793	Subtidal, underwater stills camera

Site	Intertidal Height/ Distance from Shore+Depth	*Crepidula fornicata* density (mean±SD)	Habitat type	Start Coordinate		End Coordinate		Survey Method + Date
				Long	Lat	Long	Lat	
Jenkins Point Subtidal III	n.a. channel too narrow	---	---	---	---	---	---	---
Beggars Reach Intertidal 1	1.0–1.3 m a. C.D.	5.7±9.1	Sediment with gravel	51.73807	-4.89267	51.73840	-4.89412	Intertidal, quadrat, 12/04/2009
Beggars Reach Intertidal 3	1.0–1.3 m a. C.D.	21.8±38.9	Mix of sediment, gravel and shell	51.73967	-4.89695	51.74013	-4.89753	Intertidal, quadrat, 12/04/2009
Beggars Reach Intertidal 2 (high)	**1.5-1.8 m a. C.D.**	**0.2±0.6**	**Sediment with gravel**	**n.a.**	**n.a.**	**n.a.**	**n.a.**	**Intertidal, quadrat, 07/10/2010**
Beggars Reach Intertidal 2 (mid)	**1.0–1.3 m a. C.D.**	**14.6±13.3**	**Sediment with gravel**	**51.73885**	**-4.89510**	**51.73938**	**-4.89650**	**Intertidal, quadrat, 12/04/2009**
Beggars Reach Intertidal 2 (low)	**0.5-0.7 m a. C.D.**	**23.8±34.3**	**Mix of sediment, gravel and shell**	**n.a.**	**n.a.**	**n.a.**	**n.a.**	**Intertidal, quadrat, 07/10/2010**
Beggars Reach Subtidal I	50 m distance, 2 m below C.D.	40.9±57.1	Mix of sediment, gravel and shell	51.73817	-4.89518	51.73913	-4.89765	Subtidal, underwater stills camera
Beggars Reach Subtidal II	150 m distance, 6 m below C.D.	59.6±74.2	Mix of sediment, gravel and shell	51.73718	-4.89518	51.73822	-4.89775	Subtidal, underwater stills camera
Beggars Reach Subtidal III	230 m distance, 5 m below C.D.	114.7±169.4	Mix of sediment, gravel and shell	51.73683	-4.89655	51.73783	-4.89903	Subtidal, underwater stills camera
Black Tar Intertidal 1	1.0–1.3 m a. C.D.	1.4±2.1	Sediment with gravel	51.74588	-4.90045	51.74660	-4.89932	Intertidal, quadrat, 07/04/2009
Black Tar Intertidal 2	1.0–1.3 m a. C.D.	2.1±4.6	Mix of sediment, gravel and shell	51.74708	-4.89872	51.74792	-4.89870	Intertidal, quadrat, 07/04/2009
Black Tar Intertidal 3	1.0–1.3 m a. C.D.	0	Mix of boulder, gravel and sediment	51.74863	-4.89912	51.74952	-4.89957	Intertidal, quadrat, 07/04/2009
Black Tar Subtidal I	n.a. obstructed by moorings	---	---	---	---	---	---	---
Black Tar Subtidal II	150 m distance, 1 m below C.D.	9.0±15.9	Mix of sediment, gravel and shell	51.74413	-4.89845	51.7458	-4.89710	Subtidal, underwater stills camera

Site	Intertidal Height/ Distance from Shore+Depth	*Crepidula fornicata* density (mean±SD)	Habitat type	Start Coordinate		End Coordinate		Survey Method + Date
				Long	Lat	Long	Lat	
Black Tar Subtidal III	350 m distance, 4 m below C.D.	6.1±12.3	Mix of sediment, gravel and shell	51.74287	-4.89768	51.7445	-4.89615	Subtidal, underwater stills camera

10.2. Appendix 2: List of all Subtidal Survey Stations 2009-2010

All stations in the Milford Haven Waterway in South West Wales, UK that were surveyed for the presence and abundance of *Crepidula fornicata* during four subtidal surveys between 2009 and 2010. Start and end coordinates are in decimal degrees.

