



Fouling communities and non-native species within five ports along the Bristol Channel, South Wales, UK

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ABSTRACT

Non-native species (NNS) are widely regarded to be one of the major threats to the loss of biodiversity worldwide. Maritime trade is the primary pathway for the transport and introduction of aquatic NNS around the world, and ports are central to this network. Our knowledge of port communities and the NNS they contain is limited, with ports often remaining unsurveyed for decades, which was the case within the studied region. Settlement plates were deployed for 10–11 months at five commercial ports along the Bristol Channel and Severn Estuary in South Wales, UK. We report unique communities in each of the ports with salinity being the main driver for differences among locations. Eleven NNS were identified across all ports with non-native to native species proportions ranging from 0.13 to 0.33 in each port. Most of these NNS are known to exist in the region and are 'established' species within the UK. High variation in community structure and NNS composition among all ports independent of geographic proximity highlights the importance of monitoring individual ports with a view to implementing bespoke, effective NNS management strategies.

1. Introduction

Aquatic non-native species (NNS) have long been associated with the loss of biodiversity and their direct impacts on native species, habitats and ecosystems (Bax et al., 2003; Molnar et al., 2008; McGeoch et al., 2010; Blackburn et al., 2014). Whilst documenting the impacts of NNS is vital in developing an understanding of how damaging the spread of species can be, as well as raising the profile of the problem of NNS, the focus must remain on managing species introductions in order to minimise impacts. Management of NNS is most successful following the early detection of a species introduction to a new location, with management options becoming limited as species become established (Blackburn et al., 2011; Giakoumi et al., 2019). Monitoring or screening for early NNS introductions is therefore an essential aspect of management (Pyšek and Richardson, 2010; Blackburn et al., 2011).

Maritime trade is widely considered to be the primary pathway for the spread of marine NNS worldwide (Ruiz et al., 1997; Katsanevakis et al., 2013; Seebens et al., 2013; Williams et al., 2013; Bailey, 2015). At the centre of all maritime trade are ports, making these areas particularly high risk for the introduction of NNS (Bailey, 2015). A wider concern surrounding ports is the potential role that these areas may play in the invasion of species to a region by serving as vectors for NNS into

adjacent natural systems, following an initial introduction into the port (Floerl et al., 2009). Ports are often isolated locations, where water conditions can be influenced by a range of factors including freshwater input and industrial port processes. Ports connected to the same water body may not therefore share the same, or similar, environmental conditions or communities, including NNS.

Ports are often a key focus in the monitoring of NNS, with a view to identifying novel species introductions early and allowing the most effective system of management to be implemented (Cohen et al., 2005; Marins et al., 2010; Borrell et al., 2017; Travizi et al., 2019).

Port fouling communities worldwide are often dominated by sessile benthic organisms, included a large number of ascidians, associated with the hull fouling transport vector (e.g. Cohen et al., 2005; Marins et al., 2010; Giachetti et al., 2019). However, lack of data from within UK ports and the evident variation between port communities elsewhere in the world highlights the importance of monitoring port fouling communities in unstudied regions.

Survey methodologies widely used to detect marine NNS in ports, marinas and associated habitats, generally take the form of a settlement study (e.g. Arenas et al., 2006; Floerl et al., 2012; Mineur et al., 2012; Marraffini et al., 2017). These surveys have been used extensively around the world in various habitats and are regarded to be effective in

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the detection and identification of NNS (Floerl et al., 2012; Marraffini et al., 2017). Ports can be hostile places to carry out research, with safety being a key factor when working amongst large machinery, vessels, and associated cargo. Safe locations from which to deploy materials or access existing materials, necessary for conventional survey methods, can be rare within ports. Many settlement studies also overlook temporal variation in communities, despite succession being a key feature of fouling communities (Berntsson and Jonsson, 2003; Langhamer et al., 2009; South et al., 2019). With a view to detecting all NNS that may be present within a fouling community, the application of a survey which takes temporal variation into account may prove effective.

Large scale strategic monitoring of NNS in Great Britain aims, in part, to develop 'early detection, surveillance, monitoring and rapid response' (UK Government, 2015). Efforts have so far been made to increase the involvement of various organisations and incorporating citizen science with the goal of increasing the amount of data being recorded in the public domain (UK Government, 2015). Ports, however, being privately owned and privately run industrial areas offer several complications for this strategic monitoring effort. For safety and access reasons large scale citizen science cannot be applied within ports, and certain survey types may not always be suitable for use.

It has been noted that the spatial resolution for NNS monitoring is low across the whole of Europe, with many habitats not being consistently and regularly monitored (Painting et al., 2020). Whilst legislation such as the Water Framework Directive (Council Directive, 2000/60/EC), the Marine Strategy Framework Directive (Council Directive, 2008/56/EC) and the EU Biodiversity Strategy (COM (2011) 0244, final) drive the notion of preserving natural biodiversity and the monitoring and management of NNS, there is no clear or standardised protocol to assist port operators in achieving this (Boon et al., 2020). Developing a standardised survey protocol may be a step towards improving NNS monitoring within ports, increasing the data flow into large scale management strategies and improving our ability to minimise the risk that NNS pose to our native species and habitats, as well as

coastal industry.

The aim of this study was to understand factors influencing the fouling communities in active ports, and specifically fouling of NNS. The objectives of this study were to:

1. Describe the fouling communities and detect NNS present in five ports in South Wales, UK.
2. Quantify aspects of community succession (community composition, abundance, coverage) over the course of an 11-month deployment of settlement plates.
3. Assess the influence abiotic variables have on determining fouling community composition and the proportion of NNS within port communities.

