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Research Article

Unheralded arrivals: non-native sessile invertebrates in marinas on the English coast

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Abstract

Between 2005 and 2012, 61 marinas and harbours around the English coast were surveyed to record the occurrence of non-native species (NNS) of sessile invertebrates. From these surveys, geographic distributions are described for eight species of ascidians, six bryozoans and five other species. A mean of 6.7 sessile invertebrate NNS per site (range 0–13 species) was recorded. At the 43 sites on the English Channel coast, the mean was 7.8 NNS per site, and all of the ten English sites that had ≥ 10 NNS were in the western or central region of the Channel coast. Ten sites on the Channel coast surveyed in 2004 were re-visited at least once in 2009 or 2010, and the mean number of sessile invertebrate NNS had increased from 6.0 to 7.6 species per site. Combining data from all visits in 2005–2012 for the sites surveyed in 2004, the mean number of NNS recorded per site rose to 9.2. Very rapid rates of spread along the English coast and beyond are inferred for the erect bryozoan *Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi, 1985 and the ascidian *Corella eumyota* Traustedt, 1882. At least five recently arrived species that were limited to a small number of sites in 2012 are expected to increase markedly in geographic range and prevalence: the ascidians *Asterocarpa humilis* (Heller, 1878), *Botrylloides diegensis* Ritter and Forsyth, 1917, and *Didemnum vexillum* Kott, 2002; and the bryozoans *Schizoporella japonica* Ortmann, 1890 and *Watersipora subatra* (Ortmann, 1890). Rapid assessment surveys of marinas and similar sites proved to be an effective means of documenting the arrival and spread of NNS over a relatively wide geographic range and of distinguishing different rates of progression.

Key words: rapid assessment survey, distribution, non-indigenous, marina, Bryozoa, Ascidiacea, fouling

Introduction

A substantial proportion of marine non-native species (NNS) are sessile organisms that live attached to solid substrates, and NNS are often very prominent in the fouling biota of artificial coastal structures (Glasby et al. 2007; Floerl et al. 2009; Marins et al. 2010; Mineur et al. 2012). Ports and harbours are important sites for the primary introduction of NNS carried by international shipping, while smaller commercial vessels and leisure boats are believed to be effective agents of subsequent secondary spread (Wasson et al. 2001; Minchin et al. 2006; Murray et al. 2011). Marinas can also be the site of primary introductions to new geographic regions by long-range movements of leisure craft (e.g. Bax et al. 2002; Griffith et al. 2009). Floating docks or pontoons in ports, harbours, and marinas provide solid surfaces with the distinctive feature of continuous submersion at a constant, shallow depth, and are remote from the seabed and its predators. Such surfaces support an abundant fouling biota and appear to favour NNS (Neves et al. 2007; Glasby et al. 2007; Dafforn et al. 2009). Marinas are an increasingly common component of developed shorelines and offer opportunity for the cost-effective survey of species' distributions along coasts, their pontoon walkways providing ready access from the surface to submerged fouling biotas, irrespective of the state of the tide.

Synoptic surveys of NNS along extensive coast-lines have commonly involved rapid assessment survey (RAS) protocols with standardized, timed, visits to target sites by a team of biologists. Identifications made on-site are often augmented later in the laboratory using material collected specifically for this purpose (e.g. Cohen et al. 2005; Pederson et al. 2005; Arenas et al. 2006; Minchin and Nunn 2013; Nall et al. 2015; Bishop et al. in press). The information gathered can characterize the prevalence of NNS across the surveyed region and, when repeated, document changes in the presence, abundance, and distribution of NNS. This information can contribute to government monitoring obligations arising, for instance, from the European Union (EU) Marine Strategy Framework and Water Framework Directives, and the EU Regulation on invasive alien species.

This study updates and considerably extends the 2004 RAS of marinas and harbours on the south coast of England reported by Arenas et al. (2006) and details our survey records and other occurrences to 2012. Ten of the sites surveyed in 2004 were re-visited. In addition, a substantial number of new sites were surveyed on the south coast, and coverage was extended to the northwest and east coasts of England. While the 2004 survey (Arenas et al. 2006) included algae and some motile animals, this study was restricted to sessile invertebrate species (mainly ascidians and bryozoans).

Methods

Visits were made to 61 marina and harbour sites around the English coast (Supplementary material Table S1). Visual surveys were done from the surface (i.e. from floating pontoons, without diving or snorkelling) at any state of tide. Sites expected to have markedly reduced salinity were avoided. Each marina was contacted in advance for permission to undertake the survey and to enable preparation of any required documentation or safety arrangements. During 2009 and 2010, JDDB, CAW and AY visited each location to conduct a rapid assessment survey (RAS). At each site, the pontoons were apportioned equally between the three participants, who worked independently for one hour. At small sites, the search interval was sometimes shortened to 45 min, while additional time was added at larger or more complex sites. In addition to inspection of the pontoons, submerged artificial substrates (e.g., hanging ropes, keep cages, fenders) and natural substrates (e.g., kelp) were pulled up and examined. Hooks and scrapers were used if necessary to access material for inspection. The participants then gathered to compare and record observations on a standard form. A semi-quantitative estimate of overall abundance of each species encountered was made on a three-point scale: 1 (Rare-Occasional), 2 (Frequent-Common) and 3 (Abundant-Superabundant), combining the separate estimates of the participants. Salinity and temperature were recorded using a YSI 85 or a YSI 30 meter (Xylem Analytics UK Ltd., Letchworth, Hertfordshire, UK).

An assessment of the adequacy of a one-hour search interval was made during surveys of marinas in the Solent region in early December 2009. Each person recorded the 15-minute interval within which their first sighting of each of 28 readily-recognisable species (16 non-native and 12 native) occurred.

On visits for other purposes, such as to collect specimens for research or teaching, the opportunity was taken to record observations on the same form as used for the RASs. Additional information was obtained from the examination of settlement panels. In the summer of 2006, 25 × 25 cm polymethyl methacrylate panels were deployed at 12 sites in Dorset, Devon, and Cornwall. In the summer of 2009, 15 × 15 cm panels made of twin-wall fluted polypropylene (“corrugated plastic”) were exposed for periods of 2 and 8 weeks at nine marinas in Devon and Cornwall before retrieval and scoring. Similar 15 × 15 cm polypropylene panels were exposed for a year at 7 marinas in Devon and Cornwall in 2010–11 and 2011–12.

In our survey recording after 2004, we did not include the tubeworm *Hydroides ezoensis* Okuda, 1934 (recorded in 2004 at two sites by Arenas et al. 2006), and we do not discuss here records of the motile crustacean *Caprella mutica* Schurin, 1935, restricting treatment to sessile animal species. Some sites in Devon and Cornwall, most notably FALM 3, PLYM 5, PLYM 7, TORB 1 and TORB 2, received relatively frequent visits for seasonal and experimental studies and collection of material for student classes, etc., in addition to inclusion in the periodic surveys (Tables S1 and S2). At these sites, first observations of species within the sequence of visits are likely to be relatively accurate estimates of the actual arrival dates at each place.