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
Cardigan Bay (CB), Aug09, Mya	CB - Aberaeron	Mussel Dredge	Mya 34	0.00	n.a.	52.23123	-4.29642	-	-	-	-	7
CB, Aug09, Mya	CB - Aberaeron	Mussel Dredge	Mya 35	0.00	n.a.	52.23272	-4.29400	-	-	-	-	7
CB, Aug09, Mya	CB - Aberaeron	Mussel Dredge	Mya 36	0.00	n.a.	52.23567	-4.28733	-	-	-	-	7
CB, Aug09, Mya	CB - Ina Point	Mussel Dredge	Mya 37	0.00	n.a.	52.21695	-4.33043	-	-	-	-	3
CB, Aug09, Mya	CB - Ina Point	Mussel Dredge	Mya 38	0.00	n.a.	52.21755	-4.32785	-	-	-	-	3
CB, Aug09, Mya	CB - Ina Point	Mussel Dredge	Mya 39	0.00	n.a.	52.21835	-4.32647	-	-	-	-	3
CB, Aug09, Mya	CB - New Quay Shallow	Mussel Dredge	Mya 40	0.00	n.a.	52.21645	-4.32968	-	-	-	-	2
CB, Aug09, Mya	CB - New Quay Shallow	Mussel Dredge	Mya 41	0.00	n.a.	52.21768	-4.32693	-	-	-	-	3
CB, Aug09, Mya	CB - New Quay Shallow	Mussel Dredge	Mya 42	0.00	n.a.	52.21583	-4.33110	-	-	-	-	2
CB, Aug09, Mya	CB - New Quay Bay East	Mussel Dredge	Mya 43	0.00	n.a.	52.21310	-4.35043	-	-	-	-	2

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
CB, Aug09, Mya	CB - New Quay Bay East	Mussel Dredge	Mya 44	0.00	n.a.	52.21250	-4.35132	-	-	-	-	2
CB, Aug09, Mya	CB - New Quay Bay East	Mussel Dredge	Mya 45	0.00	n.a.	52.21312	-4.35347	-	-	-	-	2
CB, Aug09, Mya	CB - New Quay Bay East	Mussel Dredge	Mya 46	0.00	n.a.	52.21358	-4.35368	-	-	-	-	1
CB, Aug09, Mya	CB - New Quay Bay West	Mussel Dredge	Mya 47	0.00	n.a.	52.21697	-4.35770	-	-	-	-	3
CB, Aug09, Mya	CB - New Quay Bay West	Mussel Dredge	Mya 48	0.00	n.a.	52.21732	-4.35897	-	-	-	-	3
CB, Aug09, Mya	CB - New Quay Bay West	Mussel Dredge	Mya 49	0.00	n.a.	52.21793	-4.35942	-	-	-	-	4
CB, Aug09, Mya	CB - New Quay Offshore	Mussel Dredge	Mya 50	0.00	n.a.	52.23465	-4.31980	-	-	-	-	16
CB, Aug09, Prince Madog	CB	Dredge	CB 18	0.00	muddy	52.23655	-4.38575	-	-	-	-	23
CB, Aug09, Prince Madog	CB	Dredge	CB 19	0.00	Slightly sandy mud, some dead shells	52.22562	-4.33988	-	-	-	-	17-20
CB, Aug09, Prince Madog	CB	Dredge	CB 20	0.00	uncertain	52.22677	-4.33090	-	-	-	-	12
CB, Aug09, Prince Madog	CB	Dredge	CB 21	0.00	Pebbles, gravel	52.22442	-4.36420	-	-	-	-	13.5
CB, Aug09, Prince Madog	CB	Dredge	CB 22	0.00	Muddy gravel with cobbles and pebbles	52.22247	-4.39345	-	-	-	-	17