2. Materials and methods

2.1. Study area

Research was conducted within the ports of Newport, Cardiff, Barry, Port Talbot and Swansea, each located along a 55-mile section of the Bristol Channel and Severn Estuary in South Wales, UK (Fig. 1). These ports are all commercial ports owned and operated by Associated British Ports (ABP) and are each connected directly to the Bristol Channel by a lock. There is only one published survey from the 1950s of Swansea (Naylor, 1957) and none from the remaining four ports. Water levels are maintained in all shipping areas to at least 10 m depth whilst the Bristol Channel itself experiences a tidal range of up to 13 m. These ports may therefore support unique subtidal communities that are influenced by a range of factors including environmental conditions as well as the potential introduction of species through maritime trade.

Salinity levels, measured using an Aquaread AP-5000 probe, varied between ports from freshwater in Port Talbot to near marine salinity in Swansea (Table 1). Barry, Cardiff and Newport all occupy a range of brackish salinities, with Cardiff the only port displaying any

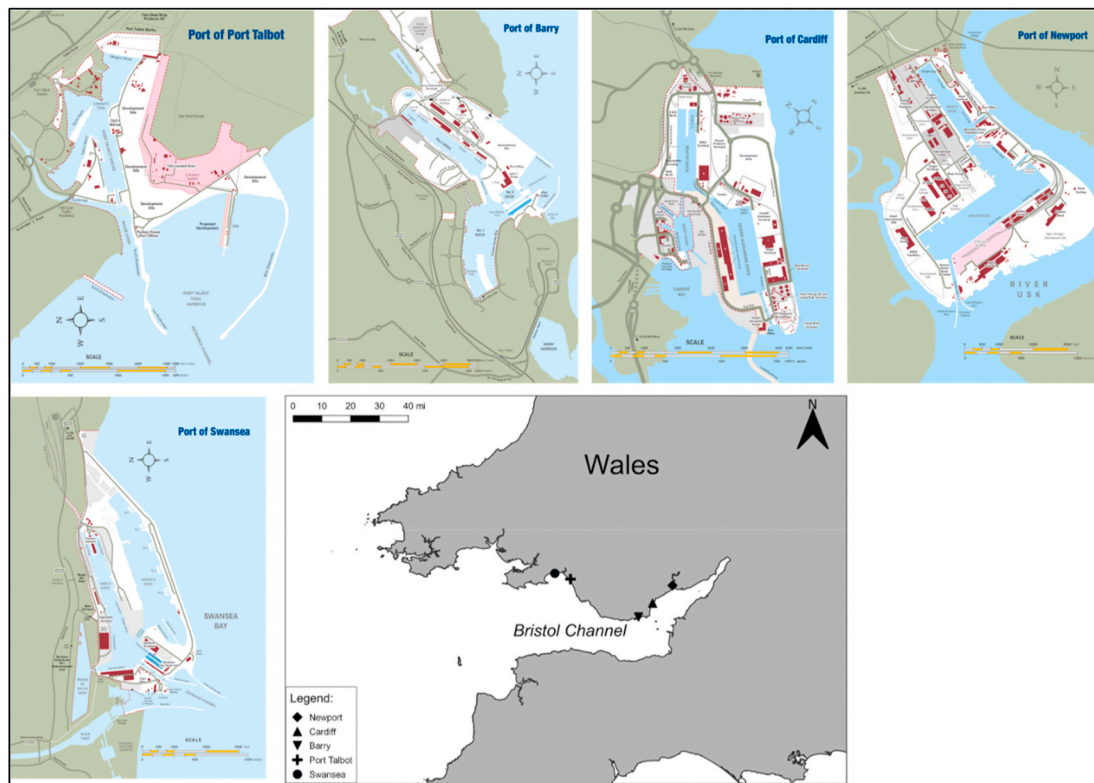


Fig. 1. Location and layout of the five ports surveyed as part of this research. Charts of ports by Associated British Ports. <https://www.abports.co.uk/>

Table 1

Salinity, shipping traffic and species richness of ports at the Bristol Channel (East to West). Salinity range over 11 months (2019), mean shipping traffic calculated from ABP logs; total number of species colonising settlement plates in 2019.

Port	Salinity	Shipping traffic (mean month ⁻¹)	Total number of species
Swansea	28–30	81	30
Port Talbot	0.1–0.3	8	6
Barry	22–24	22	25
Cardiff	1–12	42	14
Newport	8–16	73	13

stratification whereby salinity can increase from 1 in surface water to 12 at a depth of 7 m.

The variation in salinities between ports is due to the way in which water levels are maintained. Port Talbot, Cardiff and Newport all have a direct freshwater inflow from nearby rivers, whilst Barry and Swansea ports rely on the pumping of water from the Bristol Channel at high tide. Water in the Port of Port Talbot is consistently at least 3 °C warmer than the other ports due to the use of dock water for cooling within an adjacent steel works. The effluent of this process is returned into the dock which results in its warming (ABP, personal communication).

ABP provided quantitative data of the number of ships passing through port locks. The data was summarised from 2018 to 2019, and average traffic per month was calculated (Table 1). Fewer ships enter Port Talbot docks compared to the other four ports as most of the trade in Port Talbot takes place outside of the docks in a tidal harbour.

2.2. Survey design and data collection

The study was designed to record succession of ecological parameters (community composition, species richness, abundance, percentage cover) over six sampling dates during a 10–11-month deployment period in 2019. This also maximised the opportunity to detect as many species as possible over almost one year. Three sites in each port were chosen for the deployment of settlement plates and each of site was regarded as an independent replicate for the port location.

