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Research Article

Alien species of *Bugula* (Bryozoa) along the Atlantic coasts of Europe

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Abstract

Three apparently non-native species of *Bugula* occur in marinas and harbours in Atlantic Europe. The most common, *B. neritina*, was known from a few sites in southern Britain and northern France during the 20th century, following its discovery at Plymouth by 1911. During the 1950-60s it was abundant in a dock heated by power station effluent at Swansea, south Wales, where it flourished until the late 1960s, while water temperatures were 7-10°C above ambient. It disappeared after power generation ceased, when summer temperatures probably became insufficient to support breeding. Details of disappearances have not been recorded but *B. neritina* was not seen in Britain between c1970 and 1999. Since 2000, it has been recorded along the south coast of England, and subsequently in marinas in the southern North Sea, Ireland and southern Scotland, well to the north of its former range, as well as along the Atlantic coast from Spain to The Netherlands. It has also been introduced to outlying localities such as the Azores and Tristan da Cunha. We report that this rapidly spreading form has the same COI haplotype as *B. neritina* currently invasive elsewhere in the world. *B. simplex* has been reported less, with 1950s records from settlement panels in some Welsh docks. It has not been targeted in most recent marina surveys but has been observed in southwest England, Belgium and The Netherlands. There are almost no recent records of *B. stolonifera*, though it was probably introduced to a few British and Irish ports prior to the 1950s. Its current status in most of western Europe is unknown but it has been reported as expanding throughout most of the world during the last 60 years. Having poorly known distributions, *B. simplex* and *B. stolonifera* should be recorded during future monitoring of alien species in Atlantic Europe. Illustrations to aid identification are included for all three species.

Key words: *Bugula, neritina, simplex, stolonifera,* invasive, haplotype, Western Europe

Introduction

Alien marine invertebrates have increased in Atlantic European waters in recent decades (Galil et al. 2009). The increased volume of shipping, perhaps aided by quicker transit times, has brought species on ships' hulls (Minchin and Gollasch 2003), and in ballast water and its sediments (Carlton 1985). More recently, species are increasingly being transported on yachts and other small vessels (Ashton et al. 2006; Minchin et al. 2006). Following arrival, species may then spread into other habitats by a wider range of pathways (Minchin et al. 2005), where they may impact on native species. Thus, the alien ascidian *Botrylloides violaceus* Oka, 1927, which has been introduced to numerous marinas, appeared in Milford Haven (a major oil and LPG terminal) during the last decade. It now occurs in abundance on the rocky shores around Pembroke Dock, encrusting the fronds of *Fucus serratus* Linnaeus, 1753, which already support a dense epibiota (Ryland 2002) with which it is successfully competing for space. *B. violaceus* has similarly colonized natural shores in Plymouth Sound, following initial detection in local marinas. Another source of introductions has been the import of non-native oysters (*Crassostrea virginica* (Gmelin, 1791), *C. gigas* (Thunberg, 1793)) accompanied by pest species such as *Crepidula fornicata* (Linnaeus, 1758) and *Urosalpinx cinerea* (Say, 1822) (see Minchin 2007a). A recent bryozoan example is *Watersipora subtorquata* (d'Orbigny, 1852),

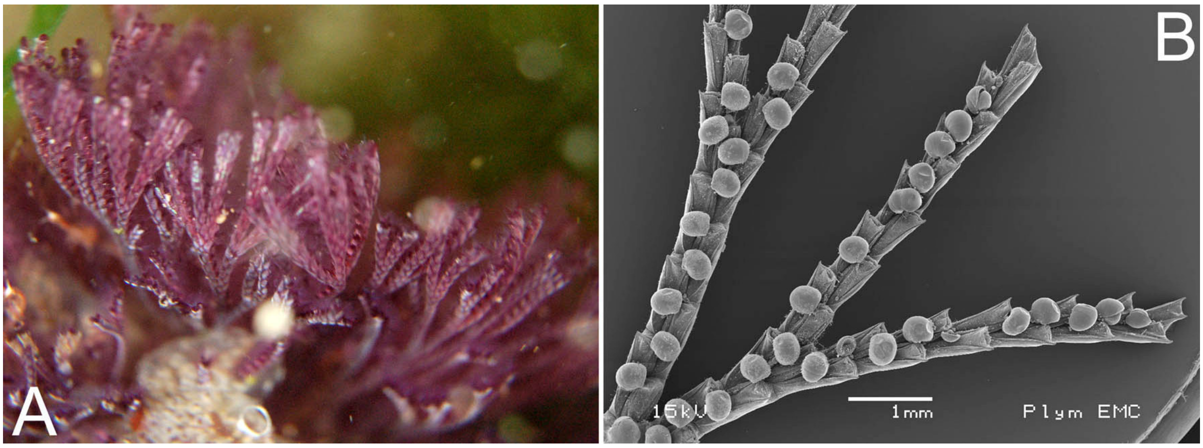

Figure 1. *Bugula neritina*. A, living material to show distinctive pigmentation; Burghsluis, The Netherlands, 2009 (photo: HDeB); B, SEM, Plymouth (photo: ALEY and JDDB).

Figure 2. Colour morphs of *Bugula neritina*: normal, with purple pigmentation (left) and pale brown, lacking purple pigmentation (right). Both colonies from Queen Anne's Battery marina, Plymouth, 2009 (photo: JDDB).

brought to French shores with *C. gigas* (d'Hondt 1984; De Blauwe 2000; Ryland et al. 2009). In part of Brittany this species has become abundant, has spread away from the oyster beds, and now competes for under-boulder space with native encrusting species (De Blauwe 2005; Ryland et al. 2009).

In this paper we update the known distributions in Britain and Ireland of non-native bryozoans of the genus *Bugula* Oken, 1815, especially the warm-water species *B. neritina* (Linnaeus, 1758). Two other species of *Bugula* that appear clearly to be non-native in Western Europe are *B. simplex* Hincks, 1886, and *B. stolonifera* Ryland, 1960, although no-one in Britain has been recording them as such. Neither species is difficult to identify and full descriptions are available (Ryland 1960; Prenant and Bobin 1966; Zabala 1986, 1988; Hayward and Ryland 1990, 1998; Ryland and Hayward 1991; De Blauwe 2009); nevertheless, for convenience with recognition, we include photographs and scanning electron micrographs (SEMs) of all three species (Figures 1, 6 and 8). It should be noted, however, that several native species of *Bugula* also occur in the region, some known to occur in fouling communities, and a key including all candidate species (e.g.

Hayward and Ryland 1998) should be used before concluding that a non-native species has been found.