When listing the details of the surveys and the sites visited (Tables S1 and S2), we have used codes for the actual localities because some marina operators did not wish their establishments to be explicitly named. In addition to RASs, a non-RAS visit to a site or a set of panels from a site was counted as a ‘survey’ if more than 8 of the 19 species discussed herein were scored as present or absent.

The detailed occurrence data given in Table S2 includes the published occurrences from Arenas et al. (2006) plus unpublished records for *Bugulina simplex*, *B. stolonifera* and *Botrylloides diegensis* from the 2004 RASs. First occurrences of species in the 2004–12 data are shown separately for ascidians (Table S3) and bryozoans (Table S4). In these tables and Table S2, zero (0) signifies that a species was consciously looked for but noted as not found, while a blank indicates that its absence was not specifically recorded (i.e. no conclusion was drawn as to its presence or absence). In Tables S3 and S4 apparent colonisation of a site, i.e. the presence of a species where it had previously been recorded as absent, is indicated by bold text and shading of the relevant cell.

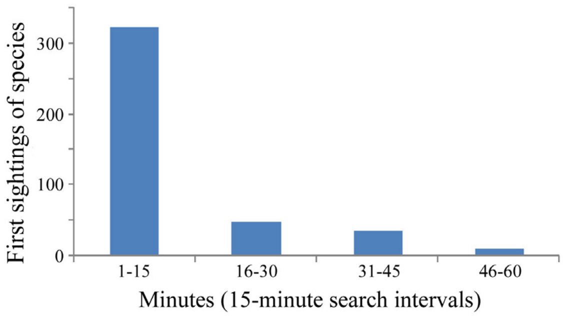

Figure 1. Timing of first sightings of 28 target species by each of three people during 1-hour surveys at eleven marinas in the Solent region.

Results

Adequacy of duration of RAS visits

During the survey of 11 marinas in the Solent region in December 2009, the three participants separately generated 417 records from a list of 28 species of sessile biota. Over three-quarters (77.5%) of the first sightings occurred in the first 15 minutes at a marina, and only 2.6% of records arose during the final 15 minutes of the 1-hour searches (Figure 1).

Species accounts

Asterocarpa humilis (Heller, 1878) (Figure 2A)

Asterocarpa humilis was first noted in autumn 2009 in Weymouth Harbour and the Kingsbridge-Salcombe estuary, and was subsequently found at several additional sites in southwestern England (Bishop et al. 2013; Table S3). It was not noted east of Weymouth in 2009, but was found in Brighton in 2011. At PLYM 5 it was first seen in 2011. To judge from new occurrences since 2009 at frequently visited sites, this species had spread rapidly in southwestern England, and it achieved considerable density at some sites such as FALM 3 (first record also 2011). However, it remained unrecorded in the Solent region. It was encountered in Holyhead Marina (northern Wales) during a visit in November 2011. *A. humilis* also occurs in Brittany (Bishop et al. 2013) and is widespread in the southern hemisphere, where it is presumed to be native.

Botrylloides spp. (Figures 2B, 2C and 3)

The ascidian *Botrylloides violaceus* Oka, 1927 was first recognised in the UK at PLYM 5 in May 2004 (G. Lambert and C. Lambert, University of Washington and California State University, Fullerton, USA, pers. comm.). In the September 2004 RAS (Arenas et al. 2006), *B. violaceus* was widespread on the south coast (and was present in a variety of colour morphs), suggesting it had been present for some time, presumably being overlooked through confusion with the putatively native species *Botrylloides leachii* (Savigny, 1816).

During the 2004 RAS, an additional *Botrylloides* species, recognisable by its distinctive two-colour pattern (Figure 3) (in contrast to the predominantly single-coloured appearance of *B. violaceus* colonies) and presumed to be non-native, was noted, but this was not included in Arenas et al. (2006) because of uncertainty over its identity. Here it is referred to as *Botrylloides diegensis* Ritter and Forsyth, 1917. During investigations of *B. violaceus* collected from both sides of the English Channel, specimens were encountered that resembled *B. violaceus* in general external appearance but, based on DNA sequencing, were conspecific with the distinctive colour morph of *B. diegensis* (F. Viard and C. Roby, Station Biologique de Roscoff, France, pers. comm.). There was thus potential for confusion of these two species, and clear morphological distinctions apart from those of the seasonally brooded larvae were not available.

Here we report the presence of *B. violaceus* only where its identity has been confirmed by DNA analysis or by the presence of the distinctive, very large, embryos and/or pink-purple larvae that are brooded in the colonial tunic after the regression of the maternal zooid. In contrast, the larvae of *B. diegensis* are much smaller, are brooded alongside the abdomen of the maternal zooid, and have c. 8 vascular ampullae compared to >20 in *B. violaceus*. Similarly, we only recorded *B. diegensis* where confirmed by DNA analysis or by the occurrence of the distinctive colour morphs (Figure 3).