Poly(methyl methacrylate) (PMMA) tiles (15 cm × 15 cm, grey in colour) were used as the settlement material. 6 tiles per site were lightly sanded using 40 grit sandpaper and mounted, using cable ties, vertically within an aluminium frame (Fig. 2). Each frame was suspended in the water column using polypropylene rope, attached to a fixed surface

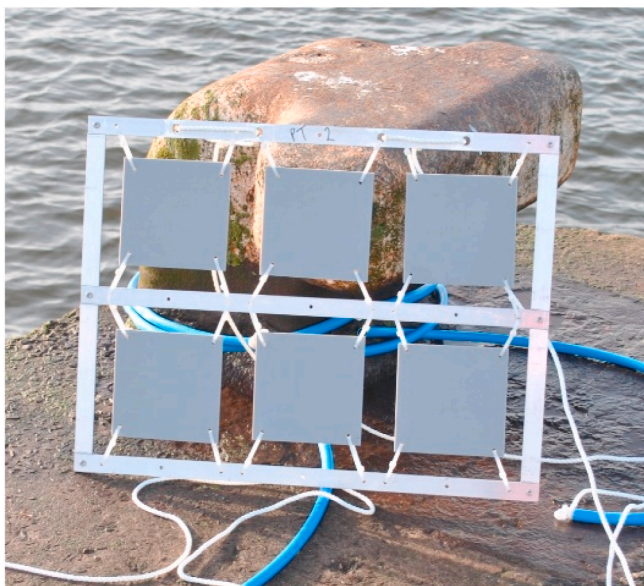


Fig. 2. Survey materials prior to deployment.

mounting point (e.g. a mooring bollard; Fig. 2). Frames were suspended initially to a depth of approximately 4 m, although the water level in the port can vary meaning that depth did not remain constant during deployment. Frames were deployed in December 2018 and retrieved in October/November 2019. One PMMA tile was removed from each frame every 6–8 weeks and returned to the laboratory for analysis, where macrofauna were visually identified to the lowest possible taxon from both the front and the reverse side of the tile using guides such as the *Handbook of the Marine Fauna of North-West Europe* (Hayward and Ryland, 2017), *British Marine Amphipoda* (Lincoln, 1979) and Linnean Society taxonomic resources. Tiles were photographed in the laboratory from which percentage cover was calculated using ImageJ software.

Temperature was measured continuously using Tinytag sensors, recording every 30 min, which were attached directly to the aluminium frame holding the settlement plates. Measures of salinity, temperature, depth, pH, dissolved oxygen (DO; mg/L and % saturation), and oxidation reduction potential (ORP) were taken periodically throughout the survey period using an Aquaread AP-5000 probe.

2.3. Data analysis

Whole community analysis, comparing samples collected within each port at each sampling occasion, was completed using Primer 6 v.6.1.13 with PERMANOVA v.1.0.3 (Anderson et al., 2008). Separate analyses outlined below were conducted using square root transformed abundance counts of countable species and the presence/absence of all recorded species to incorporate both countable and non-countable species.

All samples without colonisation were removed from multivariate analysis (January and some of March 2019). A similarity matrix using a Bray Curtis similarity index was created for all samples with colonising species. A non-metric multidimensional scaling (nMDS) plot and PERMANOVA were completed from this matrix. A PERMANOVA test was designed with the fixed factors 'Port' and 'Month' and values in the similarity matrix as response variable to analyse the effect of the different ports and months on the fouling communities. The model used the permutation of residuals under a reduced model with type III (partial) sum of squares and 9999 permutations.

Pairwise PERMANOVA analyses among 'Port' groups and 'Month' groups were also completed using this same model design. This design was also used to analyse the effect of Port and Month as factors both on the number of non-native species and the frequency of occurrence of NNS within samples based on a similarity matrix generated using Euclidian distances. Inclusion of the factor 'Month' here partially addresses aim two, meaning to better understand the temporal succession of colonisation.

Due to a high variation in community composition between ports, the factor 'Month' was also analysed independently for each port, further addressing aim two. Kruskal-Wallis tests were conducted to determine the effect of month on three measures of colonisation: number of species, total abundance (countable species), and percentage cover (all species) within each port. Pairwise Dunn's tests were used to identify significant differences in the colonisation between months. These analyses were carried out within R v.3.6.2 (R Core Team, 2017).

A distance-based linear model (DistLM) with distance-based redundancy analysis plot (dbrDA) was used to quantify how much variation between samples could be attributed to certain environmental and human driven variables, addressing the third aim of this study to understand the importance of environmental factors in the colonisation process. Variables used were temperature, salinity, pH, DO (% saturation), ORP, and ship traffic. No autocorrelation between variables was detected based on correlations generated using a draftsman plot in Primer 6. The DistLM was based on values in a Bray Curtis similarity matrix based on square root transformed abundance data. The DistLM used a stepwise selection procedure and R² selection criterion with 9999 permutations. When analysing the influence of these variables on the

number of non-native species and frequency of occurrence of NNS within samples the DistLM was based on a similarity matrix created using Euclidian distances.

3. Results

3.1. Fouling communities

Swansea had the highest recorded number of species, followed by Barry, Cardiff, Newport, with Port Talbot having the fewest (Table 1). Fouling communities were numerically dominated by different species in each port (full list of recorded taxa in the Appendix). *Mytilus edulis* and *Ciona intestinalis* were the only species to feature as the most abundant species in more than one port. Across all five ports, *Amphibalanus improvisus* was the most abundant species, with an average of over 800 individuals recorded per 450 cm² sample (front and reverse side of a 15 × 15cm tile) from the Port of Newport.

The similarity in fouling communities among ports and months was visualised using an nMDS (Fig. 3). Both 'Port' and 'Month' as fixed factors were found to significantly influence the observed fouling communities based on presence/absence data (PERMANOVA: Port, pseudo-F = 16.372, $p = 0.0001$; Month, pseudo-F = 5.024, $p = 0.0001$), as well as the abundance of countable organisms (PERMANOVA: Port, pseudo-F = 9.995, $p = 0.0001$; Month, pseudo-F = 4.436, $p = 0.0001$). Communities observed within each port were found to be significantly different to all other ports in a post-hoc pairwise analysis, based both on the presence/absence of all observed species and the abundance of countable organisms (PERMANOVAs, $p < 0.05$). Communities observed between all month pairs were significantly different to one another (PERMANOVAs, $p < 0.05$), except for March and May, September and October (both for presence/absence and abundances) and July and September (abundances only).

A SIMPER analysis was completed to identify which species are driving the dissimilarity in communities observed between ports. The dissimilarity between ports with large differences in salinity and temperature, e.g. Swansea and Port Talbot, was driven by species which

were present in one port but absent in the other.

