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# Occurrence and assemblage composition of intertidal non-native species may be influenced by shipping patterns and artificial structures

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27 This result was attributed to additional species found in rock pools during searches of complex  
28 microhabitats in natural habitats. Assemblages on artificial structures differed among regions,  
29 with regions and harbours with greater numbers of vessels supporting greater richness.  
30 Results highlight the importance of shipping and artificial structures for NNS introduction and  
31 spread.

32

### 33 **Keywords**

34 Invasive species, non-indigenous species, biodiversity, biological invasion, ocean sprawl,  
35 Rapid Assessment Surveys

36

### 37 1. Introduction

38 Habitat modification and the introduction and spread of non-native species (NNS) are  
39 impacting natural ecosystems and threatening global biodiversity (Manchester and Bullock,  
40 2000; Bax et al., 2003; Simberloff, 2005). In marine coastal systems, “ocean sprawl” (*sensu*  
41 Duarte et al., 2012) – the proliferation of artificial structures (e.g., seawalls, groynes, piers,  
42 floating pontoons, offshore platforms) – is replacing natural habitats with a variety of hard  
43 engineered structures built to support human activities (e.g., aquaculture, transportation,  
44 industry, shipping, energy extraction), as well as stabilise and protect shorelines from rising  
45 and stormier seas (Griggs, 2005; Duarte et al., 2012; Firth et al., 2016a; Bishop et al., 2017).  
46 Artificial structures provide new ‘competitor-free’ habitat for NNS settlement and establishment  
47 (Airoldi and Bulleri, 2011; Firth et al., in review), as well as increase ecological connectivity  
48 between local and global shipping hubs (Floerl et al., 2009; Airoldi et al., 2015). These novel  
49 habitats enable the spread of cryptogenic (i.e., it is unclear whether the species is native or  
50 introduced; Kinzie, 1984; Carlton, 1996a), opportunistic (i.e., a species adapted to exploit new  
51 or disturbed habitats; Whitlatch and Zajac, 1985) and non-native species (Ruiz et al., 1997;

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52 Dafforn et al., 2009; Firth et al., 2016a). Artificial structures also facilitate the homogenisation  
53 of biological communities, supporting novel species assemblages not encountered in natural  
54 habitats, and affect the structure and functioning (physical and ecological) of the surrounding  
55 environment (McKinney and Lockwood, 1999; McKinney, 2006; Dugan et al., 2011).

56 The rise in global trade has meant that harbours are characterised by a range of artificial  
57 structures, with an extraordinary amount of shipping traffic arriving from ports across the globe  
58 every day (Seebens et al., 2013; Marine Traffic, 2019; World Port Source, 2019). These mobile  
59 vectors (ranging from small, local leisure craft to large inter-continental commercial tankers)  
60 are able to spread NNS among the proliferating static structures (i.e., seawalls, breakwaters,  
61 groynes, floating pontoons) in destination ports such that the latter act as species reservoirs  
62 (Ruiz et al., 1997; Neves et al., 2007; Clarke Murray et al., 2011; Mineur et al., 2012). At a  
63 global scale, the primary vectors of initial introduction are typically transoceanic ships, barges  
64 and floating platforms (i.e., mobile vectors) that dock in large international harbours (Carlton  
65 and Geller, 1993; Ruiz et al., 1997; Molnar et al., 2008). These vessels transport species in  
66 two main ways: (1) as larvae in ship ballast water (Ruiz et al., 1997; Gollasch, 2008) and (2)  
67 as adults fouling ship hulls (Gollasch, 2002; Drake and Lodge, 2007). Thus, initial NNS  
68 colonisation and settlement tend to be highest within major shipping ports compared to  
69 surrounding areas (Eno et al., 1997; Molnar et al., 2008; Keller et al., 2011). Secondary, local  
70 spread of NNS is then probably through a combination of small mobile vectors (fishing and  
71 leisure craft) to nearby artificial structures (Clarke Murray et al., 2011; Mineur et al., 2012;  
72 Airoidi et al., 2015). Planktonic larvae can also be carried away from the port of introduction  
73 by wave-driven currents (McQuaid and Phillips, 2000), settling on artificial structures along the  
74 coast (McQuaid and Phillips, 2000; Wasson et al., 2001). In this way, artificial structures can  
75 act as stepping stones, allowing non-natives to persist or spread by provision of 'virgin' hard  
76 substrate amongst otherwise uninhabitable habitats (e.g., 'soft bottom' sediment habitat; Apte  
77 et al., 2000; Sammarco, 2015; Airoidi et al., 2015).

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78       The biological communities of artificial structures are typically less diverse, and support  
79 greater numbers of NNS, than comparable, nearby natural rocky shore habitats (Glasby et al.,  
80 2007; Vaselli et al., 2008; Dafforn et al., 2015a). This disparity is attributed to the physical  
81 design of artificial structures; they typically have steep profiles and reduced surface area and  
82 limited topographic complexity compared to their natural analogues (Moschella et al., 2005;  
83 Chapman and Underwood, 2011). The disturbance associated with human activities in  
84 harbours can also physically dislodge organisms and create space for new colonisers to  
85 exploit, thereby influencing successional dynamics of the community (e.g., removal of  
86 predators, loss of canopy algae; Stachowicz et al., 1999; Byers, 2002). Additionally, ports are  
87 usually located within sheltered bays or estuaries, which by nature, experience greater  
88 fluctuations in temperature and salinity (Whitehead et al., 2009), input of nutrients (Statham,  
89 2012) and other pollutants (Stark, 1998; Johnston et al., 2017; Hitchcock and Mitrovic, 2019)  
90 compared to open coasts. More importantly, many non-natives are generalist species that  
91 often have longer planktonic larval durations or extended reproductive seasons (Dineen et al.,  
92 2001; Muxagata et al., 2004), which means they are able to take advantage of bare space as  
93 it becomes available through creation of new substrate or after disturbance events. For  
94 example, in the UK, the non-native barnacle, *Austrominius modestus* (Darwin, 1854), is  
95 reproductive almost year-round (Muxagata et al., 2004), while native barnacle species  
96 reproduce mainly in the spring (e.g., *Semibalanus balanoides* (Linnaeus, 1767)) or summer  
97 (e.g., *Chthamalus montagui* Southward, 1976 and *C. stellatus* (Poli, 1791); Burrows et al.,  
98 1992). These physical and biological factors probably interact, leaving severely disturbed  
99 areas vulnerable to more resilient and opportunistic invaders (Stachowicz et al., 1999; Airoidi  
100 and Bulleri, 2011; Johnston et al., 2017).

101       It is important to understand the practically synergistic interaction between ocean sprawl  
102 and global shipping so that potential introduction points can be predicted and appropriate

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103 invasive species forecasting techniques can be developed. Yet to our knowledge, we know  
104 of no studies that explored the influence of shipping patterns on occurrence of NNS in  
105 intertidal habitats along the south coast of England (an area historically known as a point of  
106 introduction to the British Isles; for a review of potential sources of NNS introduction into the  
107 British Isles see Eno et al. (1997)). Even less attention has focussed on understanding  
108 differences in NNS occurrence and assemblage compositions between natural and artificial  
109 intertidal habitats (but see Glasby et al., 2007; Dafforn et al., 2012; Dafforn et al., 2015a for  
110 natural and artificial comparison in subtidal habitats). Information from natural habitats may  
111 be useful in determining the potential for NNS to spread out from points of initial introduction  
112 (Valentine et al., 2007; Carman and Grunden, 2010; Epstein and Smale, 2018).  
113 Understanding the mechanisms underpinning the differences in NNS occurrence between  
114 natural and artificial habitats is also critical to develop a robust foundation of evidence upon  
115 which to base ecological engineering (i.e., the combination of ecological and engineering  
116 design to create sustainable ecosystems that benefit humans and nature; Mitsch and  
117 Jørgensen, 2003; Odum and Odum, 2003). To address the current knowledge gaps  
118 concerning occurrence of NNS on natural rocky shores and artificial structures in intertidal  
119 habitats, we conducted surveys of NNS in intertidal natural and artificial sites in 11 harbours  
120 along the south coast of England to test the following hypotheses:

- 121 1. NNS richness would be greater, and NNS assemblage composition would differ, in  
122 artificial compared to natural habitats.
- 123 2. NNS richness and NNS assemblage composition in artificial habitats would differ  
124 among harbours and regions, but would be highest in ports with higher number of  
125 arriving vessels.

126 Our study also provided the opportunity to compare data obtained from quantitative  
127 stratified-random quadrat-based surveys with semi-quantitative methods based on timed  
128 searches, as both approaches were used here.