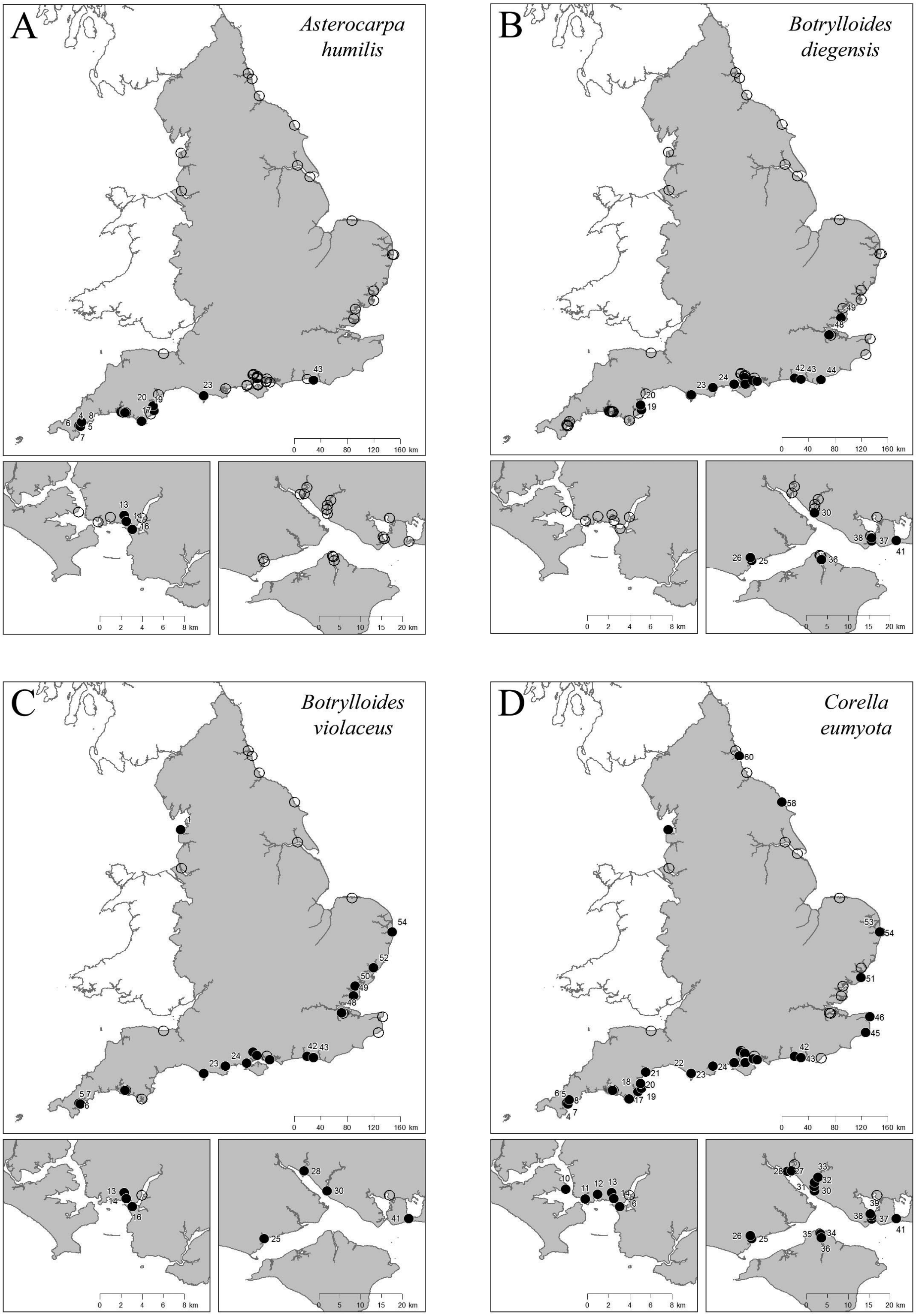

Figure 2. Distribution of four non-native ascidian species recorded in marinas and harbours over the period 2004–2012. Filled circles denote presence, empty circles denote recorded absence (equivalent to a zero in the tabulations). Site numbers are only given for presence records; refer to the enlarged sections for site numbers in Plymouth Sound and the Solent. See Table S1 for details of sites.

Figure 3. Two versions of the distinctive two-colour pattern shown by many colonies of *Botrylloides diegensis*. A, Southsea, Hampshire and B, Poole, Dorset, both in June 2011 (Images: J. Bishop).

Given the taxonomic confusion, the separate records reported here are minimum estimates of the occurrence of each species. *B. violaceus* was confirmed at 20 localities ranging from Fleetwood on the northwest coast all along the south coast and to Lowestoft (Figure 2C). *B. diegensis* was confirmed at 16 localities on the south and southeast coasts between Brixham and Burnham-on-Crouch (Figure 2B), and these records documented apparent colonisation of seven new sites on the south coast (Table S3). For the analyses of general site occupancy below, the two NNS *B. violaceus* and *B. diegensis* were combined into a single taxon since they were not distinguished at all sites; in consideration of the number of NNS per site, the two species were scored separately at sites where both were confirmed according to the criteria above.

Ciona intestinalis 'type A'

In the UK, this ascidian species is currently known only from Falmouth, Plymouth and Torquay (Nydam and Harrison 2011), and is believed native to the northwestern Pacific (Nydam and Harrison 2010). It requires a different name but has only recently been distinguished from *Ciona intestinalis* (Linnaeus, 1767), 'type B', considered native to northwestern Europe (Nydam and Harrison 2010). Photographic evidence indicates the presence of 'type A' in Plymouth (at PLYM 5) in 2003 and it was collected in Falmouth (FALM 3), Plymouth (PLYM 4 and PLYM 5) and Torquay (TORB 2) in 2007 (Nydam and Harrison 2011), so our failure to record the species in the extreme South West until 2011 relates at least in large part to being unaware of the existence of two species. Type A also appears to be seasonal in prominence, and can be relatively inconspicuous until late summer/autumn, so surveys earlier in the year can fail to record it. Field characters separating the two species were proposed by Sato et al. (2012), based on examination of specimens from Plymouth. Although molecular evidence suggests the two species diverged 2–5 million years ago (Nydam and Harrison 2007; Roux et al. 2013), DNA analysis indicates the existence of individuals of hybrid descent in populations in the region of sympatry in the western English Channel (Nydam and Harrison 2011; Sato et al. 2012) but also as far east as Brighton (F. Viard and S. Bouchemousse, Station Biologique de Roscoff, France, pers. comm.). Most or all of this introgression is probably the result of an ancient hybridisation event (Roux et al. 2013). *Ciona intestinalis* 'type A' also occurs alongside 'type B' in Brittany and was found in January 2012 in the marina at Saint-Vaast-la-Hougue, Normandy (JDDB, pers. obs.), considerably further east than its eastern limit on the English side of the Channel.

Corella eumyota Traustedt, 1882 (Figures 2D and 4)

In the UK, the ascidian *Corella eumyota* was first recorded in 2004 in Brighton, Gosport and Weymouth (Arenas et al. 2006). It appears to have rapidly colonised additional sites on the south

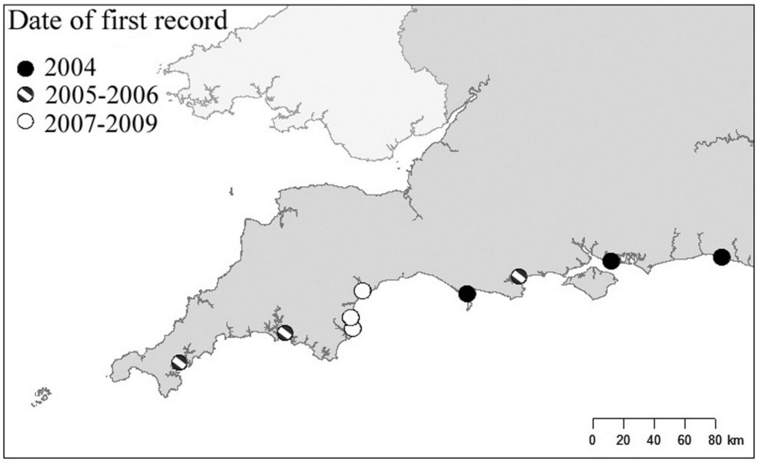

Figure 4. Timing of first detection of *Corella eumyota* at sites in southwestern England.

coast of England, and in 2009 was recorded at all seven of the sites that were re-visited where it had not been found during the 2004 surveys (Table S3). First records in 2005 at two of these, PLYM 5 (Plymouth) and FALM 3 (Falmouth), suggested that a rapid westward expansion was underway at the time of the species' discovery in 2004, but the species apparently arrived at sites between Weymouth and Plymouth and between Weymouth and Gosport some time later: EXMO (2007), TORB 1 and 2 (both 2009) and POOL (2006) (Figure 4). We also recorded *C. eumyota* in Fleetwood on the northwest coast of England and on the east coast as far north as Sunderland. In addition to artificial habitats such as marinas, the species occurs on natural and semi-natural shores, for instance around Plymouth Sound and the nearby Yealm estuary, and in Kent (Collin et al. 2010; Spurrier 2012).