Swansea and Port Talbot had an average dissimilarity of 100% of which ca. 45% was contributed by three species: *Balanus crenatus*, *Ciona intestinalis* and *Ascidella scabra*. These species were present in high abundance in the Port of Swansea (mean abundance $\pm$ SE: *B. crenatus*, 10.6 ± 2.6 450 cm⁻²; *C. intestinalis*, 57.7 ± 22.8 450 cm⁻²; *A. scabra*, 85.9 ± 29.1 450 cm⁻²) and absent from the port of Port Talbot. Ports with similar salinity had considerable overlap in the community composition and the dissimilarity between them was driven by the relative abundance of species present in both ports. Cardiff and Newport, for example, had an average dissimilarity of ca. 75% of which over 55% was attributed to three species present in both ports with different abundances: *Amphibalanus improvisus* (mean abundance $\pm$ SE: Cardiff, 65.7 ± 26 450 cm⁻²; Newport, 654.6 ± 326.7 450 cm⁻²), *Ficopomatus enigmaticus* (mean abundance $\pm$ SE: Cardiff, 197.4 ± 91.7 450 cm⁻²; Newport, 0.4 ± 0.4 450 cm⁻²), *Gammarus zaddachi* (mean abundance $\pm$ SE: Cardiff, 0.1 ± 0.1 450 cm⁻²; Newport, 3.2 ± 2.5 450 cm⁻²).

Due to the high variation in community structure among ports the influence of the factor 'month' on fouling communities was also analysed independently for each port. Whole community analysis within ports revealed 'month' to be a significant factor influencing community composition in the ports of Newport, Cardiff, Barry and Swansea (PERMANOVAs: Newport, pseudo-F = 3.9053, $p = 0.0015$; Cardiff, pseudo-F = 8.7874, $p = 0.0001$; Barry, pseudo-F = 3.1573, $p = 0.0001$; Swansea, pseudo-F = 2.802, $p = 0.0013$). Three univariate measures of colonisation were analysed (species richness, total abundance of countable species and percentage cover of all species; Fig. 4) to determine the effect of succession over time ('month') on the observed communities within each port. 'Month' was a significant factor determining the observed number of species, abundance, and percentage cover in the ports of Newport, Cardiff, Barry and Swansea (Kruskal-Wallis test, $p < 0.05$). Only percentage cover was found to be significantly influenced by the factor 'month' within the port of Port Talbot (Kruskal-Wallis test, $p < 0.05$). Pairwise tests revealed that the effect of month was largely influenced by differences in colonisation between early months (January and March) and later months (July, September,

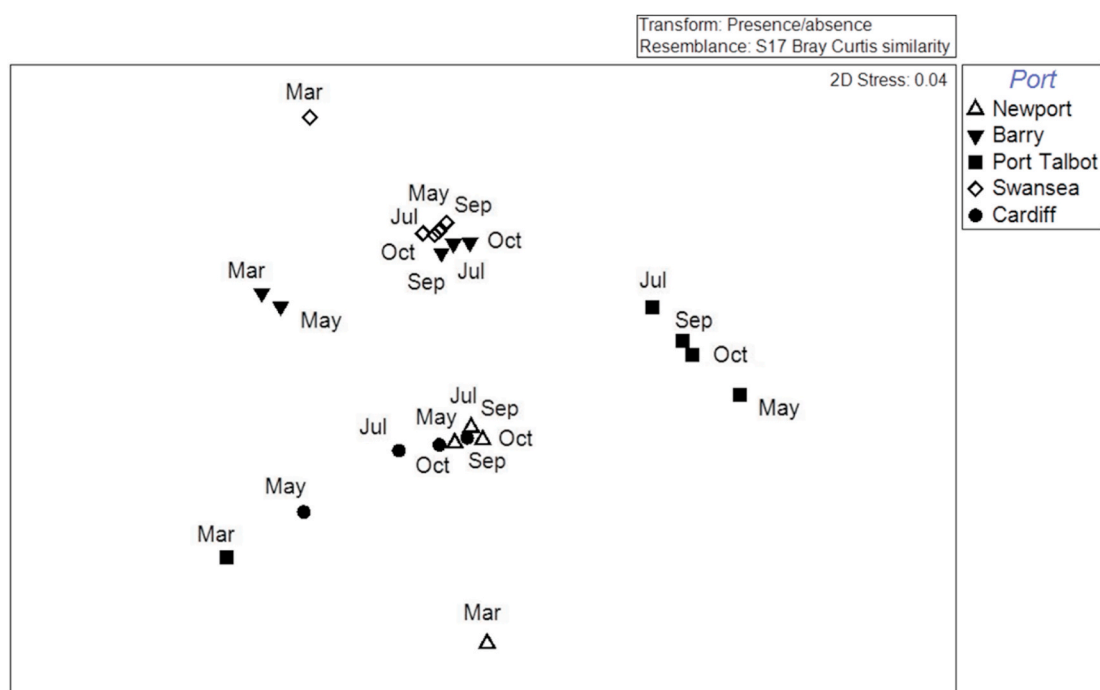


Fig. 3. nMDS plot of fouling community samples collected within 5 ports at bimonthly intervals throughout 2019. Replicate measures averaged for each port per month ($n = 2-3$) and transformed using a presence/absence transformation. Plot based on a resemblance matrix created using a Bray Curtis similarity index. Samples without any species were removed.