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## 130 2. Materials and methods

### 131 2.1. Study region

132 The English Channel is one of the busiest waterways in the world (Marine Traffic, 2019;  
133 World Port Source, 2019). The coast along the English side of the Channel is characterised  
134 by a number of harbours that support international and regional shipping and cruise traffic,  
135 military traffic, ferries to continental Europe and recreational and tourist activities (Table 1).  
136 Consequently, the south coast of England has traditionally been susceptible to invasions and  
137 is known as the point of introduction into the British Isles for many NNS from Europe and  
138 around the world (Eno et al., 1997; Bishop et al., 2015a; Bishop et al., 2015b). In this study,  
139 harbours were grouped into geographic regions following Bishop et al. (2015b) (West, Central,  
140 East; Table 1, Figure 1). One survey was done per site (hereafter referred to as 'site'), and  
141 sites were located either within natural (rocky shores) or artificial (artificial structures) habitats.  
142 Numbers of sites surveyed per harbour varied and reflected the size of the harbour. All  
143 harbours had artificial substrata, but only harbours in the West had natural rocky shore  
144 (contained within the larger natural harbour) for comparison with artificial structures (for  
145 classification of harbours within regions see Table 1). The natural versus artificial habitat  
146 assessment involved only seawalls made from naturally-sourced rock for comparison to  
147 natural rocky shores. The comparison of NNS across all harbours along the south coast of  
148 England assessed multiple types of artificial structures, which included piers, marina wave-  
149 breaker walls, seawalls, discharge pipes, groynes, boat docks, bridge support structures,  
150 wharfs and breakwaters (Table S1). As artificial structures were opportunistically sampled, not  
151 all structure types were represented in each harbour. To compare richness and assemblage  
152 composition of artificial sites (artificial structures) among harbours and regions across the  
153 entire south coast of England, all artificial structures were used for analysis. The areas



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154 surveyed were at the mouths of any estuarine complexes and generally fully saline at high

155 tides and thus comparable to non-estuarine ports (i.e., Torbay, Folkestone, Dover; Table S1).

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159

160 Table 1. Details for NNS RAS conducted along the south coast of England, including survey details, type of vessels by harbour and harbour  
 161 characteristics. Natural and artificial habitat comparisons were only done in the West region (FAL, LOE, PLY, SAL, TOR). Vessel information was  
 162 obtained from Marine Traffic (2019) and World Port Source (2019). \*International shipping describes types of destinations. \*\*Continental  
 163 passenger ferries (number of destinations) travel from south England to northern Europe. †International cruise lines describe types of destinations.  
 164 ‡Dominant natural habitat is rocky shore ('RS') or soft bottom ('SB') habitat. ††Main features include <sup>a</sup>size of harbour ('v. sm' = very small, 'sm' =  
 165 small, 'med' = medium and 'lg' = large); <sup>b</sup>type of harbour (natural coastal inlet, coastal breakwater); <sup>c</sup>freshwater input; <sup>d</sup>depth of main channel  
 166 ('shallow' = < 5 m, 'average' = 5-9 m and 'deep' = > 9 m) and <sup>e</sup>average tidal range as recorded in July 2018 from Tide Plotter (v. 5.8, Belfield  
 167 Software Ltd). Information on size and type of harbour, as well as depth of main channel were obtained from World Port Source (2019). Details  
 168 regarding type of artificial structures surveyed in each harbour is provided in Table S1.

<i>Survey details</i>			<i>Type of vessels</i>					<i>Harbour characteristics</i>	
<b>Har code</b>	<b>Harbour/ city</b>	<b>Region</b>	<b>Int'l shipping*</b>	<b>Cont'l passenger ferry **</b>	<b>Int'l cruise lines†</b>	<b>Military</b>	<b>Fishing vessels &amp; leisure craft</b>	<b>Dom nat hab‡</b>	<b>Main features</b>
FAL	Falmouth	West	0	0	0	✓	✓	RS	med <sup>a</sup> ; natural coastal inlet <sup>b</sup> ; moderate input <sup>c</sup> ; average <sup>d</sup> ; 3.6 m <sup>e</sup>
LOE	Looe	West	0	0	0	0	✓	RS	v. sm <sup>a</sup> ; natural coastal inlet <sup>b</sup> ; major input <sup>c</sup> ; shallow <sup>d</sup> ; 3.5 m <sup>e</sup>
PLY	Plymouth	West	Global	2	0	✓	✓	RS	med <sup>a</sup> ; natural coastal inlet <sup>b</sup> ; moderate input <sup>c</sup> ; deep <sup>d</sup> ; 3.6 m <sup>e</sup>
SAL	Salcombe	West	0	0	0	0	✓	RS	v. sm <sup>a</sup> ; natural coastal inlet <sup>b</sup> ; minimal input <sup>c</sup> ; shallow <sup>d</sup> ; 3.3 m <sup>e</sup>
TOR	Torbay	West	0	0	0	0	✓	RS	v. sm <sup>a</sup> ; coastal breakwater <sup>b</sup> ; no input <sup>c</sup> ; average <sup>d</sup> ; 3.0 m <sup>e</sup>
POL	Poole	Central	0	1	0	0	✓	SB	sm <sup>a</sup> ; natural coastal inlet <sup>b</sup> ; limited input <sup>c</sup> ; shallow <sup>d</sup> ; 1.0 m <sup>e</sup>
SHN	Southampton	Central	Global	0	Global	0	✓	SB	lg <sup>a</sup> ; natural coastal inlet <sup>b</sup> ; moderate input <sup>c</sup> ; average <sup>d</sup> ; 2.9 m <sup>e</sup>
PMH	Portsmouth	Central	0	6	0	✓	✓	SB	med <sup>a</sup> ; natural coastal inlet <sup>b</sup> ; limited input <sup>c</sup> ; average <sup>d</sup> ; 3.1 m <sup>e</sup>
SHM	Shoreham	East	0	0	0	0	✓	SB	v. sm <sup>a</sup> ; natural coastal inlet <sup>b</sup> ; major input <sup>c</sup> ; shallow <sup>d</sup> ; 4.5 m <sup>e</sup>
FOL	Folkestone	East	0	0	0	0	✓	SB	v. sm <sup>a</sup> ; coastal breakwater <sup>b</sup> ; no input <sup>c</sup> ; average <sup>d</sup> ; 5.2 m <sup>e</sup>
DOV	Dover	East	European	2	European	0	✓	SB	sm <sup>a</sup> ; coastal breakwater <sup>b</sup> ; no input <sup>c</sup> ; average <sup>d</sup> ; 4.7 m <sup>e</sup>

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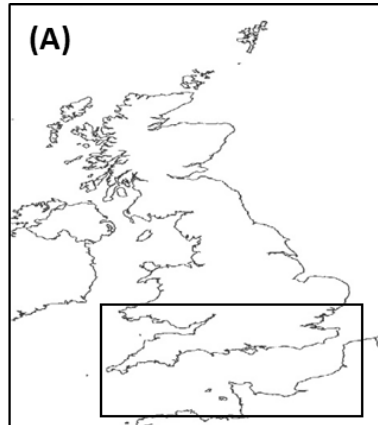
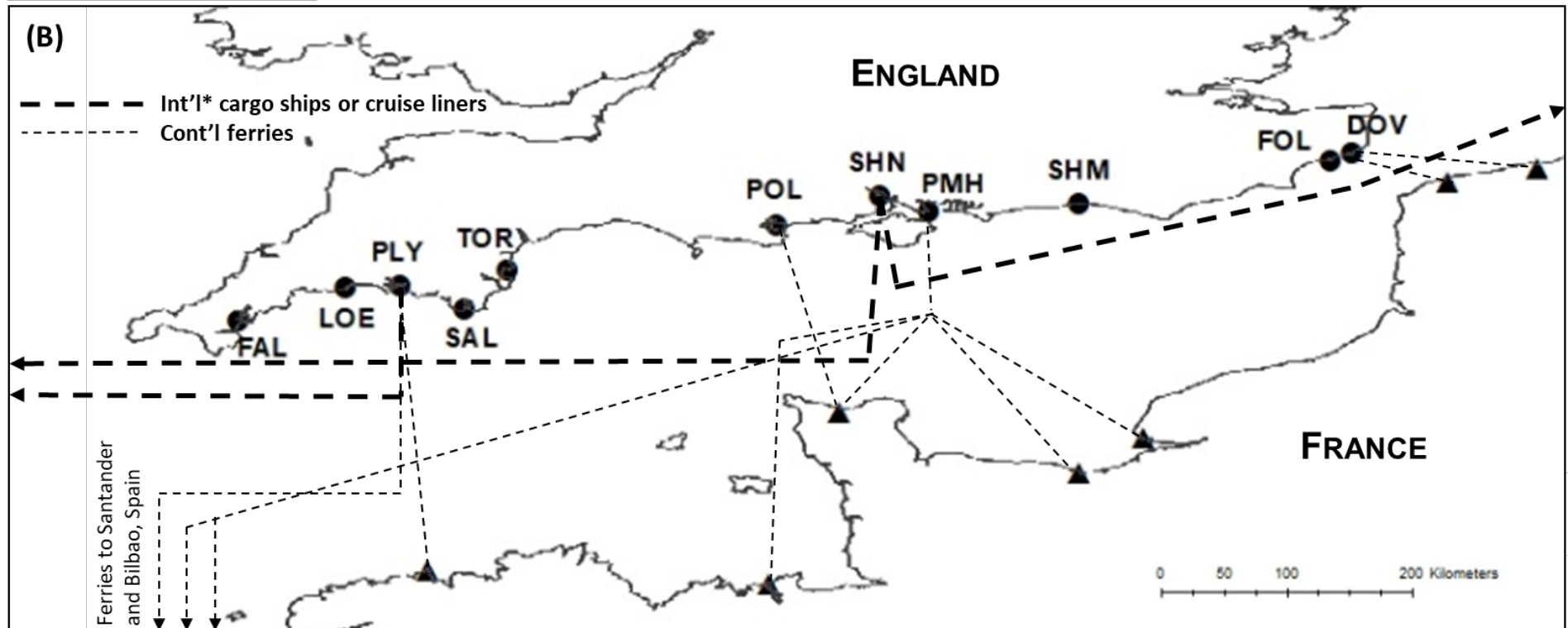