Bugula neritina

Historical review

Linnaeus (1758), listing Ellis (1755), gave the habitat of *Sertularia neritina* as Mediterranean and American seas, but Ellis had given the locality for his specimens as America – though precisely where is uncertain (Ellis 1753/1754). Good descriptions, based on Mediterranean material, are available in several languages (Gautier 1962; Ryland 1965; Prenant and Bobin 1966; Riedl 1970; Occhipinti Ambrogi 1981; Zabala 1986; De Blauwe 2009). British-sourced specimens were used for the descriptions appearing in Ryland (1960), Ryland and Hayward (1977) and Hayward and Ryland (1990, 1998), while Winston and Woollacott (2008) have recently provided a description, illustrated with SEMs, of material from Florida. Particularly notable in most freshly collected material is the purple coloration (Villela 1948), though not always as vivid as in Figure 1A and adverse environmental conditions may cause its loss. Zooids lack spines and avicularia, and the ovicells are oriented obliquely to the branch axis. *Bugula neritina* is today widely distributed in warm-temperate and subtropical coastal waters. It is a well known fouling organism in the Mediterranean Sea and features in several studies there and elsewhere (Ryland 1965, 1967; Geraci 1976; Occhipinti Ambrogi 1981). These studies led to the discovery of 'placental' nutrition of embryos (Woollacott and Zimmer 1975), of sibling attraction during settlement (Keough 1984) and – most recently – of bryostatin (Newman 1996; Wöss 2005), actually synthesised by symbiotic bacteria and now a major research endeavour (see Winston and Woollacott 2008). (Bryostatin-like compounds produced by symbiotic bacteria have more recently been reported in *B. simplex* (Lim and Haygood 2004).) The status of *B. neritina* as a ship-fouling organism has been addressed widely, particularly in regions – such as Australia, New Zealand and Hawaii – to which it appears to have been introduced on shipping (discussion in Ryland 1967 and references therein), including the known transport to Britain (where it was already established) in the 1950s on ships from Australia (Ryland 1960).

Studies encoding the DNA sequence of cytochrome c oxidase subunit I (COI) have indicated that *B. neritina* consists of at least three genetically distinct (although morphologically very similar) putative species along the coasts of the USA, with generally congruent differences in their ã-proteobacterial symbionts and the associated bryostatin products (Davidson and Haygood 1999; McGovern and Hellberg 2003; Mackie et al. 2006). Based on COI sequences, McGovern and Hellberg (2003) distinguished two cryptic, allopatric species on the eastern seaboard of the USA; these occupied northern and southern regions either side of Cape Hatteras, which could suggest a difference in thermal requirements. The southern form on the Atlantic coast (also present on the west coast of the USA) is globally distributed and is considered to have undergone widespread introduction as a fouling organism. Distinct purple and brown morphs of *B. neritina* have been recorded from the Mediterranean (Port of Naples and Corfu), Plymouth, Ireland and Spain (Figure 2). These colour forms can co-occur attached to the same substrate, suggesting that they are not ecophenotypic variants, but it is not known if they have taxonomic significance.

Bugula neritina was a known immigrant to southern Britain and northern France (Brest and St-Malo) in the mid-20th century (Ryland 1960; Prenant and Bobin 1966) but, by the end of the century, it was thought to be "No longer established [in Britain] in the wild" (Eno et al. 1997). The earliest occurrences, however, are not well documented. Ryland (1960) summarized them as: "From Shoreham to Milford Haven, from docks and harbours, especially where the water is artificially warmed". This information had been provided by DJ Crisp who, with AP Austin, was studying settlement on panels at various sites in southern Britain. In fact, since Crisp and Austin never published any results, no intermediate sites between Shoreham and Milford Haven are now known from the 1950s and 60s, although power stations cooled by sea water existed at Camber Dock, Portsmouth, and Holes Bay, Poole (Markowski 1959). [Sadly, after a distinguished career in Canada, Prof. Alan Austin died shortly before our attempt to contact him in 2009.] The supposed importance of artificially warmed sites appears to lie solely with the Harbour Canal at Shoreham, which was warmed by the discharge from the Brighton 'B' power station (Crisp and Molesworth 1951; Markowski 1959), and the well described

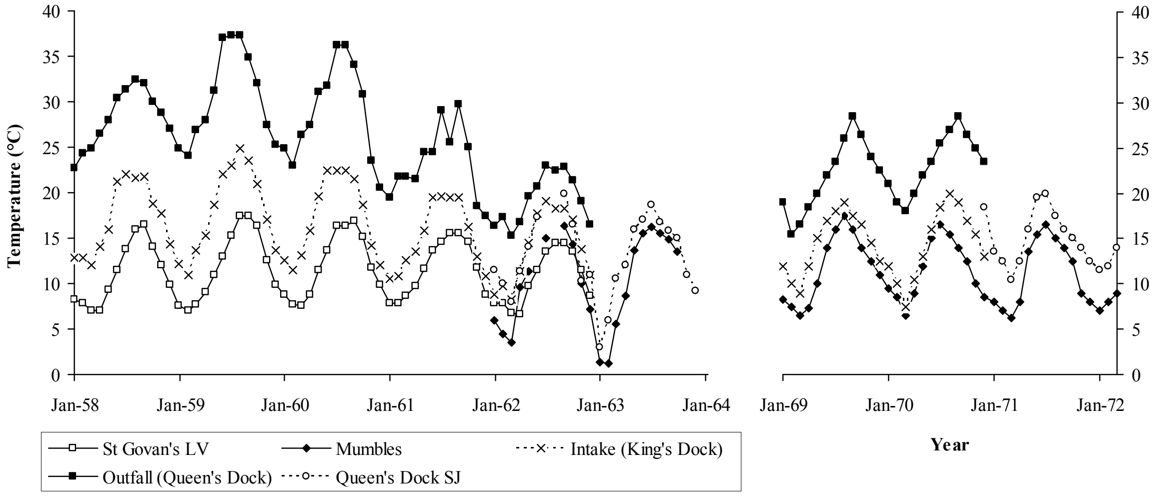

Figure 3. Water temperatures in Swansea dock system 1958–72, during the period of full generation and declining use of the Tir John Power Station. The cooling water intake is at the closed end the King's Dock and the outfall at the closed end of the adjacent Queen's Dock. Some temperatures refer to the Service Jetty (SJ) in the Queen's Dock. Ambient sea temperatures were recorded at St Govan's Light Vessel or Mumbles Pier.

Queen's Dock in Swansea (Naylor 1957; Ryland 1960, 1965), discussed below. In view of several inaccuracies in the available literature, a brief summary of the early occurrences will be given.