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
CB, Aug09, Prince Madog	CB	Dredge	CB 23	0.00	uncertain	52.21888	-4.38268	-	-	-	-	
CB, Aug09, Prince Madog	CB	Dredge	CB 24	0.00	coarse sand and gravel	52.21940	-4.38140	-	-	-	-	
CB, Aug09, Prince Madog	CB	Beam Trawl	CB 25a	0.00	n.a.	52.17742	-4.47817	-	-	-	-	15.2
CB, Aug09, Prince Madog	CB	Beam Trawl	CB 26a	0.00	n.a.	52.17988	-4.45135	-	-	-	-	
CB, Aug09, Prince Madog	CB	Beam Trawl	CB 27a	0.00	Mud	52.18067	-4.49925	-	-	-	-	
CB, Aug09, Prince Madog	CB	Beam Trawl	CB 28a	0.00	n.a.	52.18150	-4.48250	-	-	-	-	17.1
CB, Aug09, Prince Madog	CB	Beam Trawl	CB 29a	0.00	n.a.	52.18200	-4.46217	-	-	-	-	
CB, Aug09, Prince Madog	CB	Beam Trawl	CB 30a	0.00	n.a.	52.18902	-4.50418	-	-	-	-	
CB, Aug09, Prince Madog	CB	Beam Trawl	CB 31a	0.00	n.a.	52.19272	-4.46197	-	-	-	-	
CB, Aug09, Prince Madog	CB	Beam Trawl	CB 32a	0.00	n.a.	52.18903	-4.44728	-	-	-	-	
CB, Aug09, Prince Madog	CB	Beam Trawl	CB 33a	0.00	Large cobbles	52.14767	-4.62215	-	-	-	-	18.5
CB, Aug09, Prince Madog	CB	Beam Trawl	CB 34a	0.00	Pebbles and small rocks	52.14765	-4.61873	-	-	-	-	18.9

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
CB, Aug09, Prince Madog	CB	Beam Trawl	CB 35a	0.00	n.a.	52.14982	-4.57342	-	-	-	-	14.3
CB, Aug09, Prince Madog	CB	Beam Trawl	CB 36a	0.00	n.a.	52.15915	-4.54515	-	-	-	-	15.3
Skomer Marine Nature Reserve (SMNR), May10, Skalmey	Outside SMNR	Still Images	Box3_Tow1	0.00	see Sciberras 2012	51.70869	-5.24188	51.70671	-5.23989	260	11:00	29.3
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box3_Tow2	0.00	see Sciberras 2012	51.70908	-5.23747	51.70759	-5.23577		05:00	28
SMNR, May10, Skalmey	Martins Haven	Still Images	Martins Haven_Tow1	0.00	see Sciberras 2012	51.74105	-5.23856	51.73902	-5.24029	250	16:00	26.4
SMNR, May10, Skalmey	Martins Haven	Still Images	Martins Haven_Tow2	0.00	see Sciberras 2012	51.74219	-5.24288	51.74018	-5.24512	250	19:00	29.4
SMNR, May10, Skalmey	Martins Haven	Still Images	Martins Haven_Tow3	0.00	see Sciberras 2012	51.74234	-5.24488	51.74063	-5.24728	250	14:00	33.4
SMNR, May10, Skalmey	Martins Haven	Still Images	Martins Haven_Tow4	0.00	see Sciberras 2012	51.74289	-5.25111	51.74078	-5.25227	250	17:00	37.5
SMNR, May10, Skalmey	Martins Haven	Still Images	Martins Haven_Tow5	0.00	see Sciberras 2012	51.74271	-5.25444	51.74164	-5.25629	250	16:00	39.2
SMNR, May10, Skalmey	SMNR	Still Images	Skomer_Tow1	0.00	see Sciberras 2012	51.7466	-5.29232	51.74475	-5.29426	250	23:00	44.2
SMNR, May10, Skalmey	SMNR	Still Images	Skomer_Tow2	0.00	see Sciberras 2012	51.74387	-5.28968	51.74593	-5.28837	250	19:00	43