Figure 1. (A) Map of the British Isles, with the English Channel indicated by the black box. (B) Continental ferry routes across the English Channel are shown by the light dashes and internationally sailing vessels (cargo ships or luxury cruise liners) are shown by the dark dashes. Lines representing shipping routes do not reflect the numbers of vessels arriving and departing. \*International cargo ships and cruise liners include only those vessels that travel outside of northern Europe (e.g., Dover supports cargo-shipping activities, but these ships regularly sail only to European destinations). Southampton and Plymouth are the only harbours with ships that sail internationally on a regular basis (dark dashes). Harbours within the West region include Falmouth, Looe, Plymouth, Salcombe and Torbay, and were the only harbours included in the natural and artificial comparison. Harbours within the Central region include Poole, Southampton and Portsmouth. Harbours within the East region include Shoreham, Folkestone and Dover. Artificial structures in all harbours were included in analyses of richness and assemblage composition in artificial habitats. See Table 1 for Harbour codes. Information was obtained from Marine Traffic (2019) and World Port Source (2019).



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## 171 2.2. Sampling methods

172 Rapid Assessment Surveys (RAS) provide a pragmatic method of covering a large number  
173 of locations in a reasonable amount of time (Pederson et al., 2005; Arenas et al., 2006; Bishop  
174 et al., 2015a,b); they typically involve a qualitative approach, using timed searches of targeted  
175 areas and habitats (e.g., undersides of floating pontoons). In biodiversity surveys, however,  
176 the most common means of gathering data is predominantly through quantitative quadrat  
177 sampling, often avoiding topographically complex surfaces (Bulleri et al., 2005; Dafforn et al.,  
178 2012; Firth et al., 2016b). In this study, a combined approach was employed to capture NNS  
179 richness and abundance (i.e., diversity), which consisted of utilising quantitative stratified-  
180 random quadrat sampling and semi-quantitative timed searches. All artificial structures were  
181 accessed on foot at low tide. Native biota were not quantified during any of the surveys.  
182 Quantitative stratified-random quadrat sampling involved haphazardly placing 20 quadrats (25  
183 x 25 cm) in the lower intertidal within a 10 x 10 m area and recording counts of mobile  
184 organisms and percentage cover of sessile organisms. For the purpose of this study, the lower  
185 intertidal was the area of the shore that was inundated during neap low tides but exposed at  
186 spring low tides (i.e., surveys occurred only on spring low tides when tide was  $\leq 1$  m above  
187 CD). Occasionally, this area was condensed because the steeper slope of artificial structures  
188 resulted in reduced area available to survey. In these cases, a longer horizontal section was  
189 sampled to compensate for lost vertical area. All NNS visible to the naked eye within the  
190 quadrats were identified and quantified. To positively identify and quantify the non-native  
191 barnacle, *Austrominius modestus*, 5 x 5 cm photo-quadrat images ( $n = 20$ ) were taken in the  
192 densest barnacle zone and photographs were later analysed using ImageJ (Schneider et al.,  
193 2012). Slope and substrate were standardised by surveying vertical or sloping substrate ( $\geq$   
194  $45^\circ$  angle) and avoiding topographically complex surfaces (i.e., gaps, grooves, pits, crevices,  
195 rock pools). To locate rare species, one person conducted a 30-minute timed search across

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196 the study area, including complex surfaces and microhabitats (e.g., crevices, rock pools,  
197 undersides of boulders). Additional minutes were added to the search where logistical  
198 constraints delayed efficient sampling (e.g., some artificial structures had characteristics that  
199 required careful manoeuvring around the structure compared to other easily accessible  
200 structures or natural rocky shore). A semi-quantitative search-based assessment of overall  
201 abundance of each NNS was made on a scale of 0-3 (0 = absent, 1 = rare-occasional, 2 =  
202 frequent-common, 3 = abundant-superabundant; Bishop et al., 2015b). Thus, the quantitative  
203 quadrat method produced 20 quadrat replicates per site, while the semi-quantitative search-  
204 based method produced one abundance score for each NNS per site. Species that could not  
205 be identified in the field (e.g., bryozoans such as *Tricellaria inopinata* (d'Hondt & Occhipinti  
206 Ambrogi, 1985) and *Bugulina* spp.) were preserved in 70% ethanol and transported back to  
207 the laboratory for microscopic examination.

#### 208 2.2.1. Comparison of NNS in natural and artificial habitats

209 To investigate differences of occurrence of NNS between natural and artificial habitats,  
210 NNS richness and assemblage composition were recorded in ten natural sites (rocky shores)  
211 and eleven artificial sites (seawalls) in the West region (Table 1). Natural sites were chosen  
212 based on location to closest harbour and were as sheltered as possible to reduce the influence  
213 of wave exposure gradients on assemblage composition. There was no restriction placed on  
214 size of seawall.

#### 215 2.2.2. Comparison of NNS in artificial habitats along the south coast of England

216 To assess differences of occurrence of NNS in artificial habitats among harbours and  
217 regions, eleven harbours spanning three regions across the entire south coast of England  
218 were surveyed. Harbours within regions were chosen based on major harbours surveyed in  
219 Bishop et al. (2015b) and those which stretched across each region. As many artificial sites  
220 as possible with public access were surveyed in each harbour (Table 1).

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## 221 2.3. Statistical analyses

### 222 2.3.1. Comparison of NNS in natural and artificial habitats

223 To compare NNS richness and assemblage composition between natural and artificial  
224 habitats, comparisons were made between ten natural sites and eleven nearby artificial sites  
225 using both quantitative quadrat and semi-quantitative search-based data separately (i.e., data  
226 from both methods were used but were analysed separately). For both sampling methods,  
227 where abundance information was used, data were fourth-root transformed to down-weight  
228 the influence of very abundant species (Anderson et al., 2008). Bray-Curtis dissimilarity  
229 matrices were then computed, and permutational multivariate analysis of variance tests  
230 (PERMANOVA; Anderson, 2001) were used to test for differences in species richness and  
231 assemblage composition. Two-way nested designs with Habitat as a fixed factor (2 levels:  
232 natural, artificial) and Site as a random factor (nested in Habitat) were employed.  
233 PERMANOVA tests were based on 9999 permutations of residuals under a reduced model.  
234 Tests for differences were conducted in PRIMER v6 with the PERMANOVA+ add-on using  
235 the PERMANOVA routine (PRIMER-E Ltd, Plymouth, UK; Anderson et al., 2008). Ordination  
236 of samples were visualised using two-dimensional non-metric multidimensional scaling  
237 (nMDS) plots. Contributions to dissimilarities among regions from each species was  
238 determined using the similarity percentages routine (SIMPER).

### 239 2.3.2. Comparison of NNS in artificial habitats along the south coast of England

240 Differences in NNS richness and assemblage composition in artificial habitats among  
241 harbours and regions were assessed using data from both the quantitative quadrat and semi-  
242 quantitative search-based surveys. Where abundance information was used, data were  
243 fourth-root transformed. Bray-Curtis dissimilarity matrices were then computed, and  
244 permutational multivariate analysis of variance tests (PERMANOVA) were used to test for  
245 differences in species richness and assemblage composition. For quantitative quadrat data, a

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<https://doi.org/10.1016/j.marpolbul.2020.111082>

246 three-way nested design was used for each test (species richness and assemblage  
247 composition) with Site as a random factor (number of levels depended on number of sites  
248 surveyed in each harbour) nested in Harbour as a fixed factor (number of levels varied with  
249 region) nested in Region as a fixed factor (3 levels: West, Central, East). As quantitative  
250 quadrat sampling was not undertaken in Salcombe, only ten harbours were included in  
251 quantitative quadrat analyses. Because there was not replication at the 'Site' level when semi-  
252 quantitative search-based data were analysed (i.e., there was one abundance value per site),  
253 two-way nested designs were used with Harbour as a fixed factor (number of levels varied  
254 with region) nested in Region as a fixed factor (3 levels) for each test (species richness and  
255 assemblage composition). Information about vessel type and the average number of vessels  
256 per harbour over a 60-day period as a proxy for boat traffic in general was obtained from the  
257 Marine Traffic (Marine Traffic, 2019) and World Port Source (World Port Source, 2019)  
258 websites. General observations comparing numbers of NNS with numbers and types of  
259 vessels were made with no formal analyses done.