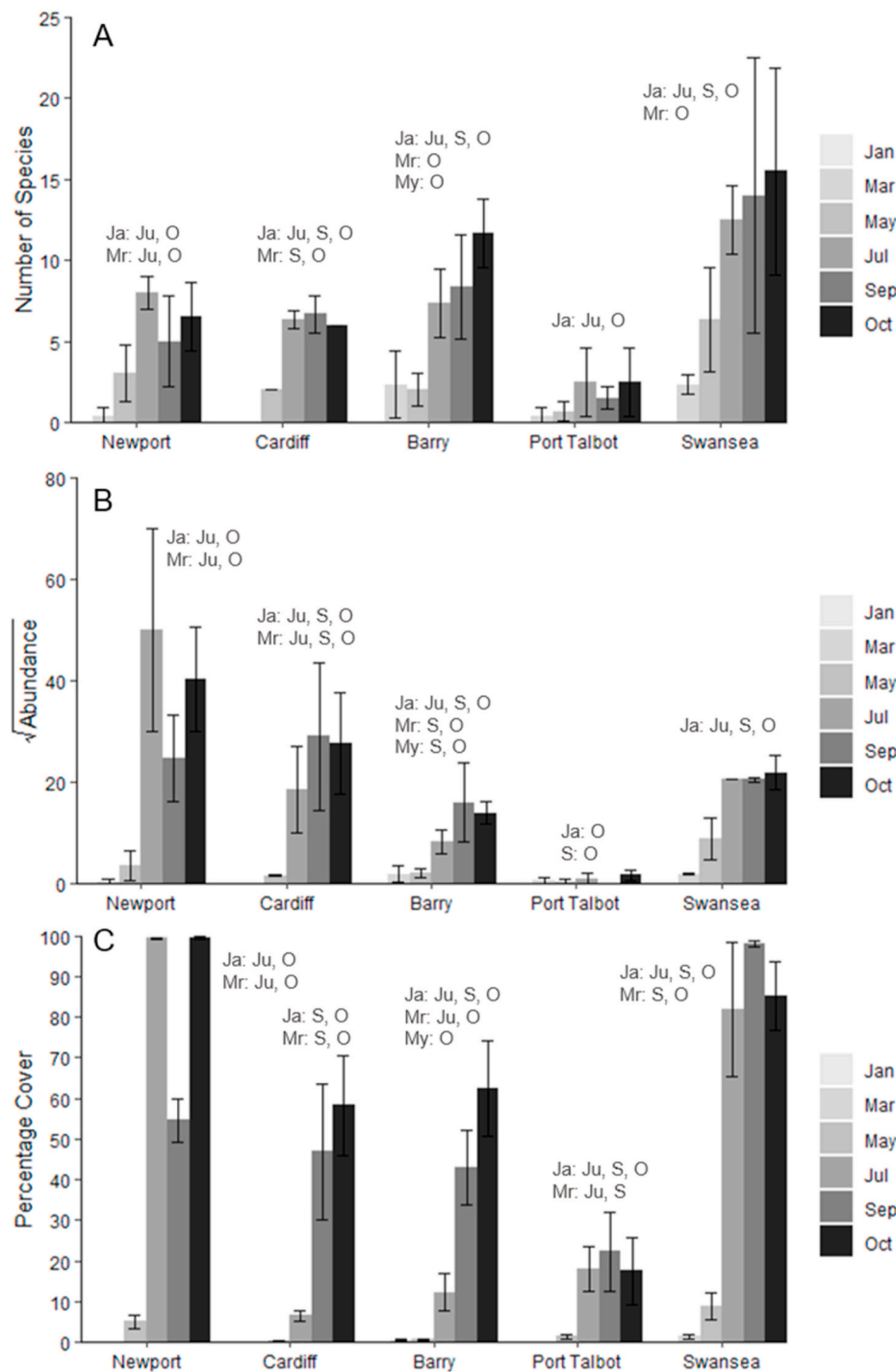


Fig. 4. Colonisation of settlement plates at five ports over 10 months. Records per sampling month in the ports of Newport, Cardiff, Barry, Port Talbot and Swansea. A: Mean species richness 450 cm⁻². B: mean square root abundance per sample. C: Mean percentage cover per sample. Error bars show standard deviation. $n = 3$ with the exception of Newport (Sep, Oct), Cardiff (Oct), Port Talbot and Swansea (Jul, Sep, Oct), where $n = 2$. Abundance based on countable organisms only, percentage cover based on all organisms. Results of significant pairwise Dunn's tests ($p < \alpha/2$, where $\alpha = 0.05$) between month groups within each port are indicated by letters above each set of bars. 'Ja: Ju, O' for example indicates a significant difference between the month pairs January and July and January and October.

October; Fig. 4).

The influence of several abiotic variables (salinity, temperature, pH, DO % saturation, ORP, ship traffic) on the observed communities was analysed using a Distance-based Linear Model (DistLM) and visualised using a dbRDA plot (Fig. 5). Salinity and dissolved oxygen concentration (DO) together were found to explain 23% of the variation observed between samples (DistLM; variable: salinity, pseudo- $F = 7.733$, $p = 0.0001$, prop = 0.132; variable: DO, pseudo- $F = 6.689$, $p = 0.0001$, prop = 0.102). Temperature was found to explain an additional 8% in variation (DistLM, pseudo- $F = 5.543$, $p = 0.001$, prop = 0.078) whilst the remaining three variables included in the analysis (ship traffic, ORP, pH) contributed only 9% combined. Ship traffic, ORP and pH were though all

significant factors in this analysis (DistLM, $p < 0.05$) despite accounting for a small percentage of the total variation. In total these six variables combined explained 40% of the variation observed among samples.