Corella eumyota has also been recorded on the west coast of Scotland (Beveridge et al. 2011). It was first recorded in the northern hemisphere in Brittany in 2002 (Lambert 2004) and is present in Ireland and Portugal and on the Atlantic coast of Spain (Minchin 2007; Varela et al. 2008; El Nagar et al. 2010). *C. eumyota* is widespread in the southern hemisphere, to which it is presumed native, occurring on all continents except Antarctica, plus several remote oceanic islands (Lambert 2004).

Didemnum vexillum Kott, 2002 (Figure 5A)

The first documented occurrence in the UK of an established population of the ascidian *Didemnum vexillum* was in September 2008 at Holyhead Marina (northern Wales), and in the same month a single colony was found and removed at PLYM 7 (Griffith et al. 2009). The only recurrence at PLYM 7 was another single colony encountered in April 2010 very close to the site of the 2008 colony, and again this was removed. There is evidence, in the form of a photograph of a single colony, that the species was present at DART in June 2005, and a colony was collected there in July 2009 (Griffith et al. 2009). Although the species was not found during visits to the marina in the period between 2005 and 2009, by the autumn of 2009, an established population of *D. vexillum* was present in DART and on a number of other pontoons adjacent to the marina. During the wider south-coast marina surveys in 2009, additional occurrences of *D. vexillum* were documented only in the Solent region, where visits to 17 marinas revealed relatively dense populations in three adjacent marinas in Gosport, plus apparently minor infestations in single marinas in Lymington (western Solent) and Cowes (Isle of Wight). The species was discovered in the Clyde on the west coast of Scotland in 2010 (Beveridge et al. 2011) and in southeastern England along the north coast of Kent in July 2011 (Hitchin 2012). It is present in northern and western France (since 1998) the Netherlands (1998, but possibly as early as 1991), Ireland (2005) and northern Spain (2008) (Lambert 2009; El Nagar et al. 2010), while the first occurrence in the Mediterranean was in Italy in 2012 (Tagliapietra et al. 2012). Globally, *D. vexillum* occurs as an introduced species in cool-temperate waters on the east and west coasts of North America and in New Zealand, and it is thought to be native to Japan (Lambert 2009).

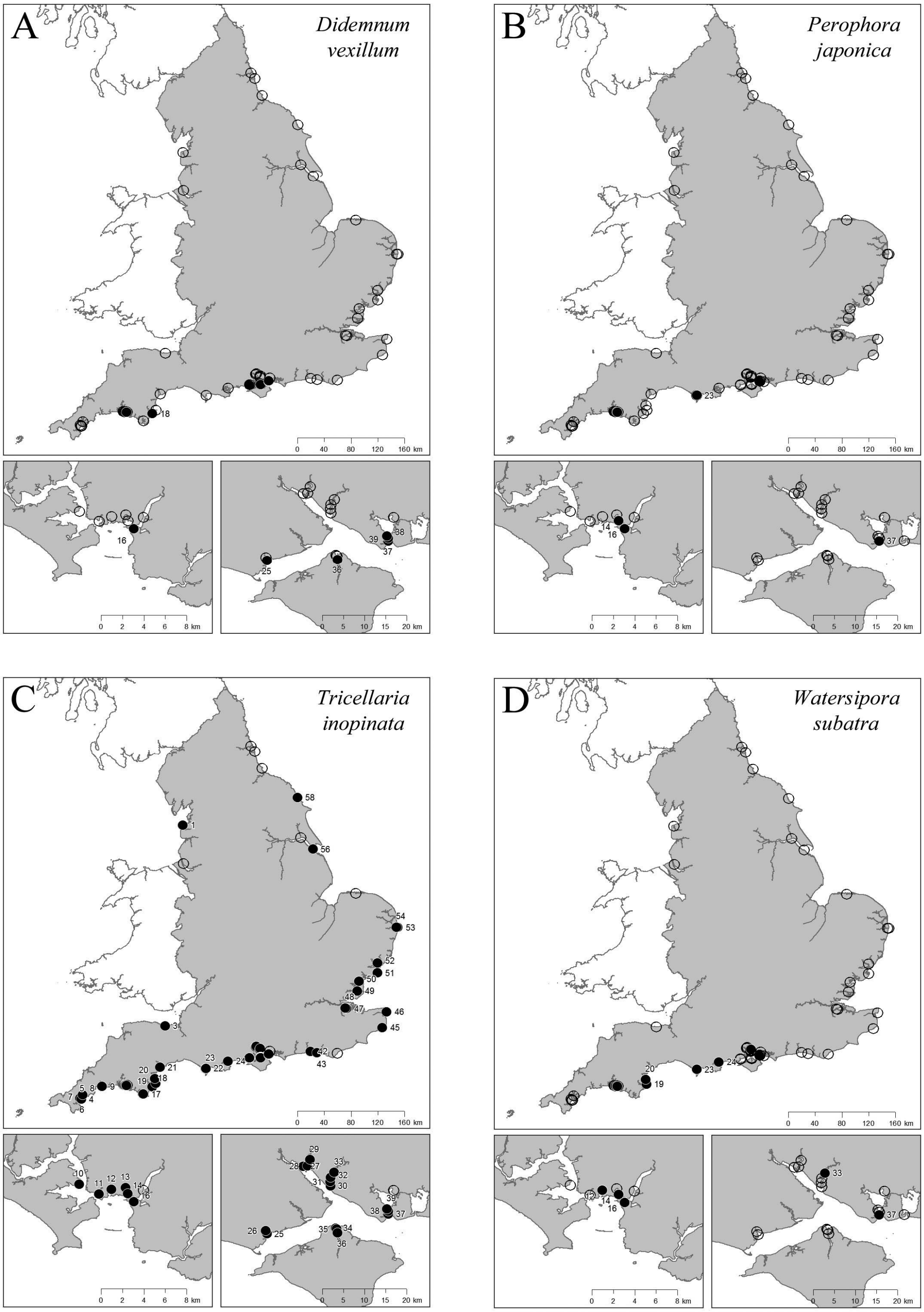

Figure 5. Distribution of two ascidian and two bryozoan NNS recorded in marinas and harbours over the period 2004–2012. Filled circles denote presence, empty circles denote recorded absence (equivalent to a zero in the tabulations). Site numbers are only given for presence records; refer to the enlarged sections for site numbers in Plymouth Sound and the Solent. See Table S1 for details of sites.