260

### 261 3. Results

#### 262 3.1. Overall results

263 A total of 26 NNS were recorded from natural and artificial habitats across the entire south  
264 coast of England (Table S1). Fifteen NNS were recorded from the natural and artificial habitat  
265 comparison in the West region (Falmouth to Torbay); 12 of these NNS were found in artificial,  
266 while 9 NNS were recorded in natural habitats (Table S1). Six species were exclusive to  
267 artificial habitats, while 3 species were exclusive to natural habitats, with 6 species common  
268 to both. Two NNS were discovered in new localities: colonies of the carpet sea squirt,  
269 *Didemnum vexillum* Kott, 2002, were found on the seaward side of a wooden wave-breaker  
270 wall and a metal pipe positioned perpendicular to the shore in Poole Harbour. Colonies were



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271 also found in Portsmouth on concrete fishing piers perpendicular to the shore. The red alga,  
272 *Botryocladia wrightii* (Harvey) W.E.Schmidt, D.L.Ballantine & Fredericq, 2017 (recently  
273 changed from *Chrysymenia wrightii*), was found in a small water-retaining pool along a  
274 stepped seawall in Portsmouth. The only previously confirmed records of *B. wrightii* in this  
275 study region were from marinas in Falmouth (Wood et al., 2015).

### 276 3.2. Comparison of NNS in natural and artificial habitats

277 Of the 15 NNS recorded across natural and artificial habitats between Falmouth and Torbay  
278 (Table S1), 9 taxa were recorded in natural (60% of total), while 12 were observed in artificial  
279 (80% of total) habitats. Species unique to natural habitats included the brown alga, *Undaria*  
280 *pinnatifida* (Harvey) Suringar, 1873 and the red algae, *Grateloupia turuturu* Yamada, 1941  
281 and *Asparagopsis armata* Harvey, 1855. Species unique to artificial habitats included the erect  
282 bryozoan, *T. inopinata*, the orange cloak sea squirt, *Botrylloides violaceus* Oka, 1927, an  
283 unidentified *Botrylloides* species, *Botrylloides* sp. indet. (Bishop et al., 2015b), the leathery  
284 sea squirt, *Styela clava* Herdman, 1881, the slipper limpet, *Crepidula fornicata* (Linnaeus,  
285 1758) and the red alga, *Bonnemaisonia hamifera* Hariot, 1891. Semi-quantitative search-  
286 based techniques found 15 NNS across natural and artificial habitats, while quantitative  
287 quadrat techniques yielded only 8 species. The use of quantitative quadrat techniques alone  
288 failed to record *B. violaceus*, *C. fornicata*, *U. pinnatifida*, *G. turuturu*, *A. armata*, *B. hamifera*  
289 and the brown alga, *Sargassum muticum* (Yendo) Fensholt, 1955.

290 Statistical analysis of quantitative quadrat data found that mean NNS richness was  
291 significantly greater in artificial compared to natural habitats (Table 2a; Figure 2a). Similarly,  
292 assemblage composition varied significantly between natural and artificial habitats (Table 2a).  
293 Statistical analysis of semi-quantitative search-based data revealed that the mean richness  
294 did not differ significantly between natural and artificial habitats, although community  
295 assemblage did differ (Table 2b; Figure 2b, c). SIMPER analysis of quantitative quadrat data  
296 showed that over 80% of dissimilarity in assemblage composition between natural and artificial

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297 habitats was attributed to *A. modestus* (32.6%), the red ripple bryozoan, *Watersipora subatra*  
298 (Ortmann, 1890) (30.9%) and the red alga, *Caulacanthus okamurae* Yamada, 1933 (23.1%),  
299 with all three species more abundant in artificial habitats. SIMPER analysis of semi-  
300 quantitative data revealed that > 50% of dissimilarity in assemblage composition between  
301 natural and artificial habitats was attributable to four species: *S. muticum* (17.3%), *W. subatra*  
302 (14.5%), the brown alga, *Colpomenia peregrina* Sauvageau, 1927 (12.4%) and the Pacific  
303 oyster, *Magallana gigas* (Thunberg, 1793) (11.8%). *S. muticum* and *C. peregrina* were more  
304 abundant in natural habitats, while *W. subatra* and *M. gigas* were more common in artificial  
305 habitats.

306

307

308 Table 2. PERMANOVA results comparing NNS richness and assemblage composition  
309 between natural and artificial habitats using (a) quantitative quadrat data and (b) semi-  
310 quantitative search-based data. Significant p-values are in bold.

**(a) Quantitative data**

Two-way PERMANOVA comparing species richness between natural and artificial habitats.

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	18976	18976	7.1199	<b>0.0009</b>
Site(Habitat)	18	47985	2665.8	33.327	<b>0.0001</b>
Residual	380	30396	79.989		
Total	399	97274			
Transformation:	pres/abs				

Two-way PERMANOVA comparing assemblage composition between natural and artificial habitats.

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	24297	24297	6.3912	<b>0.0006</b>
Site(Habitat)	18	68443	3802.4	16.724	<b>0.0001</b>
Residual	380	86397	227.36		
Total	399	179000			
Transformation:	fourth root				

This is an accepted proof.

O'Shaughnessy, K.A., Hawkins, S.J., Yunnice, A.L., Hanley, M.E., Lunt, P., Thompson, R.C. and Firth, L.B., 2020. Occurrence and assemblage composition of intertidal non-native species may be influenced by shipping patterns and artificial structures. *Marine Pollution Bulletin*, 154, 111082.

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### **(b) Semi-quantitative data**

---

One-way ANOVA comparing species richness between natural and artificial habitats.

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Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	94.912	94.912	0.59709	0.4781
Residual	19	3020.2	158.96		
Total	20	3115.1			

Transformation: pres/abs

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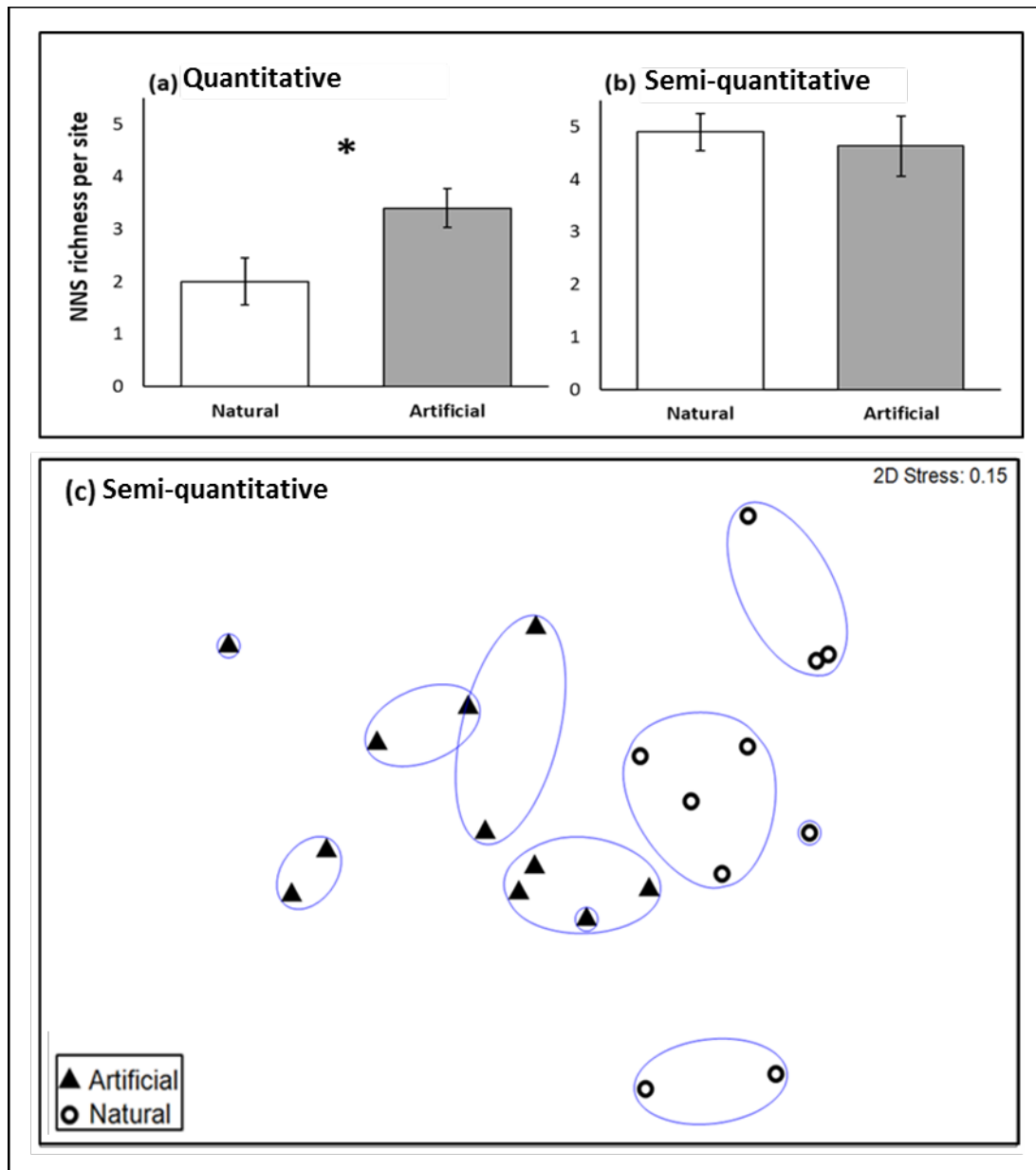
One-way PERMANOVA comparing assemblage composition between natural and artificial habitats.