3.2. Non-native species (NNS)

11 NNS were identified across the five ports surveyed within this study (Table 2). The Port of Barry had the highest recorded number of NNS with seven species, whilst Port Talbot had only two. All but one species, *Brachynotus sexdentatus*, are considered to be established species within Great Britain and all but one species (*Cordylophora caspia*) have been previously recorded from within the Bristol Channel area (NBN

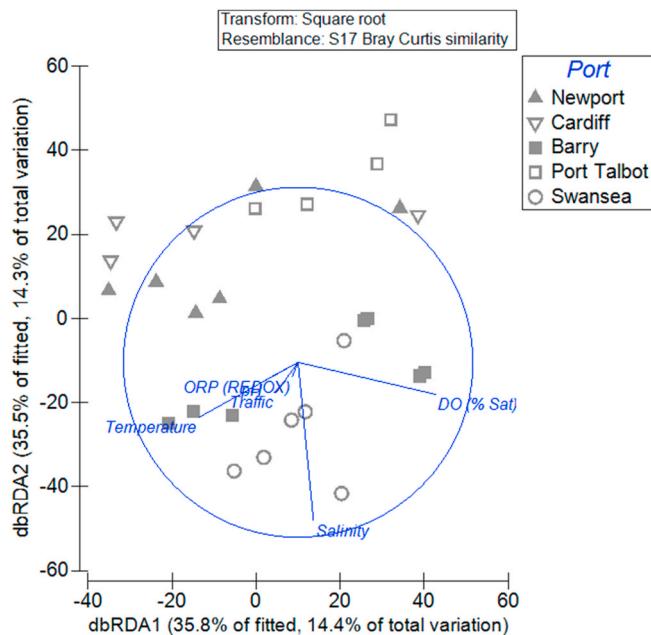


Fig. 5. Distance-based redundancy analysis (dbRDA) exploring the amount of variation between communities that may be explained by six abiotic variables (salinity, temperature, pH, DO, ORP, ship traffic). Analysis completed using a similarity matrix based on a Bray-Curtis similarity index and square root transformed abundance data for countable species.

Atlas, 2019). Port Talbot had the highest proportion of NNS within communities, whereby one in every three species was non-native, Swansea had the lowest proportion of NNS. In descending order, the proportion of NNS was Port Talbot 0.33, Barry 0.24, Cardiff 0.21, Newport 0.15, Swansea 0.13.

The colonisation of the three most dominant NNS based on total recorded abundance (*Amphibalanus improvisus*, *Bugulina stolonifera*, *Ficopomatus enigmaticus*) varied both spatially in terms of which ports they colonise, and temporally in terms of the speed of population development and how the population was sustained thereafter (Fig. 6).

Both Port and Month were found to be significant factors in determining the number of NNS recorded in samples (PERMANOVA; factor: Port, pseudo-F = 2.842, $p = 0.0362$; factor: Month, pseudo-F = 20.213, $p = 0.0001$). As environmental conditions and the amount of shipping vary between ports and months, a Distance-based Linear Model (DistLM) was used to determine whether certain environmental variables or shipping were driving the observed differences in the number of NNS between ports. Temperature and salinity combined accounted for over 30% of the observed variation between samples (DistLM; variable: temperature, pseudo-F = 25.095, $p = 0.0001$, prop = 0.241; variable: salinity, pseudo-F = 10.065, $p = 0.0016$, prop = 0.087). All other variables included in the analysis (DO, ORP, pH, ship traffic) accounted for a combined < 6% of variation in the number of NNS observed among samples (DistLM, $p > 0.05$, prop < 0.03).

By contrast, Port and Month as factors were found to have no significant influence on the observed frequency of occurrence of NNS in samples (PERMANOVA; factor: Port, pseudo-F = 1.593, $p = 0.212$; factor: Month, pseudo-F = 0.792, $p = 0.538$). Ship traffic was the only significant driver of variation in the frequency of occurrence of NNS; it explained 9% of the total observed variation (DistLM, pseudo-F = 5.41, $p = 0.0231$, prop = 0.09). All other analysed variables accounted for a remaining 1.5% (DistLM, $p > 0.05$, prop < 0.006). Combined with ship traffic all factors explained 10.6% of the variation.

Table 2

Non-native species recorded in South Wales ports. GB establishment status and existing presence in the Bristol Channel based on data from NBN Atlas (NBN Atlas, 2019). * indicates species previously known to inhabit the recorded port (s) but not the Bristol Channel.

Taxa	Port(s)	# No. samples where species was present	GB establishment status	Existing Presence in Bristol Channel?
<i>Amphibalanus improvisus</i> (Darwin, 1854)	Newport, Cardiff	13	Established	Yes
<i>Austrominius modestus</i> (Darwin, 1854)	Barry, Swansea	8	Established	Yes
<i>Brachynotus sexdentatus</i> (Risso, 1827)	Swansea	1	Unknown	No *
<i>Bugulina stolonifera</i> (Ryland, 1960)	Barry, Swansea	8	Established	Yes
<i>Caprella mutica</i> (Schurin, 1935)	Barry, Swansea	11	Established	No *
<i>Cordylophora caspia</i> (Pallas, 1771)	Cardiff, Port Talbot	5	Established	No
<i>Diadumene lineata</i> (Verrill, 1869)	Barry	1	Established	Yes
<i>Ficopomatus enigmaticus</i> (Fauvel, 1823)	Newport, Cardiff	6	Established	Yes
<i>Monocorophium sextonae</i> (Crawford, 1937)	Barry	3	Established	Yes
<i>Mytilopsis leucophaea</i> (Conrad, 1831)	Port Talbot	2	Established	Yes (in freshwater)
<i>Styela clava</i> (Herdman, 1881)	Barry	1	Established	Yes

4. Discussion

The formation of fouling communities is known to be a complex process, influenced by a range of abiotic and biotic factors (Sutherland and Karlson, 1977; Glasby, 1999, 2000; Nydam and Stachowicz, 2007; Giachetti et al., 2019; Leclerc et al., 2019). In this study fouling communities varied significantly among five ports located along the same body of water, the Bristol Channel and Severn Estuary (UK). Succession has also long been recognised as a feature in the formation of fouling communities (Berntsson and Jonsson, 2003; Cifuentes et al., 2010; Lindeyer and Gittenberger, 2011). Despite this, most studies aiming to describe fouling communities and to identify non-native species (NNS) do not consider a temporal factor (e.g. Cohen et al., 2005; Arenas et al., 2006; Floerl et al., 2012; Mineur et al., 2012). We identified succession of different aspects of community structure in each of the five studied ports. However, the patterns of succession were not consistent in all ports, with some plates being colonised rapidly early in the spring and others later in the season as well as disparity in the degree of change in community composition among ports. Variation in the degree of succession between communities is not uncommon (Berntsson and Jonsson, 2003; Nydam and Stachowicz, 2007; Ronowicz et al., 2014), and the particularly isolated nature and high variation in environmental conditions between the ports studied here likely contributed to the variation we see in the formation of their respective fouling communities.