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
SMNR, May10, Skalmey	SMNR	Still Images	Skomer _Tow3	0.00	see Sciberras 2012	51.74524	-5.28433	51.74342	-5.28662	250	10:00	43.7
SMNR, May10, Skalmey	SMNR	Still Images	Skomer _Tow4	0.00	see Sciberras 2012	51.74414	-5.28127	51.74219	-5.28245	250	13:00	43.1
SMNR, May10, Skalmey	SMNR	Still Images	Skomer _Tow5	0.00	see Sciberras 2012	51.74409	-5.27684	51.74187	-5.27744	250	15:00	44.9
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box1_Tow1	0.00	see Sciberras 2012	51.83765	-5.30694	51.83577	-5.30889	250	21:00	45.4
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box1_Tow2	0.00	see Sciberras 2012	51.83617	-5.29906	51.83473	-5.30202	250	13:00	44.9
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box1_Tow3	0.00	see Sciberras 2012	51.83177	-5.30318	51.83109	-5.30661	250	12:00	46.1
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box1_Tow4	0.00	see Sciberras 2012	51.8268	-5.30528	51.82705	-5.3089	250	10:00	47
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box1_Tow5	0.00	see Sciberras 2012	51.82689	-5.29867	51.82677	-5.30302	300	12:00	47
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box2_Tow1	0.00	see Sciberras 2012	51.76853	-5.28574	51.76634	-5.28622	250	10:00	48.2
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box2_Tow2	0.00	see Sciberras 2012	51.76324	-5.28669	51.76067	-5.28551	250	14:00	
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box2_Tow3	0.00	see Sciberras 2012	51.76637	-5.27635	51.76516	-5.2757	250	10:00	
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box7_Tow1	0.00	see Sciberras 2012	51.79871	-5.30738	51.79663	-5.30555	260	08:00	45.8

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box7_Tow2	0.00	see Sciberras 2012	51.79801	-5.29879	51.79533	-5.29745	310	09:00	45.3
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box7_Tow3	0.00	see Sciberras 2012	51.79262	-5.30422	51.79003	-5.30298	270	10:00	44.4
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box7_Tow4	0.00	see Sciberras 2012	51.78672	-5.30585	51.7843	-5.30519	250	10:00	45.5
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box7_Tow5	0.00	see Sciberras 2012	51.78808	-5.30006	51.78604	-5.29845	250	10:00	43.7
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box8_Tow1	0.00	see Sciberras 2012	51.77135	-5.3009	51.76914	-5.30033	250	11:00	45.4
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box8_Tow2	0.00	see Sciberras 2012	51.76459	-5.30437	51.76236	-5.30386	250	11:00	47.4
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box8_Tow3	0.00	see Sciberras 2012	51.76339	-5.30043	51.76124	-5.29947	250	10:00	45.7
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box8_Tow4	0.00	see Sciberras 2012	51.75743	-5.30562	51.75532	-5.30433	250	12:00	46.9
SMNR, May10, Skalmey	Outside SMNR	Still Images	Box8_Tow5	0.00	see Sciberras 2012	51.7693	-5.30395	51.76845	-5.30065	250	20:00	47.6
Milford Haven Waterway (MHW), Aug10, Pedryn	MHW	Still Images	MH_1	0.00	Mix of Sediment and Gravel	51.67673	-5.16403	51.67570	-5.16523	150	11:00	28.5
MHW, Aug10, Pedryn	MHW	Still Images	MH_2	0.00	Boulder	51.67693	-5.14887	51.67560	-5.14817	150	10:00	15.4
MHW, Aug10, Pedryn	MHW	Still Images	MH_3	0.00	Boulder with Sediment and Gravel	51.67683	-5.13502	51.67555	-5.13368	150	12:00	18.6