---

Source	df	SS	MS	Pseudo-F	P(perm)
Habitat	1	4854.7	4854.7	9.041	<b>0.0001</b>
Residual	19	10202	536.96		
Total	20	15057			

Transformation: fourth root

---



312

313 Figure 2. Comparison of mean number of NNS per site in natural and artificial intertidal  
314 habitats using (a) quantitative quadrat and (b) semi-quantitative search-based sampling  
315 techniques. \*NNS richness was significantly greater in artificial compared to natural habitats  
316 using quantitative techniques ( $p = 0.0009$ ) but not using semi-quantitative methods (natural  
317 sites,  $n = 10$ ; artificial sites,  $n = 11$ ). Error bars show standard error. (c) Non-metric multi-  
318 dimensional scaling plot (nMDS) showing significant difference in assemblage composition  
319 between natural and artificial sites using semi-quantitative search-based data. Assemblage  
320 composition between natural and artificial habitats differed significantly ( $p = 0.0001$ ). The blue  
321 envelopes show a resemblance level of 75%.

322

323 3.3. Comparison of NNS in artificial habitats along the south coast of England

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<https://doi.org/10.1016/j.marpolbul.2020.111082>

324 Overall, 26 NNS were recorded in artificial sites across eleven harbours. The barnacle, *A.*  
325 *modestus*, was encountered most (43 sites), while the erect bryozoan, *Bugulina simplex*  
326 (Hincks, 1886), the orange-tipped sea squirt, *Corella eumyota* Traustedt, 1882, *B. wrightii*, the  
327 green alga, *Codium fragile subsp. fragile* (Suringar) Hariot, 1889 and *U. pinnatifida* were only  
328 found at a single site each. Results are reported from both sampling methods, but only semi-  
329 quantitative search-based data were used to produce figures because this method captured  
330 more NNS overall.

331 Statistical analysis of quantitative quadrat data revealed that mean richness and  
332 assemblage composition were significantly different among harbours and regions (Table 3a),  
333 with the Central region supporting greater mean and total richness than the West ( $p = 0.0222$ )  
334 and East regions ( $p = 0.0039$ ). Pairwise comparisons among harbours within regions revealed  
335 significantly higher richness in Torbay compared to Looe ( $p = 0.0084$ ), Southampton  
336 compared to Portsmouth ( $p = 0.0030$ ) and Shoreham compared to Folkestone ( $p = 0.0045$ ).  
337 Pairwise comparisons showed that assemblage composition between the West and Central  
338 ( $p = 0.0012$ ) and the Central and East ( $p = 0.0012$ ) regions differed significantly. Differences  
339 in assemblage composition were found between Falmouth and Looe ( $p = 0.0232$ ), Falmouth  
340 and Plymouth ( $p = 0.0292$ ), Falmouth and Torbay ( $p = 0.0244$ ), Looe and Torbay ( $p = 0.0073$ ),  
341 Poole and Southampton ( $p = 0.0090$ ), Southampton and Portsmouth ( $p = 0.0002$ ) and  
342 Shoreham and Folkestone ( $p = 0.0034$ ). SIMPER analysis revealed that the erect bryozoan,  
343 *Bugula neritina* (Linnaeus, 1758) contributed the most to the dissimilarity between West and  
344 Central (15%; greater in Central); whilst *W. subatra* contributed the most to dissimilarities  
345 between West and East (37.3%; greater in West) and Central and East regions (22.1%;  
346 greater in Central).

347 Analysis of semi-quantitative search-based data revealed a significant difference in NNS  
348 richness among regions, with the Central region supporting greater mean and total richness  
349 per harbour compared to West ( $p = 0.0472$ ) and East regions ( $p = 0.0014$ ; Table 3b, Figures

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350 3, 4b). There were no significant differences, however, in mean richness among harbours  
351 within regions (Table 3b, Figure 4a). Assemblage composition varied significantly among both  
352 harbours and regions (Table 3b, Figure 5). Post-hoc pairwise tests comparing regions showed  
353 that the West and Central ( $p = 0.0144$ ) and Central and East ( $p = 0.0326$ ) assemblage  
354 compositions differed significantly. Comparisons of harbours within regions found that  
355 assemblage composition differed significantly between Falmouth and Plymouth ( $p = 0.0355$ ),  
356 Poole and Portsmouth ( $p = 0.0131$ ), Poole and Southampton ( $p = 0.0014$ ) and Southampton  
357 and Portsmouth ( $p = 0.0013$ ). SIMPER analysis revealed that *W. subatra* contributed the most  
358 to the dissimilarity between West and East regions (25.4%; greater in West), while *C.*  
359 *okamurae* contributed the most to dissimilarities between West and Central (11.4%; greater  
360 in West) and Central and East regions (1.6%; greater in East).

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364 Table 3. PERMANOVA results for comparison of NNS richness and assemblage composition  
365 using (a) quantitative quadrat data and (b) semi-quantitative search-based data in artificial  
366 habitats among harbours and regions. Significant p-values are in bold.

#### (a) Quantitative data

Three-way PERMANOVA comparing species richness among regions, harbours and sites.

Source	df	SS	MS	Pseudo-F	P(perm)
Region	2	60707	30354	7.0537	<b>0.0025</b>
Harbour(Region)	7	118340	16905	3.9287	<b>0.0019</b>
Site(Harbour(Region))	30	118340	4303.2	15.623	<b>0.0001</b>
Residual	760	118340	275.44		
Total	799	118340			
Transformation:	pres/abs				

Three-way PERMANOVA comparing assemblage composition among regions, harbours and sites.

Source	df	SS	MS	Pseudo-F	P(perm)
Region	2	75905	37953	4.5881	<b>0.0040</b>
Harbour(Region)	7	221400	31628	3.8236	<b>0.0001</b>
Site(Harbour(Region))	30	248160	8272	11.922	<b>0.0001</b>
Residual	760	527330	693.85		
Total	799	1155800			
Transformation:	fourth root				

#### (b) Semi-quantitative data

Two-way PERMANOVA comparing species richness among regions and harbours.

Source	df	SS	MS	Pseudo-F	P(perm)
Region	2	4014	2007	7.0275	<b>0.0012</b>
Harbour(Region)	8	2399.2	299.9	1.0501	0.4183
Residual	33	9424.5	285.59		
Total	43	18170			
Transformation:	pres/abs				

Two-way PERMANOVA comparing assemblage composition among regions and harbours.

Source	df	SS	MS	Pseudo-F	P(perm)
Region	2	12842	6420.9	7.586	<b>0.0001</b>
Harbour(Region)	8	15168	1896	2.24	<b>0.0028</b>
Residual	33	27931	846.41		

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Total	43	65127
Transformation:	fourth root	

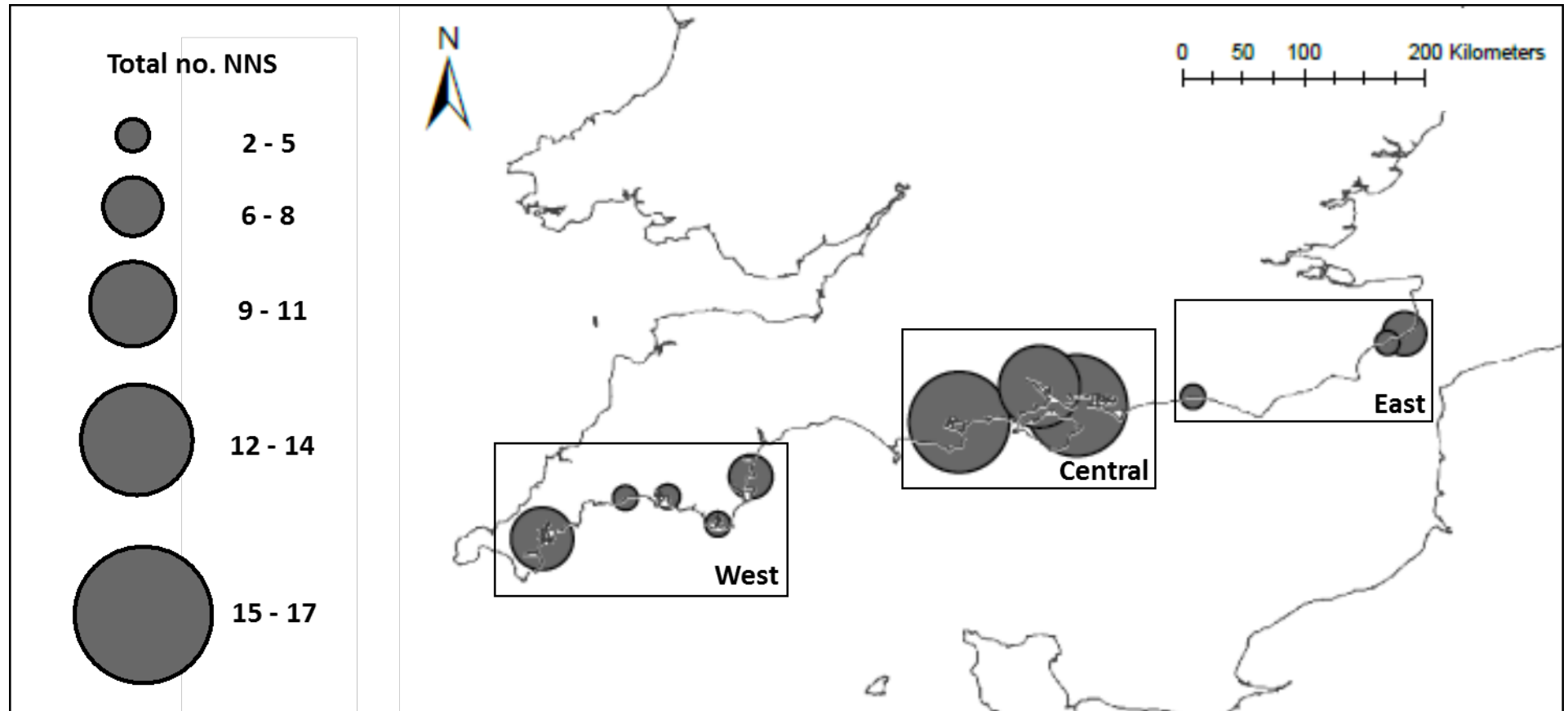
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O'Shaughnessy, K.A., Hawkins, S.J., Yunnice, A.L., Hanley, M.E., Lunt, P., Thompson, R.C. and Firth, L.B., 2020. Occurrence and assemblage composition of intertidal non-native species may be influenced by shipping patterns and artificial structures. *Marine Pollution Bulletin*, 154, 111082.