The first report of *Bugula neritina* in England was from Plymouth early in the 20th century, where M Hasper conducted trials with the species in 1911 (Hasper 1912) and Orton (1914) observed that the species "grows into huge colonies in the inner basin at the Great Western Docks" (later known as Millbay Docks) in that city (see map in Marine Biological Association 1957). Its presence had not been recorded in the 1904 edition of the *Plymouth Marine Fauna* (Marine Biological Association 1904) though, of course, it may have been overlooked. Harmer (1897), in a note on new or rare British bryozoans, written after a visit to Plymouth, did not record it either. In the second edition of the *Fauna* (Marine Biological Association 1931), it was recorded by Anna Hastings (who noted that it released larvae) as having been dredged in the Sound, and by Alice Heath (apparently unaware of Orton's (1914) paper) as present in Millbay Docks. By the 3rd edition (Marine Biological Association 1957), Dr Hastings noted its occurrence in Millbay Docks in 1928 (evidently Miss Heath's observation) again without referring to Orton's (1914) paper. The Millbay (then Great Western) Docks were built by IK Brunel to replace existing jetties, and the inner basin, accessed through lock gates, was opened in 1857 (Plymouth historical website http://www.plymouthdata.info/Millbay). For many decades the Millbay Docks were Plymouth's maritime hub, with plenty of opportunities for *B. neritina* to have arrived on ships' hulls (Ryland 1967). There was no power station and no known heated effluent, but the enclosed nature of the inner basin probably facilitated higher summer water temperatures. Commercial traffic rapidly declined during the 1960s and the old docks were converted for use as a ferry terminal in 1973-74. The date at which the inner basin lock gates were removed is not recorded. It is not known when *B. neritina* disappeared.

The next record, from the Harbour Canal, Brighton 'B' Power Station at Shoreham, comes only as a brief mention by Crisp and Molesworth (1951). The history of occurrences in Milford Haven is neither precise nor clear. Crothers (1966) appears to have misquoted Ryland's (1960) paper, though *B. neritina* was certainly present on panels deployed by Crisp and Austin in one or more dock sites (i.e. Milford, Neyland or Pembroke Dock) at about that time (c1958). It should be noted that in 1958 Pembroke Power Station had not yet been built; it was constructed on reclaimed land between 1965 and 1968, was oil fired and operated until 1997. With an output of 2000MW it presumably made a substantial hot outflow into Pennar Gut, adjacent to Pembroke Dock town. It was dismantled between 2000 and 2003 but is expected to be replaced. The period in question also precedes the development of Milford Haven as an oil terminal (the first refinery opened in 1960). There are no other reliable records from Milford Haven until 2009.

At Swansea, *B. neritina* was found in the Queen's Dock, which opened to shipping in 1920 primarily to handle crude oil imports for the Llandarcy refinery. The date of its arrival is unknown, though it was abundant in the Queen's Dock in the late 1950s (Ryland 1960). The Tir John power station, which burned powdered anthracite waste, opened in 1935. It drew cooling water from landward end of the King's Dock and returned it to the corresponding part of the parallel but much larger (35 Ha) Queen's Dock, through tunnels ~1 km in length. The King's and Queen's docks are joined by a cut near to the shared lock which links them with the open sea. The effect of the hot outflow was to maintain dock water temperatures 7-10°C above ambient (Naylor 1957, 1965a), see Figure 3. For example, in January 1946 the effluent had a temperature of 18°C, the dock water was 12°C, while the sea outside was 5°C; the summer dock water temperature was just over 26°C (Naylor 1965a). The power station worked only intermittently after 1960, as newer sources of electricity came on line, being often closed down at night. The temperature differential (as compared with the open sea at St Govan's Lightship) decreased after November 1960, to 2–5°C (Figure 3). Thus dock temperatures in January 1962 were 5°C above ambient and there was no evidence then that the abundance of *B. neritina* had diminished (Naylor 1965a). The fuel was changed to oil in 1967, but that became less economically viable in the early '70s, and generation finally ceased in 1976 (Walker 2007).

Prolonged and exceptionally cold winters occurred in 1947 and 1963. Each of these was, successively, the coldest winter in England, and Wales since 1740. In 1947, even in south-west England air temperatures were 4-6°C below average; inland, sub-zero temperatures persisted for over a month (*http://www.metoffice.gov.uk/education*). 1963 was even colder with air temperatures in southern England and Wales 5-7°C below average throughout January and most of February. Inland temperatures remained below zero from late December 1962 through January and scarcely above it until early March. Considerable damage was done to marine biota around Britain (Crisp 1964), although the fauna of the Queen's Dock, Swansea, was not mentioned. However, there is an unpublished study of settlement in the Queen's Dock using submerged 15×15 cm asbestos panels suspended at 1.7 and 4.0 m depth for either 1 or 2 months throughout 1963 (Pearce 1967). *B. neritina* began to settle in June/July, with a peak in September, some 2 months later than in the years observed by Ryland (1960), when the season was given as May–October, peak June–August (Ryland 1967, Fig. 5). Pearce attributed this difference to the lower water temperatures then prevailing (Figure 3). In a final survey of the Queen's Dock conducted by SCUBA between October 1976 and February 1977 (Bullimore et al. 1978) no *B. neritina* was found. The authors were unable to rule out that its absence was a result of the normal over-wintering dieback exhibited by this species in temperate latitudes (Numakunai 1960, Ryland 1967). Given that Pearce (1967) found it still settling heavily in September 1963, it seems unlikely that complete seasonal regression of an extant population would have occurred by October in the later study. We conclude that *B. neritina* died out in Swansea docks between 1963 and 1976. Thus, the precise reasons for the disappearance of the once flourishing Plymouth and Swansea populations of *B. neritina* remain unclear, and the severe winter of 1963 was not the direct cause of its elimination from the Queen's Dock. The most probable explanation is that in summer temperatures below about 20°C (Figure 3) the colonies never bred successfully. Certainly it had disappeared from both localities many years before being regarded as extinct in Britain (Eno et al. 1997). The improbable cluster of 1995-2003 records on the NBN Gateway (*http://www.nbn.org.uk*), from inside or just outside Milford Haven, should be discounted as misidentifications (the representative specimen seen by JSR was *B. plumosa*).

The reappearance of *B. neritina* in Britain was established during a survey of south coast marinas in September 2004 (Arenas et al. 2006), where it was present at nine out of 12 sites visited from Brighton in the east to Falmouth in the west. It was also present in St Peter Port harbour, Guernsey (Ryland et al. 2009). There are recent published records from Belgium and the Netherlands: live colonies were observed on a yacht in the marina at Ostend in 1999 (Kerckhof 2000). Then, in April 2007, colonies were found in the marina of Burghsluis, in the Oosterschelde, in which, by August of the same year, they were very common (Faasse 2007). In southern Europe, *B. neritina* has been introduced to Aveiro, Portugal, where (as is often the case) it occurs with *Tricellaria inopinata* (Marchini et al. 2007). It has also reached the Azores (material sent to JSR by PM Torres) and the remote Atlantic island of Tristan da Cunha (M Spencer Jones, personal communication). Here we add many new records to show the distribution at the end of 2009.