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
MHW, Aug10, Pedryn	MHW	Still Images	MH_4	0.00	Gravelly Sediment	51.68540	-5.14962	51.68470	-5.14775	150	10:00	21.3
MHW, Aug10, Pedryn	MHW	Still Images	MH_5	0.00	Boulder with Sediment and Gravel	51.68557	-5.13485	51.68465	-5.13315	150	11:00	16.3
MHW, Aug10, Pedryn	MHW	Still Images	MH_6	0.00	Sediment	51.68557	-5.12018	51.68523	-5.11710	190	15:00	8.8
MHW, Aug10, Pedryn	MHW	Still Images	MH_7	0.00	Gravelly Sediment	51.69413	-5.14880	51.69342	-5.14688	150	14:00	16.1
MHW, Aug10, Pedryn	MHW	Still Images	MH_8	0.00	Mix of Sediment and Gravel	51.69438	-5.13473	51.69365	-5.13278	150	17:00	16.9
MHW, Aug10, Pedryn	MHW	Still Images	MH_9	0.00	Sediment	51.69450	-5.12075	51.69478	-5.11873	150	11:00	19
MHW, Aug10, Pedryn	MHW	Still Images	MH_10	0.00	Sediment	51.70462	-5.15337	51.70420	-5.15132	150	10:00	4.8
MHW, Aug10, Pedryn	MHW	Still Images	MH_11	0.00	Sediment	51.70575	-5.15308	51.70515	-5.15108	150	10:00	5.5
MHW, Aug10, Pedryn	MHW	Still Images	MH_12	2.19 ± 5.99	Sediment	51.70882	-5.15235	51.70758	-5.15052	150	10:00	6.6
MHW, Aug10, Pedryn	MHW	Still Images	MH_13	0.00	Gravelly Sediment	51.70118	-5.13510	51.70102	-5.13287	150	11:00	20.1
MHW, Aug10, Pedryn	MHW	Still Images	MH_14	0.00	Mix of Sediment and Gravel	51.70422	-5.12070	51.70378	-5.11840	150	11:00	13.9
MHW, Aug10, Pedryn	MHW	Still Images	MH_15	4.88 ± 10.57	Gravelly Sediment	51.71205	-5.12803	51.71187	-5.12583	150	12:00	10.2

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
MHW, Aug10, Pedryn	MHW	Still Images	MH_16	0.00	Sediment	51.69888	-5.10825	51.69867	-5.10620	150	08:00	14
MHW, Aug10, Pedryn	MHW	Still Images	MH_17	0.25 ± 1.38	Sediment	51.70010	-5.09313	51.70007	-5.09560	150	09:00	13.5
MHW, Aug10, Pedryn	MHW	Still Images	MH_18	6.31 ± 14.90	Gravelly Sediment	51.70885	-5.10775	51.70907	-5.10535	150	10:00	11.2
MHW, Aug10, Pedryn	MHW	Still Images	MH_19	0.00	Sediment	51.70903	-5.09373	51.71005	-5.09520	150	09:00	10.1
MHW, Aug10, Pedryn	MHW	Still Images	MH_20	0.00	Sediment	51.71798	-5.10393	51.71653	-5.10433	150	08:00	4.6
MHW, Aug10, Pedryn	MHW	Still Images	MH_21	0.00	Sediment	51.71433	-5.10012	51.71302	-5.10105	150	08:00	8.8
MHW, Aug10, Pedryn	MHW	Still Images	MH_25	0.89 ± 3.71	Sediment	51.69025	-5.06473	51.68895	-5.06568	150	08:00	5.1
MHW, Aug10, Pedryn	MHW	Still Images	MH_26	0.00	Sediment	51.69137	-5.05932	51.68998	-5.06108	150	11:00	5
MHW, Aug10, Pedryn	MHW	Still Images	MH_27	0.00	Sediment	51.69062	-5.05535	51.69188	-5.05445	150	11:00	3.7
MHW, Aug10, Pedryn	MHW	Still Images	MH_28	2.22 ± 6.96	Sediment	51.69033	-5.05393	51.69323	-5.05327	150	11:00	3.9
MHW, Aug10, Pedryn	MHW	Still Images	MH_29	2.78 ± 8.55	Sediment with Shell	51.69497	-5.08080	51.69363	-5.07998	150	10:00	13.4
MHW, Aug10, Pedryn	MHW	Still Images	MH_30	1.52 ± 5.03	Sediment	51.69603	-5.06652	51.69450	-5.06623	150	10:00	19