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368

369 Figure 3. The number of NNS recorded per harbour from Rapid Assessment Surveys of intertidal artificial habitats along the south coast of  
370 England ranged from 2-17. Size of circles represents the total number of NNS recorded per harbour. Harbours from west to east: Falmouth,  
371 Looe, Plymouth, Salcombe, Torbay (West region), Poole, Southampton, Portsmouth (Central region), Shoreham, Folkestone and Dover (East  
372 region). Figure was produced using the semi-quantitative search-based data.

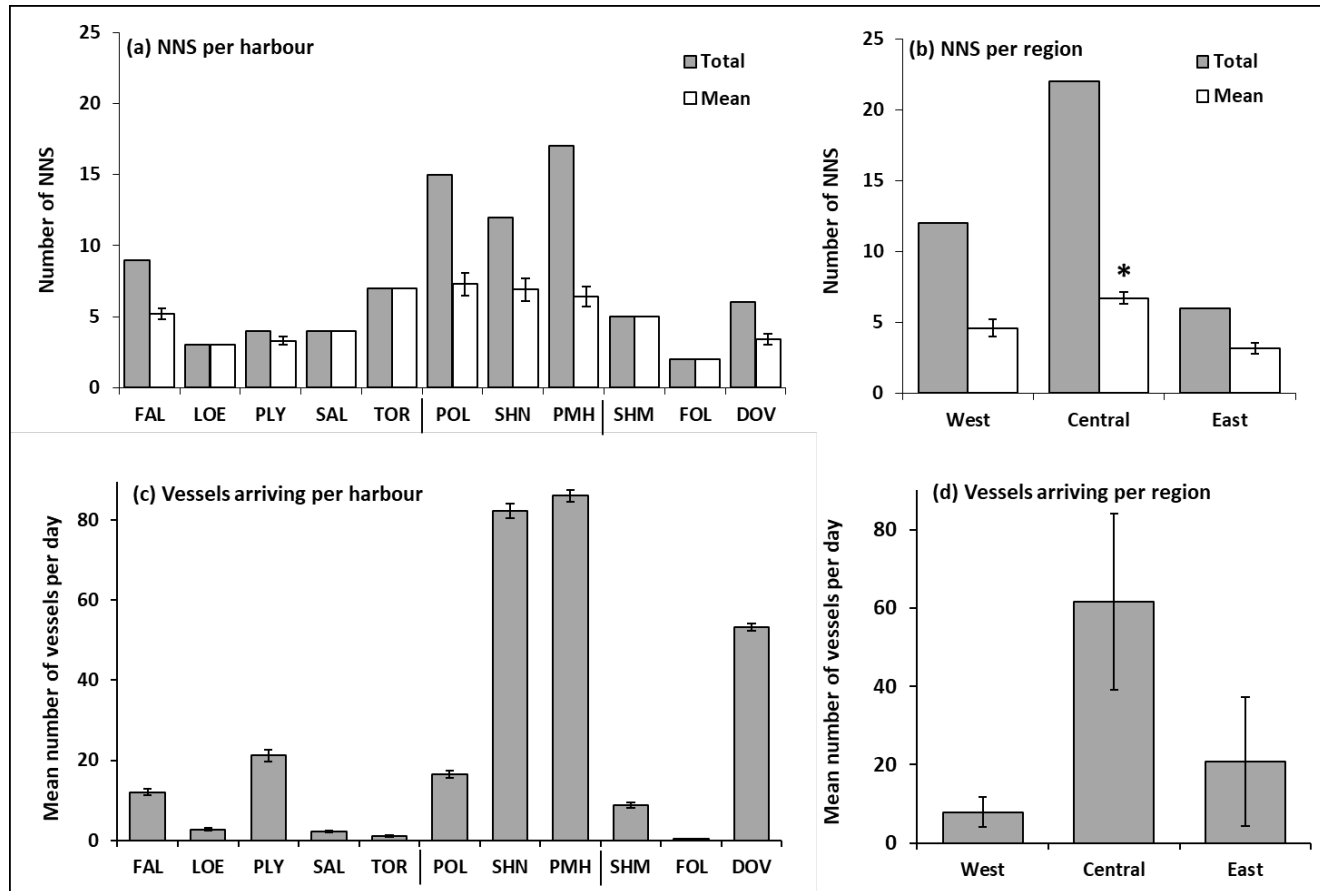
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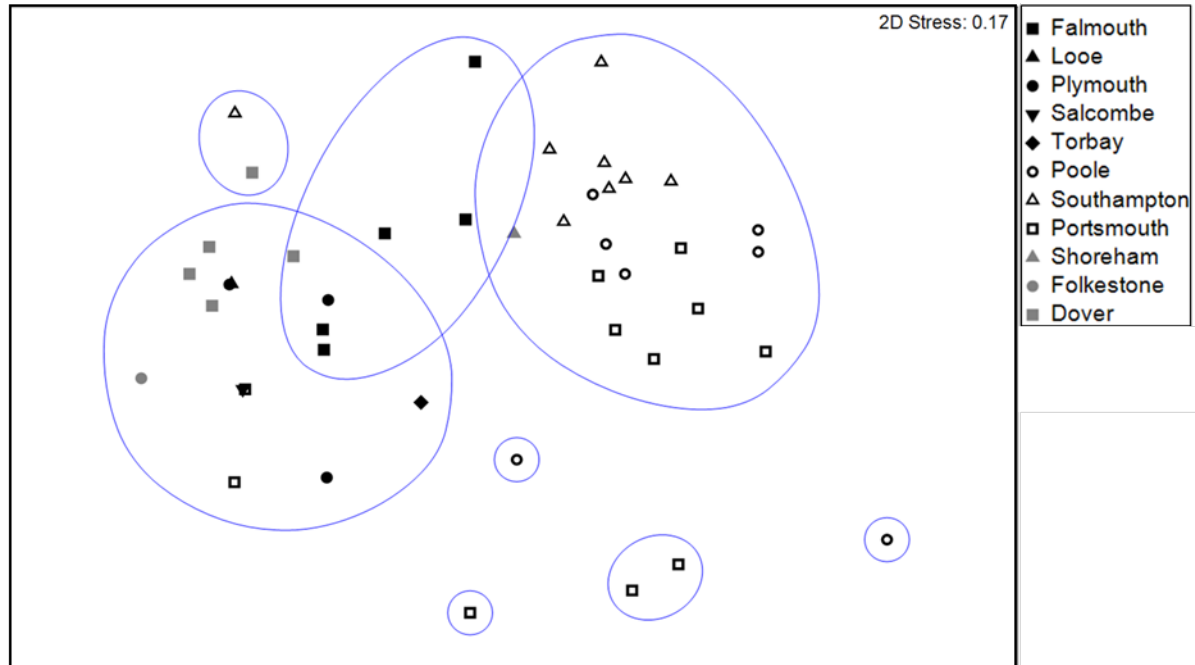
<https://doi.org/10.1016/j.marpolbul.2020.111082>

376 Figure 4. Total and mean number of NNS recorded from intertidal artificial habitats across the south coast of England per (a) harbour and (b)  
377 region. \*Numbers of NNS were significantly greater in Central compared to the West ( $p= 0.0472$ ) and East ( $p = 0.0014$ ) regions. Error bars  
378 represent standard error. Bars showing means in (a) without a standard error bar represent harbours where only one site was surveyed. Mean  
379 number of vessels arriving per day (c) by harbour and (d) by region were averaged over 60 days. Figure was produced using semi-quantitative  
380 search-based data. Information was obtained from Marine Traffic (2019) using vessel data from February and March 2019.

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381



382

383 Figure 5. Non-metric multi-dimensional scaling plot (nMDS) showing significant variation in  
384 NNS assemblage composition from Rapid Assessment Surveys of intertidal artificial sites  
385 among harbours ( $p = 0.0028$ ) and regions ( $p = 0.0001$ ) along the south coast of England. Dark  
386 shapes represent harbours in the West region, open shapes indicate harbours in the Central  
387 region and grey shapes represent harbours in the East. Figure was created using semi-  
388 quantitative search-based data. The blue envelopes show a resemblance level of 60%.

