Recent northward range extension of *Nerita yoldii* (Gastropoda: Neritidae) on artificial rocky shores in China

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(Received 6 September 2017; editorial decision 9 July 2018)

ABSTRACT

Extensive coastal infrastructures built along the Chinese coastline have effectively created a new marine ‘Great Wall’ that has had a significant effect on the biogeography of intertidal species in the region by creating new habitats for colonization. Recent colonization by *Nerita yoldii* of the artificial rocky shores in the Yangtze River Delta has contributed to a northward shift of this species’ range. Here, we study the range expansion and phylogeographic pattern of this species. Our four-year field survey showed a northward range expansion of *N. yoldii* on the artificial rocky shores. A phylogeographic analysis of populations from both artificial and natural rocky shores showed lower genetic diversity and fewer private haplotypes in newly colonized artificial shore populations. All the populations were clustered into three groups, one consisting of the three southernmost natural rocky-shore populations, a second that included all but one of the artificial-substrate populations and the two northernmost natural rocky-shore populations, and a third that included the offshore artificial-island population. These results indicate that *N. yoldii* has rapidly expanded its northern distribution limit and that the coastal artificial structures, together with increasing SST in the Yangtze River Delta, have played a crucial role in this range expansion.

INTRODUCTION

Transformations of coastal landscapes are important factors affecting the current biogeographic distribution of intertidal species (Serrano et al., 2013). Throughout the world, coastal infrastructures constructed for commercial, residential and tourist purposes have dramatically changed the coastal landscape (Bulleri & Chapman, 2010; Maes et al., 2015). The proliferation of artificial coastal structures, acting as ‘stepping-stones’ for dispersal, can promote distributional range shifts of marine species (Johannesson & Warnoes, 1990; Moschella et al., 2005; Mineur et al., 2012; Firth et al., 2013; Airoldi et al., 2015) and enhance large-scale population connectivity of rocky shore species (Firth et al., 2015; Dong et al., 2016). Ideally, combining phylogeographic patterns with data on temporal and historical geographic distributions and habitat availability can be used to infer the processes that have shaped recent changes in the geographic range of a species (Fenberg, Posbie & Hellberg, 2014).

The clear biogeographic patterns and large-scale artificial infrastructure constructions along the coast of China provide an excellent opportunity to study the recent and historical processes that have shaped the current geographic ranges of rocky intertidal species (Huang, Wang & Dong, 2015; Wang, Tsang & Dong, 2015; Dong et al., 2016; Williams et al., 2016). The Yellow Sea with a temperate fauna and the East China Sea with a subtropical fauna are two major biogeographic regions for the zoobenthic fauna in China (Liu, 2013). The distribution of many marine fauna and flora is restricted within one of these biogeographic regions (Liu, 2013) and a phylogeographic transition exists around the Yangtze River Estuary for many rocky shore species (Yu et al., 2014; Guo et al., 2015; Wang et al., 2015; Dong et al., 2016).

The landscape of the Chinese coastline is experiencing dramatic changes as a result of human activities, with about 60% of the coast modified during the past two decades (Ma et al., 2014). For example, the 884 km of coastal mudflat lacking any natural rock substrates in Jiangsu Province (Wang & Ke, 1997) is a Quaternary basin with thick sediments (Chen & Liu, 1988) that has developed over the last 6,000 years, progressing seaward with abundant sediment supply from the Yellow (1.1–1.6 × 10⁶ tons/a) and the Yangtze (0.4 × 10⁶ tons/a) Rivers (Zhu, Martini & Brookfield, 1996). The accretion rate has been 0.1–10 cm/a during the past 7,000 years and the progradation rate has gradually increased (9–13 m/a, 20–33 m/a and 49–85 m/a since 6,000, 2,000 and 500 years ago, respectively; Wang et al., 2007). However, this ‘soft’ coastal mudflat has gradually been becoming ‘hard’ over the past 70 years; about 3,000 km² of tidal mudflats have been reclaimed in this region, protected by artificial structures (e.g. concrete and rocks) that serve as coastal defences for maintaining reclaimed land (Zhang et al., 2013). These artificial structures have the
potential to alter the community and/or population structures of rocky intertidal species (Huang et al., 2015; Dong et al., 2016).