Materials and methods

Surveys. The distributions presented here are based on Marine Biological Association (MBA) surveys targeting non-native sessile fauna in England and continental Europe, and on recent visits to marinas and harbours in Britain, Ireland and southern Europe by the authors (especially DM) or collaborators (see Acknowledgements).

Floating pontoons at marina sites were examined from the surface by direct visual observation. In addition to inspection of the pontoons themselves, submerged artificial substrates such as hanging ropes, keep cages and fenders were pulled up and examined. Hooks, nets and scrapers were used if necessary to access material for inspection. In some cases, leisure craft hulls, especially idle craft immersed for more than a year, were also examined for *B. neritina*.

Molecular studies. The section of cytochrome c oxidase subunit I (COI gene) analysed by Mackie et al. (2006) and originally sequenced by Davidson and Haygood (1999) was studied. It was sequenced at the MBA in 21 colonies of *B. neritina* from Queen Anne's Battery Marina, Plymouth (UK), including purple and brown colour morphs, one colony from Falmouth Marina (UK) and 4 colonies from Albufeira Marina (Portugal), all collected during 2009. Samples were preserved in undiluted ethanol, and 4 or 5 zooids of each colony were extracted using a standard CTAB protocol. Polymerase chain reactions used 0.5 x Flexi Buffer, 0.375 mM of each dNTP (Promega), 0.017 pM of each universal primer LCO1490 and HCO2198 (Folmer et al. 1994), 2.5mM $MgCl_2$, 0.5 U of Taq polymerase (Promega), 0.7 µl template DNA in a total volume of 25 µl. A PTC Peltier-200 was used with an initial denaturation step of 94ºC for 3 minutes, followed by 45 cycles of denaturation at 94ºC for 1 minute, 40ºC annealing for 50 seconds, 72ºC extension for one minute, with a final extension of 72ºC for 10 minutes. PCR products were sent to Macrogen Korea for purification and sequencing of both strands. A 619 bp sequence was aligned by eye in BioEdit (Hall 1999) and compared with the globally distributed S1 haplotype, Genbank accession number AF061432.1, found in shallow water on the Californian coast and south of Cape Hatteras on the Atlantic coast of the USA (Davidson and Haygood 1999; McGovern and Hellberg 2003; Mackie et al. 2006).

J. Mackie additionally analysed one Mediterranean sample for us.

Results

Surveys. The data for *Bugula neritina* from the surveys in Britain and Ireland are presented in Figure 4 and Appendix 1. The British and Irish records contributed by non-MBA collaborators have been verified by JSR, but no DNA analyses have been conducted. Several new localities were recorded on the south coast of England, and colonies were recorded from the east coast as far north as Lowestoft, and on the west coast as far north as the Firth of Clyde.

In the MBA surveys of the south and east coasts of England, *B. neritina* occurred in 34 out of 45 sites visited. Some of the absences can probably be explained by unsuitable conditions, such as reduced salinity. Only three potential sites further north than Lowestoft were examined: Grimsby had a good diverse marine fauna and a salinity of 28 at the time of the survey, but no *B. neritina*. Wells Harbour had a somewhat depauperate fauna, despite full salinity (36) at the time of the visit, as did Hull Marina, where the salinity was only 18 at the time of sampling. Ten of the sites on the south coast of England that were surveyed in 2004 (Arenas et al. 2006) were re-visited in 2009. The recorded occurrence of *B. neritina* was identical in 2004 and 2009: the species was absent in Exmouth Marina, but present at the remaining nine localities (Brighton, Southsea, Gosport, Hamble Point, Poole Quay, Weymouth, Torquay, Queen Anne's Battery Plymouth, and Falmouth). One of us (JDDB) has an archived sample which was collected from Queen Anne's Battery in 1999. *B. neritina* was not targeted in Ireland during a rapid assessment study of floating pontoons in 2005-6 (Minchin 2007b) but archived material examined by JSR revealed its presence at

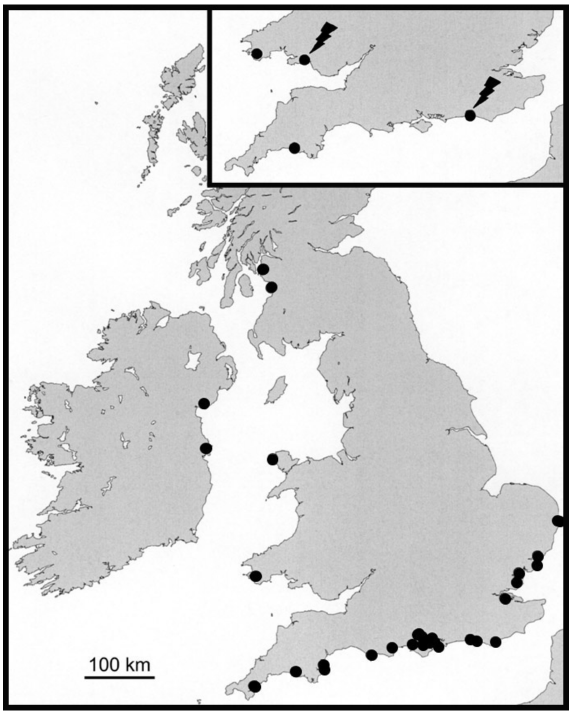

Figure 4. Known distribution of *Bugula neritina* in Britain and Ireland in the 20th century (inset) and the 21st century (main map). Lightning symbols in the 20th century map indicate artificially warmed sites.