389

### 390 3.4. Numbers and types of vessels by harbour

391 Portsmouth and Southampton supported the greatest average number of vessel arrivals  
392 per day at 86.4 and 83.1, respectively, while Folkestone supported the fewest (0.4; Figure 4c).

393 The Central region supported the greatest average number of vessels per day at 61.6, while

394 the West supported the fewest at 7.9 (Figure 4d). International shipping (container liner

395 services) occurs out of Southampton with 12 carriers, as well as Plymouth and Dover with one

396 carrier each (Table 1). Seven of the 12 container liner carriers that visit Southampton operate

397 globally, with destinations in North and South America, Asia, India, the Pacific Islands,

398 Australia, Europe, the Middle East, Africa and the Caribbean (World Port Source, 2019). The

399 carrier that operates out of Plymouth is also a global carrier (similar destinations as listed

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400 above), while the carrier out of Dover only operates out of northern Europe. International cruise  
401 liners operate out of Southampton with global destinations, while cruise liners out of Dover  
402 have European destinations only. Ferries to northern Europe (France and Spain) operate from  
403 Plymouth, Poole, Portsmouth and Dover, while military bases are located in Falmouth,  
404 Plymouth and Portsmouth (Table 1, Figure 1).

405

#### 406 4. Discussion

407 Twenty-six non-native sessile invertebrates and macroalgae were found during Rapid  
408 Assessment Surveys of artificial structures in harbours along the south coast of England.  
409 Comparisons of NNS between natural and artificial habitats found that assemblage  
410 compositions differed significantly, but differences in richness depended on the sampling  
411 technique employed. The Central region supported greater mean and total richness, as well  
412 as different assemblage compositions, compared to the West and East regions. These  
413 differences might be attributed to regional shipping patterns, as most harbours in this study  
414 with high NNS richness saw relatively large amounts of vessel traffic.

415 Our study provided mixed evidence to support the hypothesis that artificial sites would  
416 support greater NNS richness compared to natural sites, as results differed depending on  
417 sampling method employed. Analysis of quantitative stratified-random quadrat data found  
418 differences in richness between natural and artificial habitats, while analysis of semi-  
419 quantitative search-based data (obtained from timed searches including complex habitats) did  
420 not detect differences. Both sampling techniques, however, showed that NNS assemblages  
421 between natural and artificial habitats were indeed different. These results agreed to some  
422 extent with previous studies that found assemblages of NNS differed between natural and  
423 artificial subtidal habitats (Glasby et al., 2007; Tyrrell and Byers, 2007; Dafforn et al., 2012).  
424 Conversely, the result that richness did not differ between natural and artificial habitats from

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<https://doi.org/10.1016/j.marpolbul.2020.111082>

425 our study contrasts with work from these same studies listed above which showed that artificial  
426 supported more NNS than natural habitats. For example, Glasby et al. (2007) found that  
427 numbers of NNS were markedly greater on floating pontoons and pilings than on natural rocky  
428 reef. Furthermore, Tyrrell and Byers (2007) and Dafforn et al. (2012) experimentally showed  
429 that non-native fouling species outcompeted native species on artificial structures, but non-  
430 natives were not able to gain a foothold on natural substrate. Importantly, all of these studies  
431 were done in subtidal habitats (many on floating pontoons), which may explain the conflicting  
432 results. In the current study, semi-quantitative search-based sampling techniques allowed  
433 complex microhabitats to be searched (e.g., rock pools, crevices and gaps between boulders).  
434 Natural substrate generally provides more topographic complexity compared to artificial  
435 structures (Moschella et al., 2005; Chapman and Underwood, 2011). Thus, it is not surprising  
436 that many more NNS were observed during the searches in natural than artificial habitats. For  
437 example, whilst *S. muticum*, *C. pergrina*, *U. pinnatifida*, *A. armata* and *G. turuturu* were found  
438 in previous studies of artificial habitats (Arenas et al., 2006; Firth et al., 2013; Bishop et al.,  
439 2015b), they were only found in rock pools during timed searches in natural habitats in our  
440 study. This indicates the importance of water-retaining features for the successful  
441 establishment of non-native species on typically diverse natural rocky shores. These features  
442 have previously been identified as being important for providing shade and water retention at  
443 low tide to alleviate desiccation for native species in intertidal habitats (Firth et al., 2013, Firth  
444 et al., 2016). Conversely, in the subtidal zone, as desiccation is not a concern, topographic  
445 complexity may be needed for entirely different reasons, such as providing larvae and  
446 propagules refuge from predators or wave movement (Kovalenko et al., 2012; Strain et al.,  
447 2017). Different uses of topographic complexity by resident organisms between intertidal and  
448 subtidal habitats may be a reason for the differential results obtained between previous  
449 surveys and the current survey.

This is an accepted proof.

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450 The frequency of arriving vessels, types and departure points of vessels arriving in  
451 harbours, as well as the subsequent secondary destinations to which species can be  
452 transported (Carlton, 1996b; Ruiz et al., 2000; Clarke Murray et al., 2011), may explain the  
453 high number and variety of NNS around Southampton and the Central region in general. The  
454 success of an introduced species is highly dependent on propagule pressure (Lockwood et  
455 al., 2005; Copp et al., 2010), and thus it is not surprising that most of the harbours supporting  
456 relatively high species richness were also harbours that supported a high frequency of arriving  
457 vessels. For example, Southampton was unique in our study in being one of the largest cruise  
458 ship and container ports in the UK, and the busiest along the English south coast (Associated  
459 British Ports, 2019; Marine Traffic, 2019; World Port Source, 2019). As such, it sees  
460 significantly more international traffic than any other of the south coast ports. Global movement  
461 of NNS into the British Isles has been described by Eno et al. (1997) who proposed scenarios  
462 depicting likely invasion pathways. Many species were proposed to have been transferred  
463 directly to the British Isles from their places of origin, such as *B. hamifera* from Southeast Asia,  
464 *A. modestus* from Australia and *C. fornicata* from the eastern seaboard of the US. These  
465 routes of transfer explain high propagule pressure in the port of Southampton, where cargo  
466 tankers regularly arrive from international ports. However, Eno et al. (1997) suggested many  
467 other non-natives (i.e., *A. armata*, *S. muticum*, *C. peregrina*) were first transported from their  
468 origin to continental Europe, followed by a secondary transfer into the British Isles across the  
469 English Channel. Bishop et al. (2015a) provided evidence for this, as their Rapid Assessment  
470 Surveys showed a general pattern of northward movement of NNS from Brittany, France  
471 across the English Channel to South West England over time. This invasion pathway might  
472 explain the high numbers of NNS in Portsmouth (and to a lesser degree, Poole), where large  
473 passenger ferries arrive from northern European destinations. The current study can only  
474 suggest the above as invasion pathways, as identifying NNS from source ports was outside  
475 the scope of this study. Thus, future research can focus on providing evidence by ground-

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476 truthing these results or using molecular markers to show that the same NNS occurred in the  
477 departing international harbours as the receiving ports in southern England.

478 Although the relationship between NNS richness and number of vessels arriving per day  
479 was clear at the regional level (i.e., West, Central, East), at the harbour level, there were some  
480 harbours that did not follow this trend. Poole Harbour supported a relatively high number of  
481 NNS, yet the number of arriving vessels was relatively low compared to other harbours with  
482 high species richness (i.e., Portsmouth and Southampton). This suggests that factors other  
483 than propagule pressure from international shipping play a role in determining success of  
484 NNS. The geomorphology of Poole is quite different than the other harbours in this study, in  
485 that the harbour itself has a very narrow mouth, a double high tide daily and the smallest tidal  
486 range in the study area (1.8 m), as well as very poor flushing (Humphreys, 2005; May, 2005;  
487 World Port Source, 2019). Poole has been described as a lagoon-like harbour; it is a shallow  
488 and warm body of water (Humphreys, 2005; May, 2005). These conditions may be particularly  
489 favourable for NNS originating from warmer waters, such as *D. vexillum* (Zaiko et al., 2007;  
490 Lambert, 2009). Moreover, slow and incomplete flushing of the harbour means larvae of NNS  
491 are present in the water for long periods of time, potentially allowing increased settlement  
492 compared to harbours with faster flushing times. These conditions are also favourable to  
493 yachting, and so smaller leisure craft regularly travel among harbours within the Solent  
494 (Central region; SJH pers. obs.), potentially acting as secondary mobile vectors (Clarke  
495 Murray et al., 2011). On the other hand, Dover sees a relatively high number of vessels per  
496 day but supports relatively few numbers of NNS. Although the numbers of vessels are high in  
497 Dover, the origins and destinations are almost exclusively European (Marine Traffic, 2019;  
498 World Port Source, 2019). This effectively means lower propagule pressure from global  
499 invaders directly. Moreover, the geomorphology of Dover is different from the other harbours  
500 in this study, in that Dover is not a natural bay or inlet. Rather, the port was artificially created  
501 when the Dover Southern Breakwater was constructed at the beginning of the 20<sup>th</sup> century. It



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502 is therefore likely that the hydrodynamics – which can affect turbidity and scouring of structures  
503 (Govarets and Lauwaert, 2009; Dugan et al., 2011), and can dictate transport of larvae in  
504 currents and tides (McQuaid and Phillips, 2000) – differ markedly between Dover and  
505 naturally-formed ports.

