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The invasive, non-native slipper limpet *Crepidula fornicata* is poorly adapted to sediment burial

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A B S T R A C T

The American slipper limpet *Crepidula fornicata* is an invasive, non-native species (INNS) abundant along the European coast. Its further distribution may be facilitated by activities such as dredging and spoil disposal, and the aim of this study was to assess whether *C. fornicata* is able to survive sediment burial. The slipper limpet was found attached to hard substratum in intertidal areas, but it was absent at a nearby subtidal dredge spoil site. In laboratory experiments 22% of *C. fornicata* emerged when buried under a 2 cm sediment-layer; only half of them survived. When buried under ≥6 cm none re-surfaced or survived. The results provided evidence that *C. fornicata* is poorly adapted to adjust its vertical position in sediment and is killed by sudden burial underneath 2 to 6 cm of sediment. The combined laboratory experiments and field surveys suggested that *C. fornicata* has limited scope to survive the dredge spoil disposal process.

1. Introduction

1.1. Invasive non-native species

Non-native species (NNS) are not naturally found within a certain area and are also referred to as "non-indigenous", "alien" and "exotic" species (Manchester and Bullock, 2000). An invasive NNS (INNS) is a species that passed all stages of the invasion process including its release into a new environment, establishment and subsequent spread (Richardson et al., 2000; Bohn et al., 2015). INNS can cause harm to the environment and are regarded as one of the biggest threats to global biodiversity by outcompeting and dominating native species and often entire ecosystems (Thouzeau et al., 2000; Bax et al., 2003). Globalisation and human activity have both accidentally and deliberately transported INNS across major geographic barriers for centuries (Decottignies et al., 2007; Mineur et al., 2012). It is estimated that at any one time, 10,000 species are in transit around the world in ballast water, making it almost impossible to control the spread of species to new habitats (Manchester and Bullock, 2000; Bax et al., 2003). > 90 marine and brackish NNS have been identified in Britain and Ireland alone (Cook et al., 2015). Many NNS bring diseases, modify habitats and affect ecosystem functioning and can have indirect interactions with intermediate and top predators (Cook et al., 2015; Grason and Buhle, 2016). The extent to which a NNS impacts a community depends on its interactions with native species (Grason and Buhle, 2016).

The American slipper limpet, *Crepidula fornicata* is one of the most invasive non-native sessile invertebrates in Europe (Dupont et al., 2007). It is a suspension-feeding marine gastropod native to North America (Hancock, 1969; Clark, 2008). Its shell grows up to 50 mm in length, 25 mm in height, with a kidney shaped aperture and individuals attach to each other forming stacks (Clark, 2008) (Fig. 1). Human-mediated transport and its long-lived, free-swimming planktonic larvae have caused it to spread rapidly throughout Europe (Untersee and Pechenik, 2007; Rigal et al., 2010). In the UK, *C. fornicata* extends from Pembrokeshire to Yorkshire including the Bristol Channel (Clark, 2008). Hotspots include the Solent and Essex where *C. fornicata* forms a carpet over the seafloor, producing cohesive pseudofaeces as it filter feeds (Hancock, 1969; Thouzeau et al., 2000; Clark, 2008; Syvret and FitzGerald, 2008). In the UK *C. fornicata* was introduced to Essex attached to oysters, *Crassostrea virginica*, between 1887 and 1890 and is now well known as their most abundant competitor (Orton, 1912; Clark, 2008; Bohn et al., 2013). The limpet can be found in most oyster producing areas in England and Wales where it occurs in enormous numbers (Hancock, 1969; Thieltges, 2005; Clark, 2008). The limpet competes with oysters and other suspension feeders for space and food (Hancock, 1969; de Montaudoüin et al., 2001; Moulin et al., 2007). Populations of the blue mussel *Mytilus edulis* can decrease dramatically when overgrown by slipper limpets (Nehls et al., 2006). The influence of *C. fornicata* on commercially important shellfish species can have huge economic implications (Thieltges, 2005). *C. fornicata* modifies the nature and structure of habitat through biodeposition and the accumulation of its shells, often creating an unsuitable substratum for many

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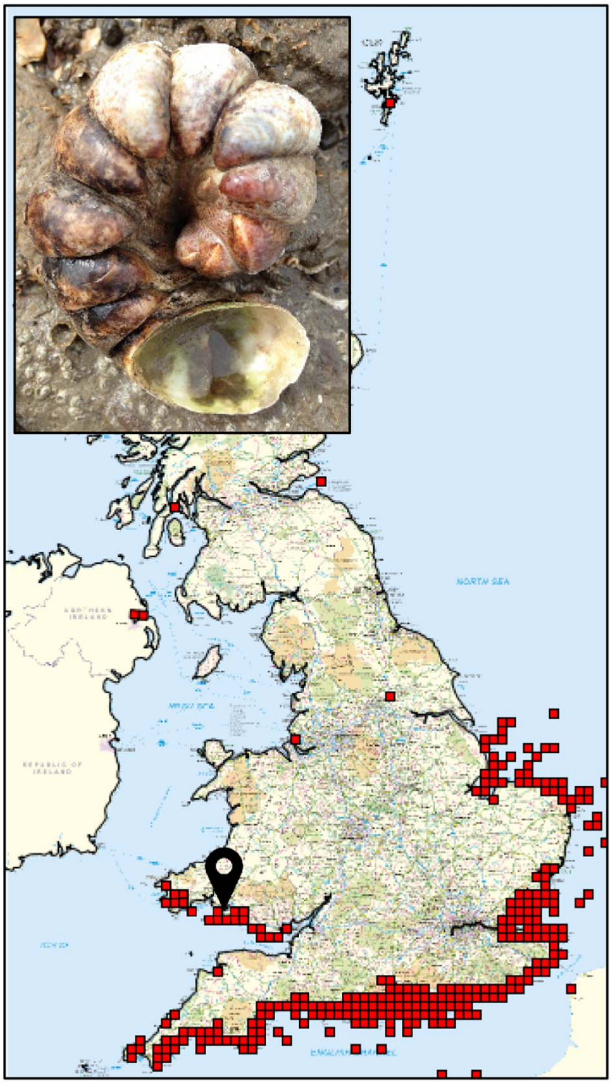