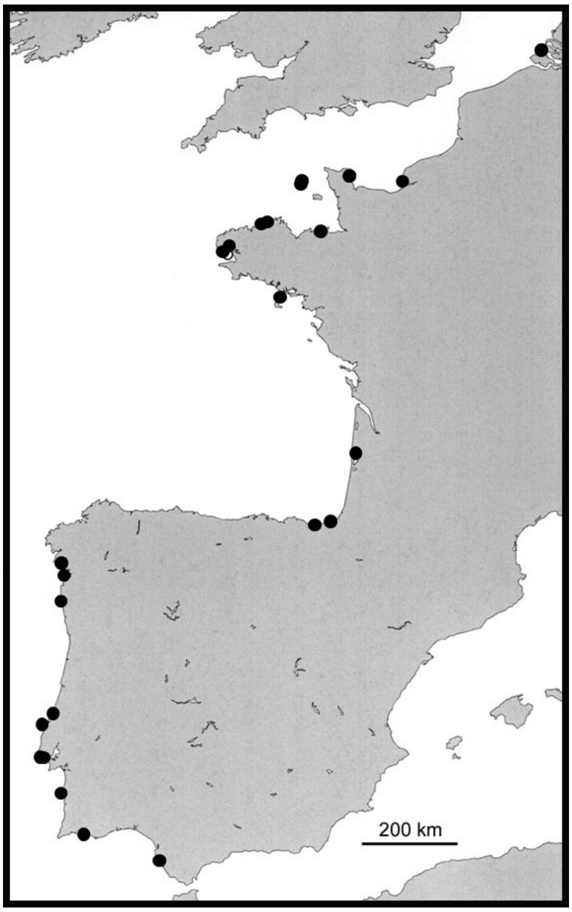

Figure 5. Recent records of *Bugula neritina* from the Atlantic coast of mainland Europe (and Guernsey).

Malahide Marina on the east coast of Ireland in January 2006, so it would have been present at this site in 2005, making it the first Irish record.

In 2008, it was found in abundance at a marina in Carlingford Lough. Both the Malahide and Carlingford marinas were visited by C Maggs on 5 August 2008 and then by DM on 11 September 2008. On 11 September *B. neritina* was found to still be locally abundant at Carlingford. However, at Malahide only a single poor quality colony of *B. neritina* could be found on 11 September. Tunicates were present at Malahide on 5 August but were absent when the site was revisited on 11 September. An event (possibly heavy freshwater runoff, causing a decline in salinity) may have taken place between 5 August and 11 September 2008 to result in change in the fouling community.

Beyond the British Isles, MBA teams conducted surveys in 2005 and 2009, and other records have been contributed by the remaining authors and collaborators (Figure 5 and Appendix 2). The non-MBA contributions have been verified by JSR or HDeB. *B. neritina* was recorded along the Atlantic coast of continental Europe from the southern Netherlands to Cadiz in Spain. The earliest record from France was from the marina at Arcachon, Gironde in August 2001, where the species persists, while the recent findings at Morgat (west Brittany) were on small boat hulls, together with *Watersipora subtorquata* (see Ryland et al. 2009) and *Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi, 1985 (HDeB). The abundant colonies at Cadiz were long and slender when compared with Irish specimens. These principally occurred close to the water surface. None of these records are from open coastlines though *B. neritina* was seen recently (by JSR, September 2003) on the rocky shore of Illa de Arousa, Galicia, north-west Spain.

Molecular studies. All colonies of *B. neritina* analysed by the MBA possessed the S1 haplo-type of COI noted by Davidson and Haygood (1999) and Mackie et al. (2006). (Thus, the purple and brown morphs collected in Plymouth shared the same haplotype.) The S1 haplotype

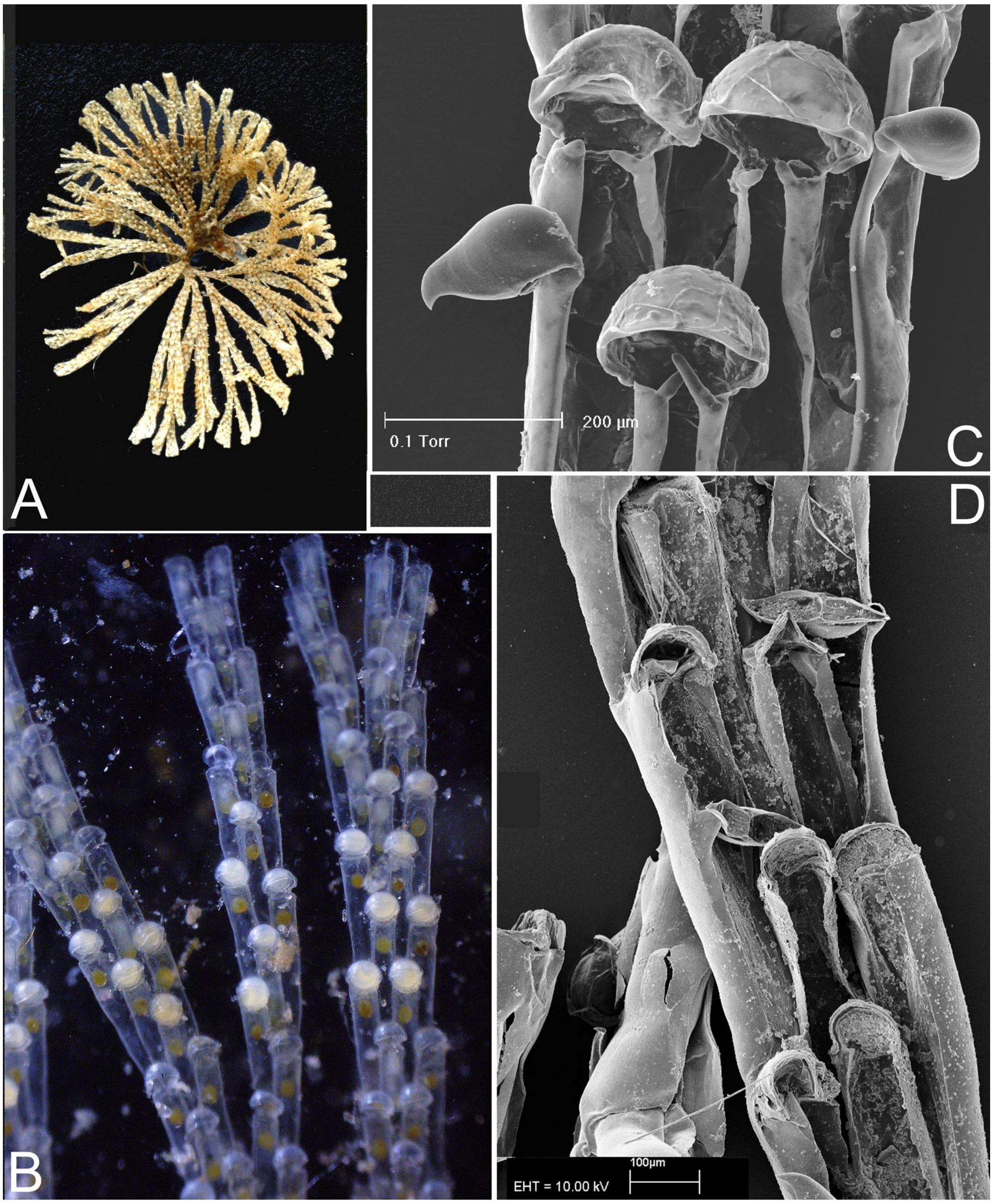

Figure 6. *Bugula simplex*. A, northern Brittany, France; B, Goesse Sas, The Netherlands; C, SEM, as A (A-C, photos: HDeB); D, SEM of material from Whangarei, New Zealand, in which the spines on the distal zooid angles are absent (photo: DP Gordon).

characterises the globally introduced populations of the putative cryptic species 'S' within *B. neritina* (Mackie et al. 2006).