506 Evidence from this study and others suggest that artificial structures probably play an  
507 important role in the initial establishment and then secondary transport of NNS away from their  
508 initial point of introduction (Eno et al., 1997; Neves et al., 2007; Mineur et al., 2012). By nature,  
509 docks and floating pontoons are constantly in close proximity to cargo tankers, passenger  
510 ferries and recreational vessels, and thus there is a high probability of species spreading from  
511 mobile vectors (vessels) to stationary structures (floating pontoons, docks; Neves et al., 2007).  
512 In a study examining the fouling communities of boat hulls and associated floating pontoons  
513 and concrete structures in an international Brazilian port, Neves et al. (2007) found that biotic  
514 communities on hulls were similar to those on the pontoons; while communities on concrete  
515 structures were a similar but smaller subset of the species found on hulls. This is because  
516 boat hulls and floating pontoons rise and fall with the tide, while concrete structures are fixed  
517 in place (similar to intertidal natural rocky shores). Hulls of recreational boats are regularly  
518 cleaned of fouling organisms (Neves et al., 2007); it is even becoming increasingly common  
519 for transoceanic vessels to undergo regular hull cleaning (Hopkins and Forrest, 2008; PML  
520 Applications Ltd, 2019). Thus, the biological communities they support are typically younger  
521 (i.e. at earlier successional stages) than those on floating pontoons and associated docks. As  
522 such, pontoons act as “reservoirs” of established NNS communities (Neves et al., 2007; Floerl  
523 et al., 2009; Foster et al., 2016), while concrete structures support fewer numbers of species,  
524 but of which have the ability to invade intertidal natural habitats (Neves et al., 2007; Epstein  
525 and Smale, 2018). In our study, harbours east of Torbay were dominated by sedimentary  
526 substrata, thus fouling organisms typical of natural rocky shores arriving from distant hard  
527 substrata have only been able to establish and survive by colonising artificial structures in

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528 these otherwise uninhabitable areas. In this way, artificial structures may affect ecological  
529 connectivity by providing “stepping stones” for the movement of species across seascapes  
530 (Sammarco et al., 2004; Airoidi et al., 2015; Bishop et al., 2017). Moreover, smaller harbours  
531 (e.g., Folkestone) with many fewer artificial structures compared to larger harbours (e.g.,  
532 Portsmouth) provided less hard substrata for NNS spread from a mobile vector to a stationary  
533 structure. These smaller harbours also supported less diverse NNS communities due to lower  
534 diversity of artificial structures (e.g., Folkestone Harbour is largely composed of rock and  
535 concrete seawalls and lacks floating pontoons). As such, these smaller harbours are less likely  
536 to act as NNS reservoirs.

537 The limitations of sampling natural and artificial sites equally are extremely challenging to  
538 overcome; yet a combined sampling approach (quantitative stratified-random quadrats and  
539 semi-quantitative timed searches), like those employed in this study, can address some of the  
540 problems associated with sampling in these habitats. By nature, complex microhabitats on  
541 gently sloping natural rocky shores (e.g., rock pools, gaps between boulders) are generally  
542 easier (and safer) to sample compared to those on artificial structures. This was acknowledged  
543 in the methods of the current study by slightly extending the timed search on structures that  
544 were difficult to sample due to safety and logistical reasons. For example, boulder groynes  
545 and riprap revetment provide internal compartments created by the stacking of boulders to  
546 maximise coastal protection. The interior of these structures provide functional niches that are  
547 absent on the exterior that protect organisms from desiccation, wave exposure and sand  
548 scour; thus species diversity tends to be greater within the internal compartments, which are  
549 difficult to access/observe (Sherrard et al., 2016; Liversage and Chapman, 2018). Traditional  
550 quadrat sampling avoids gaps between boulders and other complex microhabitats,  
551 consequently missing vital species diversity information. Therefore, numbers and abundances  
552 of NNS recorded from the exterior of these structures probably do not accurately represent  
553 the true NNS diversity of the entire structure. On the other hand, limited areal extent provided

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554 by other artificial structures, such as seawalls, means that the likelihood of these structures to  
555 be fully sampled (“censused”; Chapman et al., 2018) using quadrat sampling techniques is  
556 much greater than on a large natural rocky shore or more complex artificial structures, where  
557 many diverse habitats are likely to be missed (Chapman et al., 2018). In the current study,  
558 quadrat sampling was able to cover most of the available area on seawalls but missed areas  
559 in larger natural sites (e.g., rock pools). If quantitative quadrat sampling alone had been used  
560 (which is a typical method in biodiversity surveys), our study would have concluded that  
561 intertidal artificial habitats support greater (mean) numbers of NNS (per unit area) than natural  
562 habitats. By employing a timed search, this study came to a very different conclusion - that of  
563 which challenges the commonly accepted concept that artificial structures support greater  
564 NNS richness compared to natural rocky shores. Most NNS surveys along the south coast of  
565 England have focused on surveying marina pontoons in subtidal habitats (Arenas et al., 2006;  
566 Ashton et al., 2006; Bishop et al., 2015a,b; Foster et al., 2016), as these are known “hot spots”  
567 for introduction. Our study demonstrated that areas not labelled as “hot spots”, such as natural  
568 rocky shores, should not be ignored. A recent report cautioned that natural rocky shores might  
569 facilitate “spillover” of NNS from populations in marinas to natural habitats, facilitating the  
570 spread out from the initial sites of introduction (Epstein and Smale, 2018). Although not  
571 explicitly tested for, our study showed that intertidal natural sites do indeed support many NNS  
572 and may actually contribute to their spread between major transport hubs and surrounding  
573 bays and harbours.

574 Results from this study could be strengthened by formal tests on the effects of local  
575 environmental and physical conditions on success of NNS establishment. Physical factors,  
576 such as hydrodynamics (Horvath and Crane, 2010; Zardi et al., 2006) and pollution load  
577 (Dafforn et al., 2011; McKenzie et al., 2011) are important in influencing NNS colonisation and  
578 competition with native biota. For example, previous studies have shown that industrial and  
579 urban runoff adversely affects native composition and ecological functioning of marine

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580 communities (Johnston and Roberts, 2009; Burton and Johnston, 2010), and that species  
581 response (recolonisation) can vary depending on exposure to particular contaminants  
582 (Trannum et al., 2004). Additionally, NNS have been shown to tolerate contaminants and  
583 pollution while abundances of native species decline under the same conditions (Crooks et  
584 al., 2011; Dafforn et al., 2011; McKenzie et al., 2011). Thus, a decline in native biotic  
585 communities can easily give NNS a competitive advantage where conditions are unfavourable  
586 for native species (Johnston et al., 2017).

587 The loss of natural habitat caused by coastal development and ocean sprawl is leading to  
588 the need to explore alternative options to traditional hard built structures for coastal protection  
589 (Dafforn et al., 2015a; Firth et al., 2016a). There is therefore an increasing impetus to  
590 ecologically enhance hard structures to fulfil secondary management goals, such as increase  
591 biodiversity, enhance ecosystem services or reduce abundance of NNS (i.e., "ecological  
592 engineering"; Dafforn, 2017; Evans et al., 2017; Strain et al., 2019a,b). Results from our  
593 surveys clearly demonstrate that ecological engineering designs must consider the potential  
594 for colonisation by NNS (Sella and Perkol-Finkel, 2015; Dafforn, 2017; Strain et al., 2017).  
595 Traditionally, ecological engineering interventions that have included rock pools retrofitted  
596 onto seawalls (Chapman and Underwood, 2011; Browne and Chapman, 2014) or drilling pits  
597 into seawalls or breakwaters (Firth et al., 2014; Evans et al., 2016), have been advocated as  
598 a means of enhancing species diversity through water retention. Our survey showed that these  
599 interventions may increase the risk of colonisation by NNS, such as *S. muticum* and *U.*  
600 *pinnatifida*, which were regularly found in rock pools in natural sites. Information from  
601 biodiversity studies and Rapid Assessment Surveys should thus serve as a benchmark  
602 against which to measure change to biotic communities over time, and is an essential first  
603 step in informing management decisions concerning design details for ecological engineering  
604 of artificial structures in coastal intertidal habitats (Dafforn et al., 2015b; Mayer-Pinto et al.,  
605 2017).

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606 Ocean sprawl is accelerating the rate of NNS introduction and spread, contributing to biotic  
607 homogenisation and the growing biodiversity crisis. Understanding the ecological role of  
608 artificial structures in the marine and coastal environments is critical for preserving native  
609 biodiversity and building resilience to establishment of NNS. Our results suggest that global  
610 shipping and artificial structures may play an important role in the introduction and spread of  
611 NNS. Other factors such as local environmental conditions and geomorphology of harbours  
612 undoubtedly contribute to NNS success, but disentangling these factors is difficult. Therefore,  
613 all potential mechanisms of NNS introduction, establishment and spread need investigation  
614 so that ecologists might develop the predictive capability to identify areas at high risk of  
615 invasion, which can aid in effective forecasting for potential invaders.

616

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620

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624

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