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
MHW, Aug10, Pedryn	MHW	Still Images	MH_31	0.51 ± 2.77	Sediment with Shell	51.69875	-5.05397	51.69758	-5.05492	150	08:00	21.6
MHW, Aug10, Pedryn	MHW	Still Images	MH_32	0.28 ± 1.51	Sediment	51.70092	-5.04010	51.70017	-5.03777	150	09:00	21.4
MHW, Aug10, Pedryn	MHW	Still Images	MH_33	0.25 ± 1.38	Sediment	51.70025	-5.02353	51.70025	-5.02128	150	12:00	17.9
MHW, Aug10, Pedryn	MHW	Still Images	MH_34	3.28 ± 12.36	Sediment	51.69573	-5.01007	51.69580	-5.01255	150	10:00	4.5
MHW, Aug10, Pedryn	MHW	Still Images	MH_35	4.30 ± 15.63	Sediment	51.69662	-5.01043	51.69692	-5.01270	150	10:00	4.3
MHW, Aug10, Pedryn	MHW	Still Images	MH_36	3.79 ± 10.29	Sediment with Shell	51.69965	-5.00918	51.70005	-5.01168	150	09:00	22
MHW, Aug10, Pedryn	MHW	Still Images	MH_37	74.99 ± 80.97	Sediment with Shell	51.69710	-4.99597	51.69768	-4.99807	150	10:00	18.2
MHW, Aug10, Pedryn	MHW	Still Images	MH_38	149.47 ±206.77	Sediment	51.69518	-4.98208	51.69588	-4.98410	150	11:00	21.6
MHW, Aug10, Pedryn	MHW	Still Images	MH_39	601.20 ±576.33	Mix of Sediment, Gravel and Shell	51.68757	-4.97930	51.68943	-4.97983	150	11:00	10.2
MHW, Aug10, Pedryn	MHW	Still Images	MH_40	1151.80 ±881.09	Sediment with Shell	51.68612	-4.97803	51.68743	-4.97832	150	17:00	8.8
MHW, Aug10, Pedryn	MHW	Still Images	MH_41	18.25 ± 24.41	Sediment with Shell	51.69773	-4.97178	51.69697	-4.97388	150	12:00	15.1
MHW, Aug10, Pedryn	MHW	Still Images	MH_42	97.47 ± 158.57	Mix of Sediment, Gravel and Shell	51.70107	-4.97303	51.70002	-4.97463	160	12:00	5.4