Perophora japonica Oka, 1927 (Figure 5B)

The first UK record of the ascidian *Perophora japonica* was at PLYM 5 in 1999 (Nishikawa et al. 2000), soon followed by the Fleet Lagoon, Dorset (Baldock and Bishop 2001), from which the species subsequently disappeared (B. Baldock, pers. comm.; Pérez Portela et al. 2012). Although persisting at PLYM 5, *P. japonica* did not become common in marinas or harbours, being recorded at just three additional sites in our surveys: PLYM 7, only c. 1km from PLYM 5, where its occurrence in small numbers was intermittent, WEYM 2 (close to the Fleet) and GOSP 1. To our knowledge, it has not been found in marinas elsewhere in Great Britain (GB). However, in 2010 the species was found on chalk reefs off north Norfolk (Spray and Watson 2011), and in 2012 was encountered in Strangford Lough, Northern Ireland and Carlingford Marina (Republic of Ireland) (Minchin and Nunn 2013) and on dive surveys in the Helford estuary, Cornwall (Gall 2012). A record of *P. japonica* from Milford Haven in 2002, included on various Web sites, was based on a misidentification (specimen examined by JDDB).

The first Atlantic records of *P. japonica* were in 1982 in northwestern France (Monniot and Monniot 1985), where the species became widespread and common in marinas, on the shore, and in shallow coastal waters. In Europe it was found in the Netherlands (Faasse 2004) and northwestern Spain (El Nagar et al. 2010). Also reported as an introduced species on the west coast of the USA (Lambert 2005), *P. japonica* is thought to be native to the northwestern Pacific.

Styela clava Herdman, 1881

By far the earliest-recognised non-native ascidian in the UK—first recorded in Plymouth, in 1953 by Carlisle (1954) (as *S. mammiculata*)—*Styela clava* has been widespread for some decades and was the most frequently encountered ascidian NNS at our survey sites. The known limit on the east coast of England was extended northwards to Grimsby by Davis and Davis (2004), and the records presented here do not extend that range. On the west coast, the species reaches Scotland where northward expansion since about 2000 to Loch Carron (Highland region) has been linked to increasing summer water temperatures (Cook et al. 2013a). The history of colonisation of northwestern Europe by this species was detailed by Lützen (1999).

Bugula neritina (Linnaeus, 1758)

The history and status of this bryozoan species was reviewed by Ryland et al. (2011). First recorded in c. 1911, *Bugula neritina* was considered no longer to be present in GB in the late 1990s (Eno et al. 1997), but an apparent recolonisation and rapid expansion has occurred. The recorded range now far outstrips the few localities enjoying warm summer temperatures to which the species was restricted throughout the 20th Century. Most of the records presented here were included in Ryland et al. (2011). The species was recorded on the first visit to each of the numerous sites where it occurred during the 2004–2012 surveys, with the exception of EXMO, where it was recorded in 2009 having previously been noted as absent—the sole instance of apparent new colonisation documented for *B. neritina* (Tables S2 and S4).

Bugulina simplex (Hincks, 1886) and *B. stolonifera* (Ryland, 1960)

The occurrence of these two under-recorded bryozoan species (re-assigned to the genus *Bugulina* from *Bugula* by Fehlauer-Ale et al. 2015) was recently reviewed by Ryland et al. (2011), who argued for their inclusion in future surveys for NNS. *Bugulina simplex* was only reported from two sites in Cornwall and Devon by Ryland et al. (2011), so the records presented here yield a substantial increase in the known range of this species: from Watchet (Somerset) to Hartlepool. However, the latter site is not the northern limit of *B. simplex* on the east coast of GB: the species occurred amongst material from settlement panels deployed in Peterhead Marina, Scotland in 2009 sent to JDDB by T. McCollin and L. Brown (Marine Scotland Science, Aberdeen). It was subsequently found even further north in Kirkwall Marina, Orkney in 2012 (Nall et al. 2015). A single original record of *Bugulina stolonifera* was reported by Ryland et al. (2011); this was from Plymouth, and the occurrences noted here extend the recent records from there eastwards as far as Lowestoft.

Schizoporella japonica Ortmann, 1890

The first UK record of the bryozoan *Schizoporella japonica* was in Holyhead Marina, northern Wales, in 2010, and it was subsequently found in Stromness Marina, Orkney, Scotland, in 2011 and then in various additional locations on the Scottish coast (Ryland et al. 2014). Here we report its presence in Plymouth at PLYM 3, the only

English record thus far. *S. japonica* therefore has an extensive but apparently widely discontinuous distribution on the western side of GB. We are not aware of records of this species from continental Europe. The species is believed to be native to the northwestern Pacific and has been reported as an introduced species in the north-eastern Pacific from Alaska to California (Dick et al. 2005). The global introduced range is currently poorly defined, as *S. japonica* has possibly been misidentified as *S. unicornis* (Johnston in Wood, 1844) or *S. errata* (Waters, 1878) (Dick et al. 2005). It may also be present in Australia, where a species ascribed to *S. unicornis,* but possibly in fact *S. japonica,* was reported in 1975 following importation of Pacific oysters.

Tricellaria inopinata d'Hondt and Occhipinti Ambrogi, 1985 (Figure 5C)

Since the first UK record in Poole Harbour, Dorset in 1998 (Dyrynda et al. 2000), the bryozoan *Tricellaria inopinata* has spread rapidly. In 1999, the species was found to extend only from Swanage to Chichester Harbour (Dyrynda et al. 2000), a distance of c. 75 km, but by 2004 it had spread westwards on the south coast as far as Falmouth (Arenas et al. 2006). Here we report *T. inopinata* around the coast of England from Fleetwood in the North West to Scarborough on the east coast, but these do not represent the species' northern limits in GB, as by 2012 it occurred on both the west and east coasts of Scotland following an initial Scottish sighting in 2006 (Cook et al. 2013b). As with *Styela clava* and *Bugula neritina*, *T. inopinata* was evidently widespread and common by the time our surveys were undertaken, and it was recorded on the first visit to each of the numerous sites where it occurred, with a single exception, BRIG, where it was not recorded in 2004 but was present in 2005 (Tables S2 and S4).

Tricellaria inopinata is also found on natural GB shores, at least on the south coast. Elsewhere in Europe, it is present as an introduced species in the Netherlands and Belgium (De Blauwe and Faasse 2001), on Atlantic coasts of France and Spain (Breton and d'Hondt, 2005; Fernández-Pulpeiro 2001; Marchini et al. 2007), and in northern Italy (d'Hondt and Occhipinti Ambrogi, 1985). Globally, the species is also introduced in Australia and New Zealand (Occhipinti Ambrogi and d'Hondt, 1994), and it has more recently been reported from the east coast of North America (Johnson et al. 2012).