A sample from Genoa (Mediterranean, and therefore not included in the survey results) was analysed by J Mackie and the COI haplotype was also the widely invasive S1 haplotype. This is important because no Mediterranean material had been included in the original analyses of Mackie et al. (2006).

For comparative purposes, DNA extraction was attempted on 1950s preserved material from Swansea Docks, but no amplification was obtained.

Bugula simplex

Historical review

Until reported in the British Isles (Holyhead Harbour and Milford Docks) by Ryland (1958), *B. simplex* was known only from the Mediterranean (Calvet 1900, as *B. sabatieri*; also Gautier 1962; Prenant and Bobin 1966) and the eastern seaboard of North America (Osburn 1912, and many other authors, all as *B. flabellata*: Ryland 1960; Ryland and Hayward 1991). Osburn (1912) stated that "Verrill has recorded the species from Vineyard Sound at 6 to 8 fathoms. It has proved rather uncommon in our dredgings, but it grows abundantly on piles throughout the region." In general agreement with Osburn (1912), Grave (1930) recorded that *B. simplex* (as *B. flabellata*) occurred in the Woods Hole Eel Pond but not in Vineyard Sound (whereas another species, *B. turrita*, occurred in Vineyard Sound but not in the Eel Pond). Grave (1930) actually conducted transplant experiments with the two species, finding that the transplants survived only for a few months and never became established. This distribution was duly confirmed by Rogick (1964) "[*B. simplex*] forms thick yellow-orange tufts in protected places such as floats in the Eel Pond and piles elsewhere." In the mid-20th century larvae of this species (as *B. flabellata*) were used by WF Lynch at Woods Hole in an innovative series of papers on their behaviour and physiology (see Sears and Woollacott, in press). At the present time, a century after Osburn, it appears that *B. simplex* has a very restricted distribution in New England (JE Winston, personal communication), with a few occurrences in Rhode Island and Connecticut, but is still seasonally abundant in the Eel Pond; it is also present at several sites on Long Island. That the distribution of *B. simplex* is so restricted, in habitat and area, on the Atlantic coast of North America raises the possibility that it might have been introduced with shipping during the 18th or 19th centuries, and that the Mediterranean is its native locality. *B. simplex* is a distinctive species (Figure 6) with multi-serial branches, hemispherical ovicells, and long avicularia on the marginal zooids only (see Ryland 1960; Ryland and Hayward 1991; Hayward and Ryland 1998).

Recent British records (NBN Gateway http://www.nbn.org.uk) are from Brighton Marina and Suffolk Yacht Harbour (R. Orwell), southeast England. This source also includes a record from 18-30m, off Ardnamurchan Point, western Scotland, which seems a highly improbable site for a warm water species, falling well outside its known habitat and geographic range.

Like *B. neritina*, *B. simplex* has now been recorded from other parts of the world, including Australia and New Zealand (Brock 1985; Gordon and Mawatari 1992), presumably introduced from either the Mediterranean or North America (or both). In the New Zealand material (Gordon and Mawatari 1992, Pl. 6G, and specimens from Whangarai (Inglis et al. 2006) sent to JSR by D Gordon) the distal spines are reduced to prominences or lacking (Figure 6D), but in other respects it conforms with Northern Hemisphere morphology and appears correctly identified. It is not included by name in the book on species introduced to Western Australia (Wells et al. 2009) but the colour photograph attributed to *B. flabellata* looks like *B. simplex*. The description, insufficiently detailed for critical distinction, also conforms more to *B. simplex* than *B. flabellata*. It should be noted that *Bugula flabellata* (Thompson in Gray), a native and widely distributed species in Western Europe, has also been recorded from Australia and New Zealand (e.g., Brock 1985; Gordon and Mawatari 1992; Hayward and Ryland 1998), presumably having travelled on ships.

Results of surveys

In the majority of recent surveys, with the exceptions of those made by HDeB in The Netherlands, Belgium and France, and the MBA in England, no search has been made for *Bugula simplex* and *B. stolonifera*. The records of *B. simplex* are shown in Figure 7 and detailed in Appendix 3. It is generally found only during a short time of the year, August-September in the Netherlands, where it is abundant in marinas located in the Ooster- and Westerschelde; even in Trébeurden (northern Brittany) the species was abundant in July (2002) but very scarce in March (2003). It was also found in Plymouth and Falmouth, southwest England in summer 2009. This accords with the findings of Grave (1930) in the Eel Pond at Woods Hole: colonies did not mature until June and erect portions never survived the winter. Survival was dependent on small colonies (8–16 zooids) or regeneration from old stolons (as in *B. neritina*). Failure to record the species during MBA surveys of the

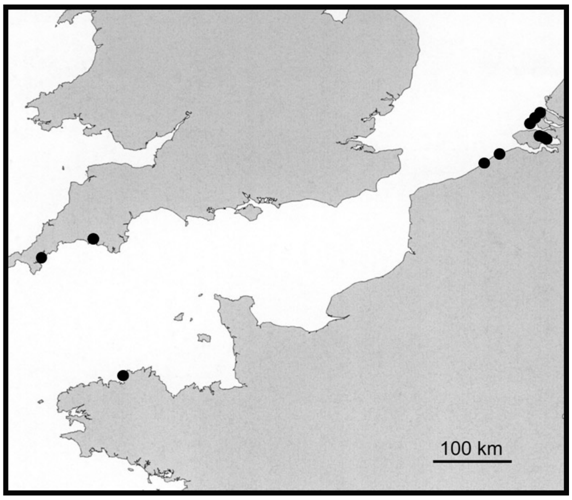

Figure 7. Recent records of *Bugula simplex* in NW Europe.

south and east coasts of England in October, November and December of 2009 might be attributable to its strong seasonality.