The snail *Nerita yoldii* is a common gastropod found on rocky intertidal shores along the coast of southern China. During its spawning period (April–August), adult snails lay benthiic egg capsules on hard substrates. After approximately 30 days, eggs develop into planktonic veliger larvae with a pelagic larval duration (PLD) of 1–2 months, with recruitment typically occurring from June to December (Yeung, 2006). The long PLD suggests that the pelagic larvae of *N. yoldii* can potentially disperse over long distances under the influence of coastal currents. The northern limit of *N. yoldii* occurs south of the Yangtze River Estuary in the Shengsi Archipelago (a natural rocky shore; 30°34’37”–30°52’08”N, 122°01’37”–122°50’52”E; Fig. 1) (Zhang et al., 1963). Several factors may have contributed to this historical northern range limit around the Yangtze River Estuary: (1) freshwater discharge from the Yangtze River, which may impede the northward dispersal of pelagic larvae; (2) an approximately 10°C difference in seawater temperatures north and south of the river in winter and (3) muddy shores north of the Yangtze River Estuary, which lack hard substrates and are unsuitable for the settlement of *N. yoldii*. However, *N. yoldii* was reported north of the Yangtze River Estuary on oyster reefs at Layashan Oyster Reef (32°08’45”N, 121°32’59”E; Fig. 1) in the 1980s, based on a field survey along the Jiangsu coastline and on subsequent records (Tong & Meng, 1985; Quan et al., 2012). However, there have been no reports of the occurrence of *N. yoldii* north of the Liyashan Oyster Reef.

As a consequence of extensive coastal construction along the Jiangsu coastline that has created habitat suitable for rocky-shore organisms, *N. yoldii* might be extending its range northward via these artificial stepping-stones. In the present study, we investigated the role of these artificial structures in facilitating the northward geographic range expansion of this rocky intertidal species north of the Yangtze River Estuary. From July 2013 to December 2016, we continuously monitored the distribution of *N. yoldii* in the Yangtze River Delta and characterized the population genetic structure of this species in both artificial and natural rocky-shore populations.

**MATERIAL AND METHODS**

**Field surveys, sampling and sequencing**

From July 2013 to December 2016, 3-h field surveys were conducted at 12 localities to document the distribution of *Nerita yoldii* in summer and winter each year along the coast of Jiangsu Province (Fig. 1). A total of 193 *N. yoldii* samples were collected from nine localities (17–30 individuals per locality), including four localities from artificial rocky shores and five localities from natural rocky shores in the south (Table 1). Samples were preserved in 100% ethanol before DNA extraction.

Genomic DNA was extracted from foot muscle of each specimen using TIANamp Marine Animals DNA Kit (Tiangen Biotech Co., Beijing). The universal primers LCO1490 and HCO2198 (Folmer et al., 1994) were used to amplify a partial sequence of the mitochondrial COI gene. PCR reactions were conducted in a 25-μl reaction volume containing 2.5 μl of 10X buffer (Mg2+ Plus), 2 μl of 25 mM dNTPs, 1 μl of each 10 mM primer, 0.25 μl (1.25 U) of Taq DNA polymerase and 200 ng DNA template. Amplification was initiated with denaturing at 94°C for 3 min, followed by 35 cycles of 94°C for 45 s, annealing at 50°C for 45 s and 72°C for 1 min, and then a final extension at 72°C for 10 min. The target amplicon was visualized on 1.5% agarose gels and PCR products were sent to a commercial company for sequencing (Invitrogen Biotechnology Co., Shanghai). All sequences were deposited in GenBank with accession numbers KX831721-KX831867 and MG924940-MG924983.

**Genetic variation analyses**

Complimentary sequences were assembled and edited by comparing both strands using DNAMAN v. 7 software (LynnonBioSoft, Quebec), then all sequences were aligned with MUSCLE (Edgar, 2004) implemented in MEGA v. 6 (Tamura et al., 2013) with default settings. For each locality, the number of haplotypes (Nh), the number of private haplotypes (Nhp), the number of polymorphic sites (S), the haplotype diversity (h) and the nucleotide diversity (π) were calculated using ARLEQUIN v. 3.5 (Excoffier & Lischer, 2010). To test for evidence of selective sweeps or population expansions, Fu’s Fs and Tajima’s D were calculated with ARLEQUIN. In addition, pairwise mismatch analysis was performed with ARLEQUIN to test for past population expansions.