Watersipora subatra (Ortmann, 1890) (Figure 5D)

This bryozoan was previously referred to as *Watersipora subtorquata* in its northwestern European introduced range, but was re-identified by Vieira et al. (2014). In the UK, *Watersipora subatra* was first detected in 2008 in marinas in Plymouth (Devon) and Poole (Dorset), although the species had been found in Guernsey (Channel Islands) in 2007 (Ryland et al. 2009). Here we report a range on the south coast of England from Plymouth to Gosport, representing only a modest eastward extension beyond the two sites we recorded in 2008, but with progressive infilling between them—apparent colonisation of six new sites on the south coast in southwestern England is documented (Table S4). The species was recorded in Ireland in 2011 (Kelso and Wyse Jackson 2012) and has been present for some time on the Atlantic and western Channel coasts of France, where it occurs on natural shores (Ryland et al. 2009) in addition to the harbour or marina habitats typical of English occurrences. Globally, *W. subatra* is also introduced in the USA (California), Australia, and New Zealand.

Other species

The barnacle *Austrominius modestus* (Darwin, 1854) arrived on the south coast of England during the Second World War. Its subsequent spread around the coast of GB involved progressive movement along the coast attributed to larval dispersal from a number of geographic foci founded by anthropogenic dispersal (Crisp 1958). *Austrominius modestus* was established in at least one site in Shetland, in the extreme north of GB, by the mid-1970s (Hiscock et al. 1978) and is widely distributed in northern Scotland (Nall et al. 2015). The species is very widespread, especially in habitats subjected to fluctuating salinity, and accordingly was often recorded during surveys of marinas. However, *A. modestus* is most prevalent on tidal surfaces of fixed structures, and our recording of its presence will have been influenced by the state of the tide during visits.

Occurrences of the Pacific oyster *Crassostrea gigas* (Thunberg, 1793) derive ultimately from recruitment from commercially cultured stocks. Self-sustaining wild populations are now established, particularly on the southeast coast of England, where commercial exploitation of wild stocks is underway (Herbert et al. 2012). This species is frequently most conspicuous on intertidal surfaces, which were not visible during

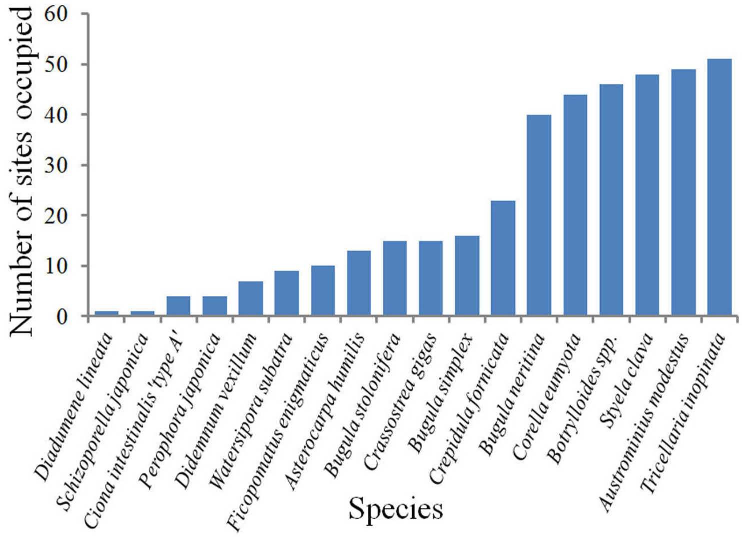

Figure 6. Frequency of occurrence of 18 non-native sessile invertebrate taxa at 61 sites around the English coast, ranked from least to most frequent.

marina visits that coincided with high tide, so this species was probably under recorded.

The slipper limpet *Crepidula fornicata* (Linnaeus, 1758) was widely encountered on the south coast of England. Although surfaces raised above the seabed, such as those examined, would not be regarded as prime habitat for *C. fornicata*, the species was regularly recorded on visits to marinas in Poole Harbour and the Solent region, where it appeared to be very common.

A general association with low salinity was evident in the records of the polychaete tube-worm *Ficopomatus enigmaticus* (Fauvel, 1923). However, low surface salinity values were not recorded during the visits to LYMI 1 and SOUT 4, where the species was recorded, and *F. enigmaticus* was not noted at North Shields (surface salinity 11.5). Brackish-water sites were generally under-represented in our data set.

Only one record of the anemone *Diadumene lineata* (Verrill, 1869) was obtained, again possibly reflecting the poor representation of brackish-water sites in our data set, since *D. lineata* is regarded as a common species favouring brackish habitats (Barnes 1994).

Species comparisons

The rankings of species by the number of sites where they occur (Figure 6) and by their total recorded abundance scores (not shown) were very similar, and the following six taxa were clearly more prevalent than the remainder: *Tricellaria inopinata*, *Austrominius modestus*, *Styela clava*, *Botrylloides spp.* (this category probably dominated by *B. violaceus*), *Corella eumyota,* and *Bugula neritina*. As noted above, the surveys did not target intertidal surfaces, which represent prime habitat for *A. modestus*, and taxonomic uncertainty affected the recording of *B. violaceus*, so these species were probably more prevalent than the current data suggest.

A plot of species occurrence versus time since their first records in GB (Figure 7) identifies *Schizoporella japonica*, *Didemnum vexillum, Watersipora subatra*, *Asterocarpa humilis, Botrylloides diegensis*, and *Ciona intestinalis* 'type A' as a cluster of recently arrived species that, in 2012, were still limited to a small number of sites in England. *Perophora japonica* is on the edge of this cluster as a slightly older arrival that had so far failed to colonise more than a handful of scattered sites. In Figure 7, *Botrylloides violaceus* plots only just above this set of species according to the limited number of confirmed records. However, indeterminate non-native *Botrylloides* (i.e. non-brooding *B. violaceus* and/or less distinctive colour morphs of *B. diegensis*, but not *B. leachii*) was noted in 26 additional sites in these surveys, and most of these additional records probably include *B. violaceus*. Furthermore, *B. violaceus* had possibly been overlooked for some years at the time of its recognition, already being widespread on the south coast of England