Bugula stolonifera

Bugula stolonifera Ryland (1960) colonies form dense tufts quite lacking the spiral branching patterns of superficially similar species such as *B. avicularia*, *B. plumosa* and *B. turrita* (Figure 8). It has biserial branching, generally two spines on the zooid outer angle, and sub-globular ovicells (see Ryland 1960; Ryland and Hayward 1991; Hayward and Ryland 1998). In a major contribution to our understanding of morphological variation in *Bugula*, Rodgers and Woollacott (2006) studied the number of spines found on the distal angles of >10 000 ancestrulae of *B. stolonifera* in the Eel Pond at Woods Hole. They found that nearly 50% of the ancestrulae had spine formulae that differed from that regarded as typical for the species, namely 3 on each distal angle and one situated proximally (Ryland 1960). This finding should be borne in mind when identifying young *Bugula* colonies as it must be assumed likely to occur to a similar extent in other species.

Its status in western Europe is unclear. Apart from the 1950-1960 British and Irish records (Swansea, Milford Haven, Neyland, and Cobh: Ryland 1960, see also NBN Gateway *http://www.nbn.org.uk*), all from docks or harbours, Ryland (1960) had specimens only from the Mediterranean, where it had been confused with other species (such as *B. avicularia* and *B. plumosa*). The existence of one nineteenth century specimen, possibly from the British Isles, made it difficult to assert that the species was then a recent introduction; but the absence of this reasonably distinctive species from Hincks' (1880) comprehensive and accurate monograph makes it unlikely to have been present in the nineteenth century. There is also a possible nineteenth century record from the former Zuiderzee in The Netherlands (Horst 1885, as *B. avicularia*) but *B. stolonifera* was not recorded from Nieuwpoort by Loppens (1906). The first Belgian record is from Polk (1976, as *B. avicularia*) in a centre of oyster culture in Oostende. At the present time *B. stolonifera* is common in marinas in Belgium and The Netherlands but is also present on groynes (Koksijde), the seaside of Brouwersdam, the Netherlands Institute for Sea Research (NIOZ) harbour on Texel, and in canals and inland water bodies in Zeeland (De Blauwe 2009).

Ashelby (2005) has recently recorded *B. stolonifera* from the Outer Harbour, Harwich, noting that as the first record from the east coast of England. Unverified but plausible British records on the NBN Gateway (*http://www.nbn.org.uk*) are from the Fal estuary (1985) and the Kenmare River (southwest Ireland, 2007); other unverified records at subtidal locations off Skomer (southwest Wales), off Hartlepool (northeast England) and off Jura (western Scotland) seem inherently unlikely, on habitat grounds in all cases and geographically also for Hartlepool and Jura (*B. stolonifera* is manifestly a warm water species). The Mediterranean distribution was given fully by Gautier (1962) – from Tunis to Venice – emphasizing its occurrence as "fréquente sur les quais et appontements portuaires, comme *B. neritina*". Koçak (2007) extends that range to the Turkish Aegean. Since its description *B. stolonifera* has been recorded in warm temperate waters worldwide: Azores (Morton et al. 1998); east coast USA (Maturo 1966; Winston 1982, Ryland and Hayward 1991); east coast of South America (Ramalho et al. 2005; Albano et al. 2006); west coast USA (Okamura 1984); Hawaii (Zabin 1999); Japan (Scholz et al. 2003); Australia (Ryland 1974; Brock 1985; Wells et al. 2009); New Zealand (Gordon and Mawatari 1992; Inglis et al. 2006); Arabian Gulf (Jones 1986).

During the surveys reported here, *B. stolonifera* was found only in Queen Anne's Battery Marina, Plymouth on 24/8/09 (MBA data; locality details given in Appendix 1).

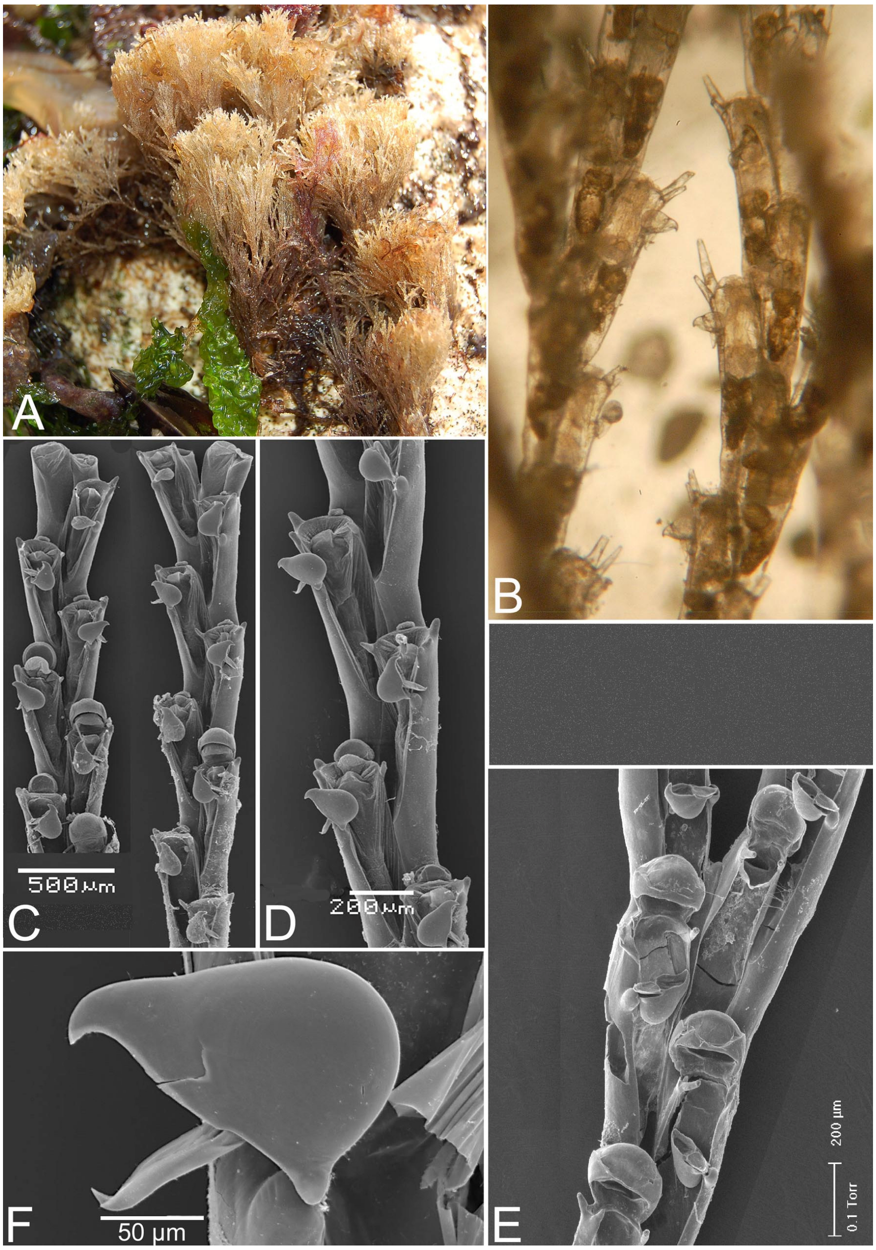

Figure 8. *Bugula stolonifera*. A, living colonies, Zeebrugge, Belgium; B, branches and zooids, Koksijde, Belgium; C-D, SEMs, Plymouth; E, SEM, Goesse Sas, The Netherlands; F, SEM of avicularium, Plymouth. (Photos: A, B, E, HDeB; C,D,F, ALEY and JDDB.)