**Population structure analyses**

The best-fitting substitution model (HKY) was inferred with jModelTest v. 2.1.4 (Darriba et al., 2012) using the Bayesian information criterion and a maximum likelihood (ML) tree was constructed with 1,000 bootstraps in RAXML v. 8.2 (Stamatakis, 2014). A Bayesian tree was also built with MrBayes v. 3.2 (Ronquist et al., 2012). Markov-chain Monte Carlo (MCMC) searches were run with four chains for 5,000,000 generations, sampling every 100 generations. Convergence was evaluated by the standard deviation of split frequencies (0.01) and potential scale-reduction factor (close to 1.0 for all parameters). Ten thousand sampled trees were used to infer the consensus tree and the posterior probabilities (PP) for node support, after discarding the
The annual survey data gathered from July 2013 to December 2016 indicated that *Nerita yoldii* had gradually colonized the artificial structures beyond its previous northernmost distributional limit (Fig. 1). The first field investigation (July 2013) showed that the northern limit of *N. yoldii* occurred on an artificial rocky shore in Yangguangdao (YGD) (Fig. 1). *Nerita yoldii* was recorded for the first time on artificial rocky shores in Xinglongzhong (XZD) in July 2015 and in Zhonganpeng (ZAP) in January 2016.

**Table 1.** Sampling localities and summary of diversity indices of *Nerita yoldii.*

<table>
<thead>
<tr>
<th>Type of substratum</th>
<th>Sampling locality (Abbr.)</th>
<th>Latitude (°N)</th>
<th>Longitude (°E)</th>
<th>N</th>
<th>Nh</th>
<th>Npr</th>
<th>S</th>
<th>h</th>
<th>τ</th>
<th>Tajima’s D</th>
<th>Fu’s Fs</th>
<th>HRag</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artificial hard substratum</td>
<td>Zhonganpeng (ZAP)</td>
<td>32°51.069’</td>
<td>120°58.306’</td>
<td>20</td>
<td>4</td>
<td>0</td>
<td>8</td>
<td>0.2842 ± 0.1284</td>
<td>0.001442 ± 0.000173</td>
<td>−2.0409</td>
<td>−0.2767</td>
<td>3.000 0.332</td>
</tr>
<tr>
<td>Xindongshen (XZD)</td>
<td>32°39.281’</td>
<td>120°58.062’</td>
<td>30</td>
<td>5</td>
<td>0</td>
<td>10</td>
<td>0.3080 ± 0.1075</td>
<td>0.001181 ± 0.001007</td>
<td>−2.2527</td>
<td>−1.4644</td>
<td>3.000 0.267</td>
<td></td>
</tr>
<tr>
<td>Yangguang Island (YGD)</td>
<td>32°31.472’</td>
<td>121°24.169’</td>
<td>20</td>
<td>5</td>
<td>1</td>
<td>9</td>
<td>0.5684 ± 0.1188</td>
<td>0.002340 ± 0.002340</td>
<td>−0.3852</td>
<td>1.0266</td>
<td>0.201 0.121</td>
<td></td>
</tr>
<tr>
<td>Dayanggang (DYG)</td>
<td>32°04.830’</td>
<td>121°36.362’</td>
<td>20</td>
<td>6</td>
<td>2</td>
<td>5</td>
<td>0.5158 ± 0.1316</td>
<td>0.000951 ± 0.000888</td>
<td>−1.7800</td>
<td>−4.0148</td>
<td>0.725 0.143</td>
<td></td>
</tr>
<tr>
<td>Natural rocky shore group</td>
<td>Artificial rocky shore</td>
<td>90</td>
<td>10</td>
<td>3</td>
<td>14</td>
<td>0.4087 ± 0.0654</td>
<td>0.001778 ± 0.001303</td>
<td>−1.6659</td>
<td>−3.6652</td>
<td>3.250</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Natural rocky shore</td>
<td>Shenjianwan (SJW)</td>
<td>30°36.103’</td>
<td>122°08.110’</td>
<td>19</td>
<td>5</td>
<td>3</td>
<td>4</td>
<td>0.3860 ± 0.1389</td>
<td>0.000682 ± 0.000725</td>
<td>−1.8612</td>
<td>−3.5705</td>
<td>0.500 0.170</td>
</tr>
<tr>
<td>Zhoushan (ZS)</td>
<td>29°55.052’</td>
<td>122°25.193’</td>
<td>21</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>0.3476 ± 0.1276</td>
<td>0.000602 ± 0.000669</td>
<td>−1.4567</td>
<td>−2.1992</td>
<td>0.441 0.198</td>
<td></td>
</tr>
<tr>
<td>Dongtou (DT)</td>
<td>27°51.430’</td>
<td>121°11.600’</td>
<td>30</td>
<td>10</td>
<td>4</td>
<td>15</td>
<td>0.7310 ± 0.0787</td>
<td>0.003589 ± 0.002266</td>
<td>−1.3886</td>
<td>−2.6795</td>
<td>1.328 0.029</td>
<td></td>
</tr>
<tr>
<td>Pingtan (PT)</td>
<td>25°29.168’</td>
<td>119°51.359’</td>
<td>16</td>
<td>8</td>
<td>2</td>
<td>15</td>
<td>0.8500 ± 0.0750</td>
<td>0.005067 ± 0.003103</td>
<td>−1.1948</td>
<td>−1.3398</td>
<td>0.623 0.031</td>
<td></td>
</tr>
<tr>
<td>Xiamen (XM)</td>
<td>24°33.433’</td>
<td>118°09.083’</td>
<td>17</td>
<td>11</td>
<td>4</td>
<td>12</td>
<td>0.9118 ± 0.0561</td>
<td>0.002955 ± 0.002000</td>
<td>−1.8248</td>
<td>−7.6965</td>
<td>2.020 0.099</td>
<td></td>
</tr>
</tbody>
</table>