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
MHW, Aug10, Pedryn	MHW	Still Images	MH_43_2	90.95 ± 79.98	Sediment	51.70043	-4.97645	51.70183	-4.97410	210	19:00	5.4
MHW, Aug10, Pedryn	MHW	Still Images	MH_45	4.04 ± 6.52	Sediment with Shell	51.70240	-4.95838	51.70253	-4.96087	150	11:00	16.9
MHW, Aug10, Pedryn	MHW	Still Images	MH_46_2	514.39 ±736.98	Mix of Sediment, Gravel and Shell	51.70132	-4.94398	51.70043	-4.94577	150	09:00	19
MHW, Aug10, Pedryn	MHW	Still Images	MH_47	330.28 ±355.81	Mix of Sediment, Gravel and Shell	51.70722	-4.93225	51.70633	-4.92963	200	13:00	23.9
MHW, Aug10, Pedryn	MHW	Still Images	MH_48	224.98 ±174.84	Mix of Sediment, Gravel and Shell	51.70200	-4.92122	51.70145	-4.91843	200	14:00	16.8
MHW, Aug10, Pedryn	MHW	Still Images	MH_49	74.77±141.19	Mix of Sediment, Gravel and Shell	51.70212	-4.91627	51.70357	-4.91450	200	13:00	5
MHW, Aug10, Pedryn	MHW	Still Images	MH_50_2	32.20±48.43	Mix of Sediment and Gravel	51.70710	-4.90873	51.70590	-4.91007	150	10:00	5.4
MHW, Aug10, Pedryn	MHW	Still Images	MH_51	26.90 ± 30.56	Mix of Sediment and Gravel	51.70645	-4.91082	51.70772	-4.90867	200	12:00	3.4
MHW, Aug10, Pedryn	MHW	Still Images	MH_52	11.36 ± 15.38	Mix of Sediment and Gravel	51.70658	-4.91237	51.70798	-4.91043	200	14:00	8.1
MHW, Aug10, Pedryn	MHW	Still Images	MH_53	131.19 ±148.67	Mix of Sediment, Gravel and Shell	51.70877	-4.89480	51.70990	-4.89258	200	15:00	15.1
MHW, Aug10, Pedryn	MHW	Still Images	MH_54	61.09 ± 70.93	Mix of Sediment, Gravel and Shell	51.71665	-4.88912	51.71833	-4.88793	200	16:00	11.8
MHW, Aug10, Pedryn	MHW	Still Images	MH_55	63.31 ± 40.34	Mix of Sediment, Gravel and Shell	51.71595	-4.88810	51.71777	-4.88708	210	14:00	5.5

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
MHW, Aug10, Pedryn	MHW	Still Images	MH_56	378.40 ±433.81	Mix of Sediment, Gravel and Shell	51.72468	-4.88588	51.72648	-4.88615	200	18:00	15.6
MHW, Aug10, Pedryn	MHW	Still Images	MH_57	98.16 ±152.16	Mix of Sediment, Gravel and Shell	51.73402	-4.88603	51.73518	-4.88830	200	18:00	5.1
MHW, Aug10, Pedryn	MHW	Still Images	MH_58	59.55 ± 74.16	Mix of Sediment, Gravel and Shell	51.73718	-4.89518	51.73822	-4.89775	200	12:00	9.1
MHW, Aug10, Pedryn	MHW	Still Images	MH_59	40.93 ± 57.13	Mix of Sediment, Gravel and Shell	51.73817	-4.89518	51.73913	-4.89765	200	13:00	4.9
MHW, Aug10, Pedryn	MHW	Still Images	MH_60	114.70±169.37	Mix of Sediment, Gravel and Shell	51.73683	-4.89655	51.73783	-4.89903	200	12:00	10
MHW, Aug10, Pedryn	MHW	Still Images	MH_61_2	8.96 ± 15.88	Mix of Sediment, Gravel and Shell	51.74413	-4.89845	51.74580	-4.89710	200	18:00	5
MHW, Aug10, Pedryn	MHW	Still Images	MH_62	6.12 ± 12.25	Mix of Sediment, Gravel and Shell	51.74287	-4.89768	51.74450	-4.89615	200	15:00	7.3
MHW, Aug10, Pedryn	MHW	Still Images	MH_63	0.00	Sediment	51.75437	-4.89640	51.75247	-4.89725	180	15:00	6.4
MHW, Aug10, Pedryn	MHW	Still Images	MH_64	0.00	Sediment	51.76507	-4.89492	51.76328	-4.89523	200	15:00	7.4
MHW, Aug10, Pedryn	MHW	Still Images	MH_E1	0.00	Sediment	51.69418	-5.10185	51.69430	-5.10413	150	09:00	16.7
MHW, Aug10, Pedryn	MHW	Still Images	MH_E2	2.31 ± 10.02	Sediment	51.69302	-5.08897	51.69290	-5.09115	150	09:00	7.3
MHW, Aug10, Pedryn	MHW	Still Images	MH_E3	6.53 ± 21.06	Sediment	51.69167	-5.07462	51.69192	-5.07690	150	10:00	6.6