Discussion

The history of *Bugula neritina* in a few localities in southern Britain is interesting and puzzling. That it was present in the enclosed Millbay Docks in Plymouth since before 1912 has been widely overlooked. While summer temperatures may have been quite high in the dock, there is a reliable statement that breeding colonies had been dredged from The Sound (Hastings in Marine Biological Association 1931). It is frustrating that there are no later observations and it is unknown – even approximately – when the bryozoan disappeared. At two localities during the mid-20th century, Shoreham and Swansea, *B. neritina* flourished for a time in docks that were warmed by power station effluent: only the latter is reasonably documented. As power generation declined and became intermittent, the water temperature in the

Queen's Dock fell from 7-10°C above ambient to about 3° above, or less. This decline coincided, at the outset, with two cold winters, 1961-62 and, particularly, 1962-63. However, the cold temperatures (only 2-3°C in early 1963) in the Queen's Dock did not kill *B. neritina*, which was still present and breeding in late 1963 (Pearce 1967). The breeding season (in *B. stolonifera* also) was late and short in 1963, occurring mainly in September-October instead of from May onwards, as had previously been the case for both species (Ryland 1960; Pearce 1967). This may have led to the local extinction of *B. neritina* as it had almost certainly disappeared from the dock by the time of a final survey in 1976 (Bullimore et al. 1978), though *B. stolonifera* was then still present and breeding late in the year. Examination of the water temperature data from Queen's Dock suggests that a summer temperature of ~20°C may have been necessary for successful breeding of *B. neritina*. *B. neritina* is assumed to have died out in all British localities by the end of the 20th century (Eno et al. 1997).

It was, therefore, unexpected to find *B. neritina* well established at 10 sites during a survey of marinas along the south coast of England in 2004 (Arenas et al. 2006). Searches in ~50 marinas in the previous five years by one of those authors (PEJ Dyrynda) had first identified it at a few sites and it was certainly present at Plymouth by 1999. It was suggested that the enclosed nature of the marina basins was conducive to water temperatures being relatively high during summer (as was assumed above for the Millbay Docks, Plymouth), so that breeding could take place. The rapid spread away from the south coast of England (eastwards to Lowestoft and The Netherlands, and northwards to Carlingford Lough in Ireland and the Firth of Clyde in Scotland) seems inconsistent with that being the only explanation. The research on bryostatins determined that these products occurred in some populations but not in others, suggesting that cryptic species might be involved. Various contemporary studies using DNA confirm that *B. neritina* sensu lato does indeed comprise a number of cryptic species. It seems possible that the present invasive strain of *B. neritina*, which can be characterized by its COI haplotype worldwide (Mackie 2003; Mackie et al. 2006, present results), is different from that formerly present, i.e. represents a second introduction, and is better adapted to breed at lower temperatures than that which colonized southern Britain in the 20th century. Unfortunately, no usable DNA could be extracted from museum material of *B. neritina* collected from Swansea docks in 1958 (JA Mackie, pers. com.). The likely source (or sources) of the invasive animals is not known. It has been noticed in collections from Corfu, Naples, Plymouth and Carlingford that some colonies show reduced purple pigmentation of the polypide, resulting in colonies with a golden-brown overall hue (Figure 2), while the new settlement on panels in two marinas in the Firth of Clyde was colourless. While the genetic explanation for this – if it is genetic – is unknown, it suggests that changes may be taking place, although the purple and brown colour forms are shown here to share a common COI haplotype. Clearly, this requires further investigation.

We wish to draw attention to the probable under-recording of *Bugula simplex* in western Europe. It has not been found recently in Milford docks, where it occurred in the 1950s, and its status in Holyhead harbour is unknown. Since being characterised as a fouling species (Ryland 1960) it has been recognized as invasive (often with both *B. neritina* and *B. stolonifera*) worldwide. The situation for *B. stolonifera* is similar, recognized as an alien worldwide (see above) but not being recorded as such in most of western Europe (cf. De Blauwe 2009 in regard to both species). There are several other species of *Bugula* in western Europe and some, such as *B. fulva* and *B. plumosa* (described in standard works such as Ryland 1960 and Hayward and Ryland 1990, 1998), frequently occur in harbour situations. It seems important at a time of rapid distributional change that all alien species should be recognized and recorded. It is also stressed that colonies of *Bugula*, like those of many other branching species, die down during the winter months and surveys for invasive species should be scheduled accordingly.

It is clear that Bryozoa are a significant fouling component of leisure craft, erect branching, encrusting, and foliose forms being found on hulls (e.g. *Watersipora subtorquata* is initially encrusting but may become foliose (Ryland et al. 2009)). Even uncalcified bryozoans such as *Zoobotryon verticillatum* have been recorded attached to leisure craft hulls and this propensity may have been responsible for its recent appearance in Madeira (Wirtz and Canning-Clode 2009), Lanzarote in the Canary Islands (noted by D Minchin in March 2010), and Ponta Delgada in the Azores (September 2009, PM Torres coll., JSR det.). Further spread of bryozoans by leisure craft may be expected world-wide. In addition, it is has been suggested that commercial shipping, long recognized as a vector, will pose an increased threat in the spread of many marine fouling organisms following periods of idleness as a result of global economic conditions (Floerl and Coutts 2009).

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Supplementary material

The following supplementary material is available for this article.

Appendix 1. Locations of marinas and harbours in Britain and Ireland surveyed by the authors and collaborators. Y = *Bugula neritina* recorded; N = *B. neritina* not observed.

Appendix 2. Locations in The Netherlands, Guernsey, France, Spain, Portugal and the Azores surveyed by the authors and collaborators. Y = *Bugula neritina* recorded; N = *B. neritina* not observed.

Appendix 3. Recent records of *Bugula simplex* from marinas in The Netherlands, Belgium, France and southern England. Y = *Bugula simplex* recorded; N = *B. simplex* not observed.

All records will be available at the Regional Euro-Asian Biological Invasions Centre information system (http://www.reabic.net).

This material is available as part of online article from:
http://www.aquaticinvasions.net/2011/AI_2011_6_1_Ryland_etal_Supplement.pdf