For each locality, individual numbers (N), haplotypes numbers (Nh), private haplotype numbers (Npr), the number of polymorphic sites (S), haplotype diversity (h), nucleotide diversity (τ), neutral test (Tajima’s D and Fu’s Fs), mismatch distribution estimate (τ), and Harpending’s raggedness index (HRag) for mitochondrial COI DNA are listed. Bold values are significant at P < 0.05 for D and HRag, and P < 0.02 for Fs.

Haplotype relationships and genetic variation among sampling localities

A total of 31 polymorphic sites were found in the 620 bp alignment of 193 COI sequences, yielding 26 different haplotypes (Fig. 2). The dominant haplotype (Hapl1) was widely distributed and accounted for a high percentage (30–65%) at each sampling locality (Fig. 3). In addition to Hapl1, there were eight haplotypes shared by more than two populations (Hapl2–Hapl7, H16 and H22). For populations on artificial rocky shores, no private haplotypes were found in the newly colonized populations (ZAP and YGD), while the other two populations (YGD and DYG) had their own private haplotypes (Table 1). All natural rocky-shore populations (SJW, ZS, DT, PT, XM) had private haplotypes, and XM and DT had the most private haplotypes (Npr = 4, Table 1). All other haplotypes differed from Hapl1 by at most eight mutations (Fig. 2). Haplotype relationships based on ML and Bayesian trees revealed no clusters of sequences corresponding to sampling localities (data not shown).

Relatively low levels of haplotype diversity (h, mean ± SD) were observed in the six northernmost populations (ZAP, XZD, YGD, DYG, SJW, ZS; h = 0.2642 ± 0.1264 to 0.5684 ± 0.1188) in comparison with the three southern populations (DT, PT, XM; h = 0.7310 ± 0.0787 to 0.9110 ± 0.0561; Table 1). Haplotype diversity was lowest in the two most recently (2015–2016) colonized populations (ZAP, h = 0.2842 ± 0.1284; XZD, h = 0.3080 ± 0.1073) as compared with natural rocky-shore populations to the south (SJW, ZS, DT, PT, XM; h = 0.3476 ± 0.1276 to 0.9118 ± 0.0561; Table 1). Haplotype diversity of the other two artificial-substrate populations that were colonized earlier (2006–2013) was greater (YGD, h = 0.5684 ± 0.1188; DYG, h = 0.5158 ± 0.1316; Table 1), but not as high as the three southernmost natural-substrate populations (DT, PT, XM). The two northernmost natural rocky-shore populations had intermediate levels of haplotype diversity (SJW, h = 0.3860 ± 0.1389; ZS, h = 0.5476 ± 0.1276; Table 1).
Figure 2. Median-joining network of COI haplotypes for *Nerita yoldii*. Each circle represents a single haplotype and sizes are proportional to haplotype frequencies. Colours within circles denote localities (see Table 1 for locality abbreviations).

Figure 3. Spatial distribution of *Nerita yoldii* COI haplotypes. Colours within circles denote different haplotypes (see Table 1 for locality abbreviations).
NERITA ON ARTIFICIAL ROCKY SHORES

Table 2. Pairwise $\Phi_{ST}$ values (below diagonal) and $P$ values (above diagonal) between different populations of Nerita yoldii.