Fig. 1. *Crepidula fornicata* stack (image) and records of the species' presence in the UK (map from National Biodiversity Network Gateway UK, 2011). Location icon marks study site Swansea Bay, Wales, UK.

native species (Thieltges, 2005; Valdizan et al., 2009).

Its success can be explained by its strong reproductive viability and opportunistic feeding strategies together with the fact that it has few natural predators (Dupont et al., 2007; Clark, 2008; Syvret and FitzGerald, 2008; Valdizan et al., 2009). It is also tolerant to a wide range of salinities (Syvret and FitzGerald, 2008; Rigal et al., 2010) and is found attached to a variety of substrates in the low intertidal and subtidal (Bohn et al., 2013; Cook et al., 2015). *C. fornicata* is a protandrous hermaphrodite that breeds from February to October and has a long-distance dispersal ability (Dupont et al., 2007). The availability of suitable substratum for settlement is crucial in determining its distribution (Barnes et al., 1973).

1.2. Methods of controlling the spread of *Crepidula fornicata*

Numerous methods have been employed to eradicate *C. fornicata*. Earliest attempts focused on eradication by dumping dredged *C. fornicata* above the high water mark and removing them by hand (Hancock, 1969; Bolam et al., 2010; Cook et al., 2015). Since the 1950s, brine dipping has been trialed (Syvret and FitzGerald, 2008); brine immersion for over 5 min resulted in 100% mortality (Syvret and FitzGerald, 2008). This method is however not practical, especially for large amounts of material (Cook et al., 2015). Other attempts crushed *C. fornicata* stacks and fed their flesh to scavenging birds, or it was used as whelk bait (Hancock, 1969; Clark, 2008; Valdizan et al., 2009). Chain riddles were used to break up stacks in Kent and Essex (Cook et al., 2015). This disturbance had, however, the unintended consequence to act as a dispersal vector for *C. fornicata*, further exacerbating the problem (Clark, 2008; Cook et al., 2015). The slipper limpet was successfully eradicated from a commercial mussel lay in Wales, UK, by smothering with seed mussels of double the usual stocking density (Syvret and FitzGerald, 2008; Cook et al., 2015). In the United States, INNS including *C. fornicata*, have been smothered with heavy duty polythene sheeting and then relayed with oysters (Hancock, 1969), but this method was extremely costly and time consuming.

1.3. Dredge spoil disposal

The disposal of dredged material during the construction and maintenance of coastal infrastructure represents a significant problem in coastal management (Marmin et al., 2014; Callaway, 2016). > 40 million tons of sediment must be disposed of appropriately each year (Bolam, 2011). Following dredge spoil dumping, changes in benthic communities are commonly reported since many species are smothered with sediment (Hutchinson et al., 2016). The greatest ability to emerge from burial for a range of macroinvertebrates is 2 cm depth (Hendrick et al., 2016). Changes in the community structure are not restricted to the site of disposal and are often found kilometers away from the dumping area (Hendrick et al., 2016). The ability of species to escape burial through vertical migration is not well understood (Bolam, 2011). The tolerance and responses of species to burial are species specific and cannot be generalized; species tolerance to burial depends on its adaptation and behaviour (Hendrick et al., 2016). Following burial, benthic invertebrates may recover by vertical or lateral migration and/or the planktonic recruitment of larvae (Bolam, 2011). Emergence from sediment burial is central to the chance of survival since failure to re-surface is assumed to eventually lead to death (Bolam, 2011; Hendrick et al., 2016).

During the construction and maintenance of coastal infrastructure dredged spoil is disposed at designated sites. Dredged material may contain INNS, but legislation prohibits their release and spread (http://www.legislation.gov.uk/ukpga/1981/69/section/14). However, *C. fornicata* may not survive the dredging and disposal process. We hypothesized that smothering methods may kill any alive *C. fornicata* in dredge spoils. While some speculative assessment of the intolerance of *C. fornicata* to burial has been made there is a lack of evidence to support assumptions for informed management decisions (Johnson, 1972; Rayment, 2008; Cook et al., 2015; Syvret and FitzGerald, 2008). The aim of this study was therefore to assess the mortality of *C. fornicata* under sediment burial to determine whether smothering could be an effective way to prevent its spread. A multifactorial experiment was conducted to test burial intolerance using various burial depths and durations, and both stacks and individuals of *C. fornicata* were assessed.

This study had the following objectives

i) Identification of the preferred habitat of *C. fornicata*;
ii) Assessment of *C. fornicata* presence at a dredge spoil disposal site;
iii) Quantification of survival rates of *C. fornicata* under different sediment burial regimes.

2. Materials and methods

2.1. Study site

Intertidal and subtidal *C. fornicata* surveys were carried out in Swansea Bay, South Wales, UK (Fig. 2). Swansea Bay is located along the northern coastline of the Bristol Channel and has the second largest tidal range in the world with mean spring tides of 8.5 m and neap tides