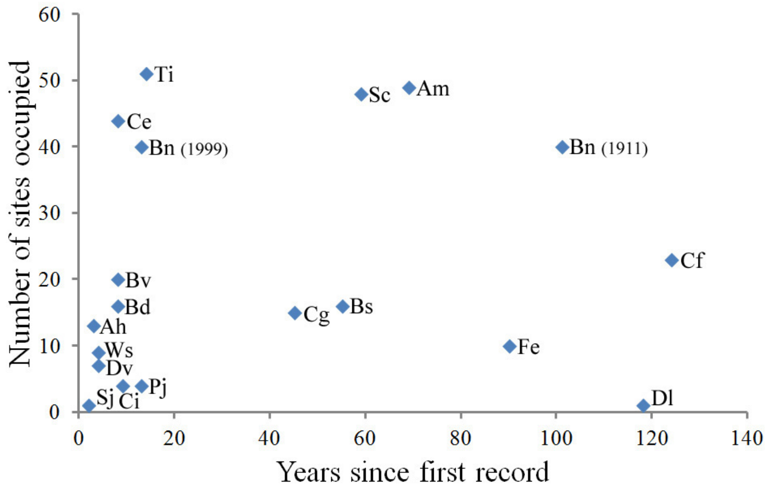

Figure 7. Scatter plot of the number of years (in 2012) since the first record of each NNS and the number of English sites at which the species was recorded in the surveys reported here. First records were in England, except for *Didemnum vexillum* (Wales and England), *Bugulina simplex* and *Schizoporella japonica* (Wales). Year used for *Crassostrea gigas* (1967) refers to simultaneous growth trials at ten field sites in Wales, Scotland and England using Asian stock from an experimental hatchery (Walne and Spencer, 1971) since wild populations attributable to earlier culture of the '*C. angulata*' ('Portuguese oyster') strain are not documented. Year used for *Diadumene lineata* (1894) from estimate of arrival by Barnes (1994). Ah = *Asterocarpa humilis*, Am = *Austrominius modestus*, Bd = *Botrylloides diegensis*, Bn = *Bugula neritina* (two points shown, taking first record to be 1911 and 1999 respectively; see text), Bs = *Bugulina simplex*, Bv = *Botrylloides violaceus*, Ce = *Corella eumyota*, Ci = *Ciona intestinalis* 'type A', Cf = *Crepidula fornicata*, Cg = *Crassostrea gigas*, Dl = *Diadumene lineata*, Dv = *Didemnum vexillum*, Fe = *Ficopomatus enigmaticus*, Pj = *Perophora japonica*, Sc = *Styela clava*, Sj = *Schizoporella japonica*, Ws = *Watersipora subatra*. *Bugulina stolonifera* is not plotted because its year of first occurrence is unclear (Ryland et al. 2011).

in 2004 (Arenas et al. 2006). Thus *B. violaceus* may in fact be an older arrival, and present in a higher proportion of sites, than shown in Figure 7. *Bugulina simplex* is possibly still under-recorded as it is relatively inconspicuous and its identification requires microscopical examination, although the present data constitute a considerable advance over information available to Ryland et al. (2011); similar comments would apply to *B. stolonifera*. Two other species, *C. eumyota* and *T. inopinata* do seem to be genuine examples of very rapid spread and efficient colonisation of available habitats. If it is accepted that *B. neritina* has recolonised GB following extinction in the late 20th Century, its subsequent rate of colonisation (represented by the '1999' data point in Figure 7) groups it with *C. eumyota* and *T. inopinata* as a rapid spreader. As two species that appear to have arrived at approximately the same time, the present distributions of *T. inopinata* and *P. japonica* in marinas provide a stark contrast: *T. inopinata* is clearly the superior coloniser of these sites. Longer-established species recorded from relatively few places include *Ficopomatus enigmaticus* and *Diadumene lineata*, species primarily restricted to brackish sites, which are poorly represented in this data set, and *Crepidula fornicata*, for which substrates suspended above the seabed are not a prime habitat.

Geographic trends

The mean number of sessile invertebrate NNS recorded at a site at least once during any visit between 2004 and 2012 was 6.7 (modal value 8 species and median value 7 species, range zero to 13 species) in the 61 English sites (Figure 8A). On the same basis, the English Channel coast (43 sites) had a mean of 7.8 NNS per site (modal and median values both 8 species, range 1 to 13 species) (Figure 8B). All of the ten English sites that had 10 or more NNS were in the western or central region of the Channel coast (Figure 9A). A modelling study by Pearce et al. (2012) identified the Solent, the Kent Coast, and the Thames estuary as regions having particularly high likelihood for introduction and establishment of marine NNS. The numbers of

NNS recorded at sites in our surveys (Figure 9A) do not identify these regions as particular hotspots for sessile invertebrate NNS diversity. However, any such pattern could be partially obscured in our full data set by unequal survey effort (number and nature of visits), both between sites and regions, and by the inclusion of data gathered over several years. These concerns are partially addressed by combining 2010 data in southwestern England and 2009 data for the remainder of the south and east coasts to produce a reduced data set comprising a single RAS at each available site (Figure 9B). Again, the sites within the hotspots indicated by modelling do not stand out as having particularly high counts of NNS. A possible explanation, if the hotspots do indeed exist, is that secondary spreading of NNS from sites of initial entry is sufficiently fast to erase any signal of regional variation in primary introductions. The examples of very rapid secondary spread identified in the ‘Species comparisons’ section above support this possibility.

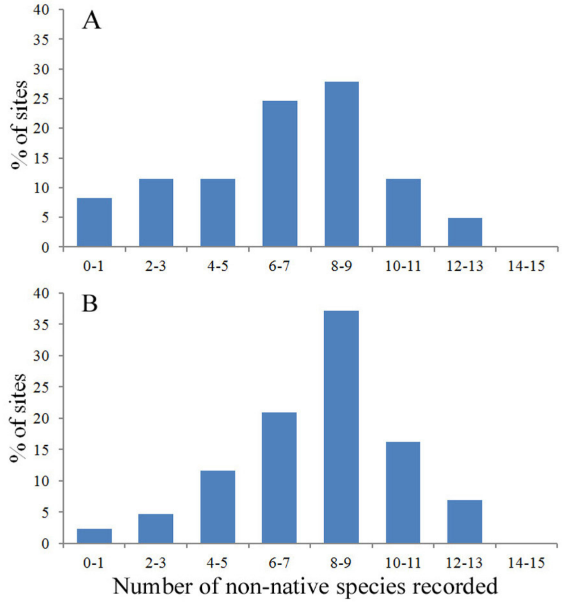

Figure 8. Frequency distributions of sites on the English coast in terms of number of sessile invertebrate NNS recorded per site. A: 61 sites around whole coast; B: 43 sites on English Channel coast.