<table>
<thead>
<tr>
<th></th>
<th>ZAP</th>
<th>XDZ</th>
<th>YGD</th>
<th>DYG</th>
<th>SJW</th>
<th>ZS</th>
<th>DT</th>
<th>PT</th>
<th>XM</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZAP</td>
<td>0.629</td>
<td>0.217</td>
<td>0.241</td>
<td>0.273</td>
<td>0.786</td>
<td>0.357</td>
<td>0.258</td>
<td>0.140</td>
<td></td>
</tr>
<tr>
<td>XDZ</td>
<td>0</td>
<td>0.045</td>
<td>0.617</td>
<td>0.749</td>
<td>0.837</td>
<td>0.188</td>
<td>0.057</td>
<td>0.141</td>
<td></td>
</tr>
<tr>
<td>YGD</td>
<td>0.01510</td>
<td>0.07583</td>
<td>0.006</td>
<td>0.013</td>
<td>0.052</td>
<td>0.178</td>
<td>0.397</td>
<td>0.041</td>
<td></td>
</tr>
<tr>
<td>DYG</td>
<td>0.00108</td>
<td>0</td>
<td>0.10701</td>
<td>0.613</td>
<td>0.230</td>
<td>0.039</td>
<td>0.015</td>
<td>0.284</td>
<td></td>
</tr>
<tr>
<td>SJW</td>
<td>0.00725</td>
<td>0</td>
<td>0.11228</td>
<td>0</td>
<td>0.542</td>
<td>0.074</td>
<td>0.013</td>
<td>0.107</td>
<td></td>
</tr>
<tr>
<td>ZS</td>
<td>0</td>
<td>0.008799</td>
<td>0.01149</td>
<td>0</td>
<td>0.103</td>
<td>0.029</td>
<td>0.174</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DT</td>
<td>0.00408</td>
<td>0.02337</td>
<td>0.01832</td>
<td>0.04329</td>
<td>0.03867</td>
<td>0.03023</td>
<td>0.888</td>
<td>0.442</td>
<td></td>
</tr>
<tr>
<td>PT</td>
<td>0.01464</td>
<td>0.04777</td>
<td>0</td>
<td>0.06118</td>
<td>0.06507</td>
<td>0.06283</td>
<td>0</td>
<td>0.551</td>
<td></td>
</tr>
<tr>
<td>XM</td>
<td>0.01584</td>
<td>0.01596</td>
<td>0.07329</td>
<td>0.06118</td>
<td>0.06507</td>
<td>0.06283</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

All negative $\Phi_{ST}$ values were adjusted to 0.

Bold values are significant at $P < 0.05$. See Table 1 for locality abbreviations.

Figure 4. Multidimensional scaling analyses of $\Phi_{st}$ genetic matrices based on mitochondrial COI sequences for populations of Nerita yoldii (see Table 1 for locality abbreviations).

Table 3. Results from analysis of molecular variance (AMOVA) of Nerita yoldii.

<table>
<thead>
<tr>
<th>Among groups</th>
<th>Among populations within groups</th>
<th>Within populations</th>
</tr>
</thead>
<tbody>
<tr>
<td>d.f.</td>
<td>$\Phi_{CT}$</td>
<td>% Var</td>
</tr>
<tr>
<td>2</td>
<td>0.06445</td>
<td>6.45</td>
</tr>
</tbody>
</table>

The grouping refers to the results from SAMOVA and population difference analyses: group 1 (YGD); group 2 (ZAP, XDZ, DYG, SJW, ZS); group 3 (DT, PT, XM) (see Table 1 for locality abbreviations).

Multidimensional scaling based on $\Phi_{CT}$ showed that the three southernmost natural rocky-shore populations (DT, PT, XM) clustered together, while the rest of the populations to the north (except for the YGD population) also clustered together (Fig. 4).

According to the SAMOVA, $F_{CT}$ was maximized ($F_{CT} = 0.07538; P = 0.006$) when all populations were divided into three groups (group 1: YGD; group 2: ZAP, XDZ, DYG, SJW, ZS; group 3: DT, PT, XM). Based on the SAMOVA groupings, an AMOVA revealed that the 6.45% of the variation was among groups ($F_{CT} = 0.06445; P = 0.002$), -1.48% among populations within groups ($P = 0.002$) and 95.04% within populations ($P = 0.025$) (Table 3).