Overall, 40% of the variation in the observed fouling communities could be explained by six abiotic variables recorded and analysed within this study (salinity, temperature, dissolved oxygen, pH, ORP, and ship

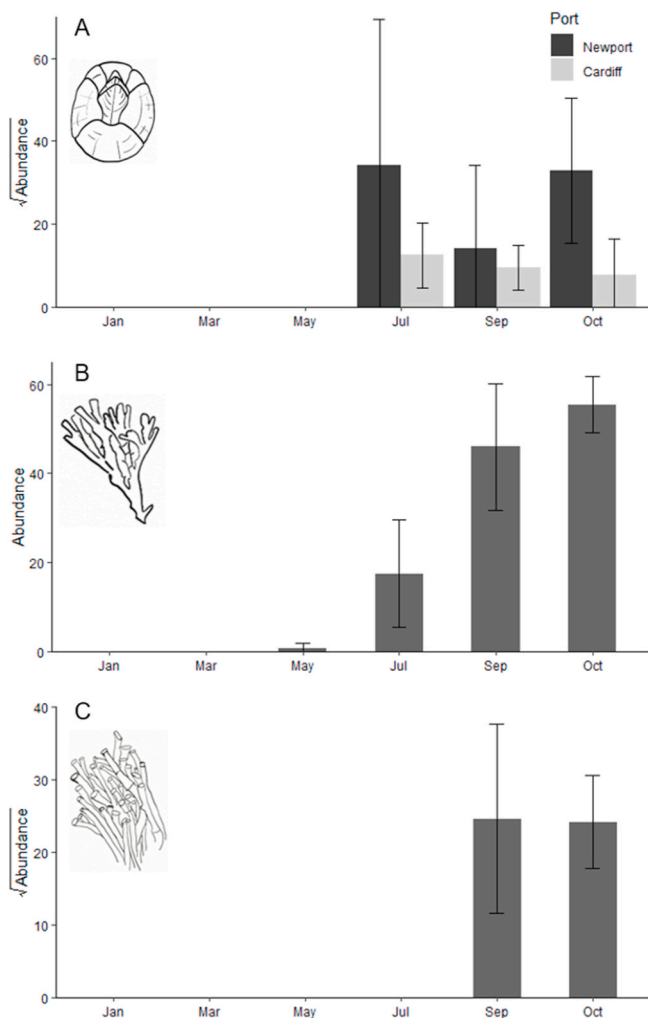


Fig. 6. Spatial and temporal distribution of the three most abundant non-native species. A: *Amphibalanus improvisus* as recorded in the ports of Newport and Cardiff. B: *Bugulina stolonifera* as recorded in the port of Swansea. C: *Ficopomatus enigmaticus* as recorded in the port of Cardiff. *B. stolonifera* and *F. enigmaticus* were each present in only one sample from within the ports of Barry and Newport, respectively, and these data were omitted from the figure.

traffic). 13% of the variation was explained by salinity alone which is concurrent with previous studies highlighting salinity as a significant factor in shaping fouling communities (MacGinitie, 1939; Charles et al., 2018; Pinnell and Turner, 2020). It appears though that other abiotic or biotic factors which were not measured within this study influenced the observed succession.

Reported factors include founder effects (Lindeyer and Gittenberger, 2011; Vieira et al., 2018), predation (Nydam and Stachowicz, 2007; Giachetti et al., 2019), and habitat type (González-Duarte et al., 2018; Leclerc et al., 2019). The latter can be considered negligible or absent from this study given that the studied ports are artificial sites with similar habitat types.

Founder effects and predation, however, may play a significant role in the succession and formation of the observed fouling communities. The effects of predation varied between studies, with some reporting a reduced species diversity in the presence of macropredators, while other studies found no significant effect (Nydam and Stachowicz, 2007; Giachetti et al., 2019; Leclerc et al., 2019). Founder effects may have influenced the succession and composition of the fouling communities. Solitary ascidians, found in high abundance in the ports of Barry and Swansea, may have served as founder species in community development (Lindeyer and Gittenberger, 2011). *Ascidella scabra* has indeed

been linked with succession in fouling communities within the Port of Swansea in a previous study (Holmes and Callaway, 2020). Habitat complexity is known to influence the species diversity of a community (Sueiro et al., 2011; Mendez et al., 2015). Solitary ascidians can colonise rapidly, forming complex 3-dimensional habitats capable of supporting a wide range of other taxa (Svane and Gröndahl, 1988). By contrast, barnacles, such as *Amphibalanus improvisus*, recorded in high abundance in the Port of Newport, form dense mats with little habitat complexity in comparison to solitary ascidians.

It follows then that the observed lower total abundance and higher species diversity in the ports of Barry and Swansea were possibly facilitated by the abundant solitary ascidians present. However, these biotic variables are inherently linked to environmental conditions within each port, particularly salinity. For example, whilst *A. improvisus* would be able to thrive in the environmental conditions in the Port of Swansea (Dineen Jr. and Hines, 1992) and may have been spatially outcompeted by ascidians, *A. scabra* would likely not tolerate the lower salinity environment in the Port of Newport (Hiscock, 2006).

Brackish environments also tend to support lower diversity in general (Cognetti and Maltagliati, 2000), which likely contributed to the lower observed diversity in the brackish ports of Newport and Cardiff. It seems plausible that whilst founder effects may be crucial in forming the observed communities within each port, salinity remains the underpinning variable in determining community composition and explaining the variation in communities between these ports.