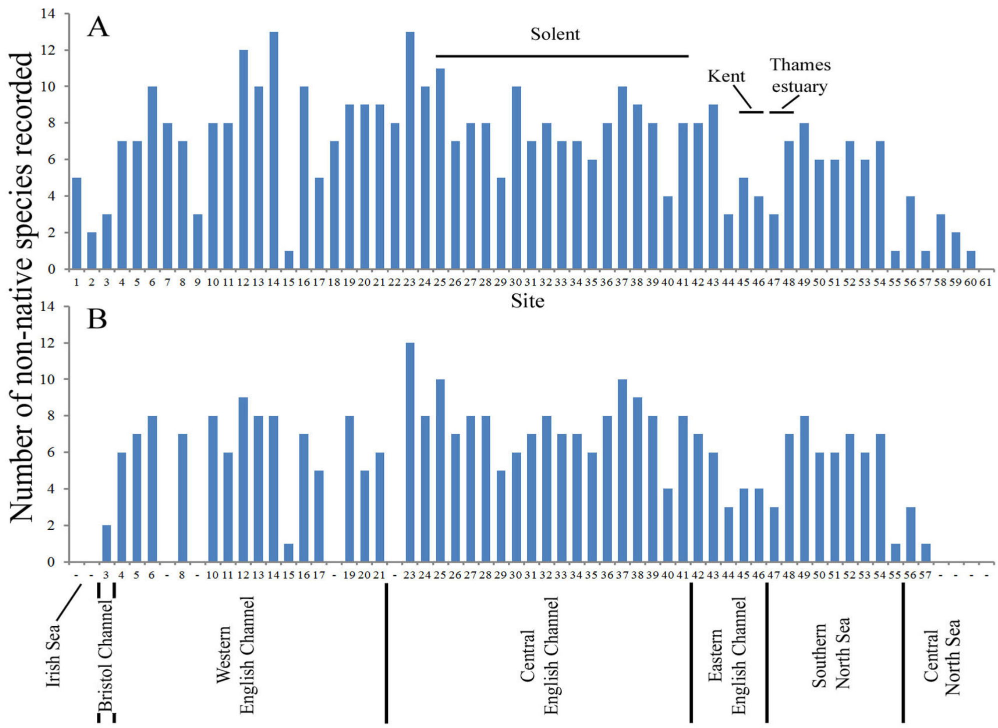

Figure 9. Counts of sessile invertebrate NNS recorded at individual sites around English coast. A: all data 2004–2012. B: data from single RAS survey at each site, 2009–10. Un-numbered sites in B: no survey undertaken. See Table S1 for details of sites.

Although relatively few sites were surveyed there, northeastern England (Central North Sea in Figure 9) did appear to host fewer NNS (range 0 to 4 NNS at the six sites, Figure 9A) than the coasts further south. Of the six most prevalent species in the total data set (Figure 6), *Bugula neritina* was not recorded in northeastern England, while *Styela clava* and non-native *Botrylloides* were found only at Grimsby, the most southerly survey site in this region, and *Tricellaria inopinata* was recorded only at Grimsby and Scarborough. Low salinity at the time of the visits to Hull (surface salinity 18.0) and North Shields (11.5) suggests that freshwater influence might contribute significantly to the low diversity of NNS recorded at those two northeastern sites.

Discussion

The low percentage (2.6%) of species first records generated during the final fifteen minutes at 11 Solent marinas in December 2009 suggests that a one-hour search of a site is generally adequate to detect the target species present. It would of course be expected that abundant species would be detected quickly and that late-detected species would predominantly be rarer taxa. Salinity recorded as single readings on generally infrequent visits to sites showed very little correlation with NNS diversity at the sites, and is thus little mentioned in our account. It is clear that automated salinity measurements at frequent intervals over a period of time to capture patterns of fluctuation and to document brief but potentially influential extreme salinity excursions would be much more informative.

The 2004 to 2012 surveys recorded an average of 6.7 sessile invertebrate NNS per English marina. The complete resolution of the non-native species of *Botrylloides* would increase this figure somewhat. Furthermore, in this figure there was minimal contribution from Cnidaria and none from Porifera. Within these phyla, few non-natives are recognised in GB (e.g. Minchin et al. 2013). This is despite the likelihood that these two taxa have been widely dispersed by human activities. For instance, amongst the Cnidaria, hydroids could be transported both in ballast water (as larvae or, if present, as the medusa stage), and on hulls or shellfish (as the sessile polyp stage). Motile animal species could also be added to the total of NNS, and it is probable that surveys of non-native algae would produce figures broadly comparable to, or exceeding, those for the sessile animals reported here (e.g. Arenas et al. 2006).

By 2012, four non-native sessile marine invertebrates had appeared in England since the published 2004 surveys reported by Arenas et al. (2006): *Asterocarpa humilis*, *Didemnum vexillum*, *Schizoporella japonica* and *Watersipora subatra*. A fifth species, *Ciona intestinalis* ‘type A’, had been distinguished from its native congener (*C. intestinalis* ‘type B’) and might have been present at surveyed sites in 2004 but would have been unrecognised: as stated above, photographic evidence indicates that the species was present at PLYM 5 in 2003. Even in the absence of regularly repeated surveys, progressive colonisation of additional marinas has been documented since 2004 (or since the species’ more recent first appearance) by *A. humilis*, *Botrylloides diegensis*, *Corella eumyota* and *W. subatra*, with lesser contributions from other species. Ten sites that were surveyed in 2004 were subsequently re-surveyed. At these sites, arrivals and range expansions produced an increase in the mean number of sessile invertebrate NNS recorded per site from 6.0 in 2004 to 7.6 in RASs in 2009 or 2010, an average increase of 1.6 NNS per site in five or six years. (These figures were calculated in both periods with the inclusion of species already noted during the 2004 surveys but not reported as NNS in the resulting publication by Arenas et al. (2006): *Botrylloides diegensis*, *Bugulina simplex* and *Bugulina stolonifera*.) Combining site-occurrence data across all visits up to 2012 results in a further increase to 9.2 NNS recorded per site, partly reflecting further colonisation after 2010 but also the effect of more complete inventories achieved by multiple surveys.

In 2004 *C. eumyota* was recorded at three widely spaced sites. Its subsequent spread appeared to involve relatively large saltatory movements, followed by infilling of vacant sites within the new range, rather than a progressive wave of expansion along the coast. This process presumably involved anthropogenic vectors of dispersal, since *C. eumyota* broods its embryos and releases tadpole larvae that are ready to settle, and is thus expected to have very limited natural dispersal (Lambert 2004).

In this study, RAS data augmented with additional information appeared effective in documenting the arrival and spread of NNS over a relatively wide geographic range. However, the data presented here were acquired in a somewhat piecemeal manner. Stronger inferences and better earlier detection would doubtless be possible from surveys repeated according to a fixed protocol at regular intervals, enabling better mapping of extent, fuller comparison between years, and thus improved understanding of patterns and rates of spread.

We would expect most or all of a suite of recently arrived species currently showing relatively limited distributions to increase markedly in geographic range and prevalence in GB in the coming years: *Schizoporella japonica*, *Didemnum vexillum, Watersipora subatra*, *Asterocarpa humilis, Botrylloides diegensis,* and possibly *Ciona intestinalis* 'type A'. *Botrylloides violaceus* is still under-recorded because of difficulties of definite identification and thus has the potential to be more widely recorded within its known range but also may colonise further stretches of the coast of GB. Despite its rather slow colonisation of marinas in England to date, *Perophora japonica* could be added tentatively to this 'of concern' list on the basis of its common occurrence in northern France, where it was recorded 17 years before the first occurrence in GB, and its recent discovery in widely-separated natural habitats in the UK.

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The following supplementary material is available for this article:

Table S1. Details of sites visited (with number of 'surveys' at each).

Table S2. Occurrence of non-native sessile invertebrates at 61 sites on the English coast in 2004–12, with site and visit details.

Table S3. First records of ascidian species in authors' surveys 2004–2012; apparent colonisation.

Table S4. First records of bryozoan species in authors' surveys 2004–2012; apparent colonisation.

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