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
MHW, Aug10, Pedryn	MHW	Still Images	MH_E4	0.00	Sediment	51.70598	-5.02783	51.70560	-5.03008	150	11:00	5
MHW, Aug10, Pedryn	MHW	Still Images	MH_E5	430.38 ±585.51	Sediment with Shell	51.69453	-4.98963	51.69420	-4.98742	150	09:00	7.6
MHW, Aug10, Pedryn	MHW	Still Images	MH_E6	76.35 ±169.11	Mix of Sediment, Gravel and Shell	51.70007	-4.96460	51.70042	-4.96258	150	09:00	7.3
MHW, Aug10, Pedryn	MHW	Still Images	MH_E7	112.37 ±193.30	Mix of Sediment, Gravel and Shell	51.70018	-4.95308	51.70002	-4.95073	150	09:00	5.2
MHW, Aug10, Pedryn	MHW	Still Images	MH_E8	19.33 ±35.27	Mix of Sediment, Gravel and Shell	51.70115	-4.94567	51.70255	-4.94348	150	08:00	6.2
MHW, Aug10, Pedryn	Entrance of MHW	Still Images	Outside_1	0.00	Mix of Sediment, Gravel and Boulder	51.69702	-5.23440	51.69827	-5.23513	150	10:00	34.5
MHW, Aug10, Pedryn	Entrance of MHW	Still Images	Outside_3	0.00	Mussel bed mixed with sediment, gravel, shell and boulder	51.67767	-5.23568	51.67833	-5.23760	150	10:00	50.5
MHW, Aug10, Pedryn	Entrance of MHW	Still Images	Outside_4	0.00	Mussel bed mixed with sediment, gravel, shell and boulder	51.67810	-5.20737	51.67927	-5.20845	150	12:00	37
MHW, Aug10, Pedryn	Entrance of MHW	Still Images	Outside_7	0.00	Mix of sediment, gravel and shell	51.65938	-5.20587	51.66053	-5.20477	150	15:00	51.6
MHW, Aug10, Pedryn	Entrance of MHW	Still Images	Outside_8	0.00	Mix ofsediment, gravel and shell	51.65972	-5.17783	51.66035	-5.17983	150	08:00	48
MHW, Aug10, Pedryn	Entrance of MHW	Still Images	Outside_9	0.00	Mix of Sediment and Gravel	51.65933	-5.15025	51.66017	-5.15212	150	11:00	42.5

Survey (Location, Date, Boat)	Location	Survey Method	Sample ID	*Crepidula fornicata* density (mean±SD)	Habitat	Start Coordinate		End Coordinate		Tow length (m)	Tow length (min)	Depth (m)
						Long	Lat	Long	Lat			
MHW, Aug10, Pedryn	Entrance of MHW	Still Images	Outside _10	0.00	Mix of Sediment, Gravel and Boulder	51.65927	-5.12042	51.66055	-5.12130	150	18:00	33.7
MHW, Aug10, Pedryn	Entrance of MHW	Still Images	Outside _11	0.00	Sediment	51.65920	-5.09218	51.65982	-5.09010	150	12:00	21.9

Data Archive Appendix

Data outputs associated with this project are archived at [NRW to insert relevant server pathway and / or reference numbers] on server–based storage at Natural Resources Wales.

Or

No data outputs were produced as part of this project.

The data archive contains: [Delete and / or add to A-E as appropriate. A full list of data layers can be documented if required]

[A] The final report in Microsoft Word and Adobe PDF formats.

[B] A full set of maps produced in JPEG format.

[C] A series of GIS layers on which the maps in the report are based with a series of word documents detailing the data processing and structure of the GIS layers

[D] A set of raster files in ESRI and ASCII grid formats.

[E] A database named [name] in Microsoft Access 2000 format with metadata described in a Microsoft Word document [name.doc].

[F] A full set of images produced in [jpg/tiff] format.

Metadata for this project is publicly accessible through Natural Resources Wales' Library Catalogue http://194.83.155.90/olibcgi by searching 'Dataset Titles'. The metadata is held as record no [NRW to insert this number]

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