A major concern regarding ports is the role they may play in the spread of NNS by serving as vectors into a region (Floerl et al., 2009). Eight of the 11 NNS recorded across the five ports have an existing presence within the Bristol Channel and Severn Estuary, the immediately adjacent water body to each port (NBN Atlas, 2019). Known effects of propagule pressure in aquatic invasion biology (Lockwood et al., 2005; Colautti et al., 2006; Wilson et al., 2008; Bacon et al., 2014) indicate a likelihood that the studied ports contributed to the introduction and establishment of NNS in this region, although it is impossible to quantify the role they played in this process due to a lack of historical data. The focus here will be on the three NNS that have to date not been recorded outside of the ports within this region: *Brachynotus sexdentatus*, *Caprella mutica* and *Cordylophora caspia*. Based on the environmental tolerances of each of these species, *B. sexdentatus* and *C. caspia* are at a low risk of spreading out of the ports where temperatures can range from <5 °C to 23 °C and salinities from 17 to >30 (Henderson et al., 2012). *B. sexdentatus* is native to the Mediterranean Sea and is thought to have become resident within the Port of Swansea whilst artificial warming was taking place within the port, which ceased in the 1970s (Arenas et al., 2006). It is likely that *B. sexdentatus* has become adapted to the cooler water temperatures over time, and therefore may be able to tolerate the temperature ranges within the Bristol Channel, however it remains to be seen whether this is the case since *B. sexdentatus* has not been recorded from outside of the ports to date. It may be that the salinity range within the Bristol Channel is not favourable for this species, or that the low abundance within the port is limiting the potential for dispersal.

C. caspia is a freshwater/brackish species of hydroid, capable of tolerating salinities below 16 (Folino-Rorem and Indelicato, 2005), therefore unlikely to survive in the considerably higher salinities of the Bristol Channel.

In contrast, *C. mutica* has the environmental tolerance to survive in these conditions (Ashton et al., 2007a). *C. mutica* has a strong link to human activity in the marine environment, and particularly the maritime trade industry, having regularly been recorded within ports and marinas worldwide and rarely within natural habitats (Willis et al., 2004; Ashton et al., 2007b). This suggests that *C. mutica* is not successful at dispersing beyond enclosed environments, perhaps due to the lack of a larval stage in Caprellid amphipods (Thiel, 1998; Cook et al., 2007). It may also be due to the relatively recent dispersal of this species around the world, and the spread of populations out of ports may accelerate

over time. A lack of records from outside of ports and marinas should therefore not be used to downplay the risk of spread. The relatively low abundances recorded for *C. mutica* across the five surveyed ports (total abundance of 50) does though reduce the risk of wider dispersal as recruitment is most likely low within the ports.

When considering the abiotic variables which drive the number of NNS within ports, temperature and salinity alone accounted for over 40% of the observed variation between samples. In general, the number of NNS was greater in samples collected from environments with higher salinity and temperature. Most aquatic NNS tend to be marine species, owing to the necessity to survive interactions with marine bodies of water in most ship transits (Carlton, 1996; Seebens et al., 2013; Bailey, 2015). This may contribute to the increased number of NNS in ports of near marine salinity, as observed within this study. The amount of ship traffic was not found to be a significant factor in determining the number of NNS, yet was a significant factor in determining the frequency of NNS within a samples.

We believe this to be driven by the high proportion of NNS found in Port Talbot, where one in every three species was non-native, coupled with the considerably lower ship traffic by comparison with the four other ports. This does nevertheless highlight the importance of monitoring a range of port types and not focussing on the ones with the busiest traffic.

Surveying within these challenging environments limited the number of settlement plates that could be deployed, and therefore the number of replicates obtained. It also led to loss of some replicates during deployment. It should be noted that the low number of replicates here may have played a role in the observed statistical variation both spatially among ports and temporally between month groups. The use of frames with six settlement tiles was intended to accommodate increased total replicates as well as allowing for a temporal factor in the study. Such a survey design does however introduce potential pseudo-replication when comparing between month groups in individual ports, since settlement tiles are housed in close proximity within a single frame, thus reducing their independence due to possible interaction between species of individual tiles. The limited number of safely accessible deployment sites limited survey design option, and we feel that on balance the importance of surveying for temporal variation justified the less than desirable survey design. Results should though be viewed with caution and, for example, standard variations should not be over-interpreted, due to the limitations in terms of replication and sampling design.

In terms of management of NNS in ports, the findings of this study suggest that short-term monitoring efforts and resources could be focussed on ports which are more likely to support a larger number of NNS based on the environmental conditions. However, with a view to documenting all NNS within a region and therefore developing the most effective management strategies, long-term monitoring must not focus on any one port. Whilst larger and more active ports may be more at risk to novel introductions based on the amount of ship traffic they experience (Seebens et al., 2013, 2016; Sardain et al., 2019), smaller and historically active ports are likely harbouring NNS and may therefore pose a similar risk to the neighbouring natural systems.

Developing an understanding of the species present within these ports may prove decisive in understanding if, how, and over what timescale NNS spread from a port into a natural habitat.

5. Conclusion

The high degree of spatial variation in the observed communities between ports showed that it cannot be assumed that any two ports, even in close proximity, will be colonised by similar fouling communities. Whilst environmental conditions can provide an indication as to the potential diversity within a port community, the high level of complexity surrounding the formation of fouling communities limits our ability to make assumptions based on environmental conditions alone.

This is of importance when considering the monitoring of non-native species (NNS) within ports or similar isolated environments. The high degree of variation in the NNS recorded among ports highlights the importance of monitoring individual ports, with the aim of documenting the introduction of NNS and minimising the risk of spread. Increasing the spatial and temporal resolution of community data from within the port environment could prove essential in implementing the most effective NNS management strategies.

Data availability statement

If the manuscript is accepted for publication data will be made available via the Pangaea database (<https://www.pangaea.de/>).

CRediT authorship contribution statement

Samuel Holmes: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Project administration. **Ruth Callaway:** Conceptualization, Validation, Resources, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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