Demographic analysis

Mismatch distribution analyses indicated that within each population most haplotypes differed by only 0–1 nucleotides (Fig. 5). The largely unimodal peaks and nonsignificant Harpending’s raggedness index (Table 1) were all consistent with recent demographic expansions. Neutrality tests (Table 1) showed a similar pattern, with significantly negative values of either Tajima’s $D$ or Fu’s $F_{s}$ for most samples.

DISCUSSION

Previous studies have shown that artificial structures can act as ‘stepping stones’ to facilitate dispersal of invasive species (Airoldi et al., 2005; Bulleri & Airoldi, 2005; Hidas et al., 2007; Adams et al., 2014; Dong et al., 2016). Similarly, our intertidal survey conducted from 2013 to 2016 along the coast of Jiangsu Province revealed that recently constructed coastal infrastructures were rapidly occupied by Nerita yoldii. In July 2013, the northern limit of $N$. yoldii was found at YGD (32°31.472′N, 121°24.169′E) on coastal defence structures that were begun in 2006 and completed in 2011. Specimens of $N$. yoldii were found for the first time at XDZ (32°39.281′N, 120°38.062′E) in July 2015 and at ZAP (32°51.069′N, 120°58.306′E) in January 2016, where seawalls were built in July 2013. Similar rapid colonization of artificial structures has also been observed for other rocky intertidal species with planktonic larvae in China (e.g. Siphonaria japonica, Littoraria saxatilis, Fistulobalanus alticostatus; Dong et al., 2016) and even for a species with direct development, Littorina saxatilis, on Belgian breakwaters (Johannesson & Warmoes, 1990).

Populations on artificial rocky shores are expected to have relatively low haplotype diversity and fewer private haplotypes, as shown in the limpet Patella caerulea (Fauvelot et al., 2009). As expected, the two most recently colonized (2015–2016) artificial shore populations (ZAP and XDZ) of $N$. yoldii were characterized by low genetic diversity and an absence of private haplotypes, likely due to a founder effect. However, another two artificial...
rocky-shore populations (YGD and DYG) that were colonized earlier (2006–2013) had relatively higher haplotype diversity than nearby natural-shore populations (SJW and ZS). One possible explanation for higher diversity in YGD and DYG is multiple invasions, since these two populations (2006–2013) could be as much as 9 years older than the more recently colonized ZAP and XDZ populations (2015–2016). Bock et al. (2015) discovered that genetic variability in invaders largely depends on whether they result from single or multiple introductions, and successful invasions are highly associated with multiple introductions and subsequent mixing (Dlugosch & Parker, 2008). Genetic diversity in the two northernmost natural-shore populations (SJW and ZS) was unexpectedly low, similar to nearby artificial-substrate populations, suggesting that the northward range expansion of this species may have started earlier, with the colonization of natural rocky shore at ZS in response to another factor, such as increased

Figure 5. Mismatch distributions of observed COI haplotypes for each locality. Histograms are the observed frequencies of pairwise divergences and line shows expectation under sudden population-expansion model, tested with Harpending’s raggedness index (HRag). See Table 1 for locality abbreviations and HRag values (all P > 0.05).
sea surface temperature (SST) in the past. As SJW and ZS were at the historic northern limit of N. yoldii, the habitats and/or conditions at SJW and ZS may have been marginal, such that the two peripheral populations maintained low genetic diversity as a consequence of smaller effective population size.

The population genetic structure analyses suggest the putative source for most of the artificial rocky-shore populations (ZAP, XDZ, DYI) and the invasion routes. The MDS and SAMOVA results, which both grouped the two northernmost natural rocky-shore populations (SJW and ZS) with the artificial-shore populations, indicate that the putative source populations are the two northernmost natural rocky-shore populations south of the Yangtze River. During spring and summer spawning seasons of N. yoldii, the northward coastal currents likely carry pelagic larvae from the source areas south of the Yangtze River to the invaded areas north of the river (Wang et al., 2015; Dong et al., 2016).

Among the artificial-substrate populations, the offshore YGD population had higher genetic diversity and is relatively isolated from the other artificial shore populations, 20 km offshore. The construction of this artificial island may have changed the local hydrodynamic conditions in the offshore areas of Jiangsu Province (Chen et al., 2008; Xin et al., 2017) by reducing the velocity and direction of flow near the construction area, potentially influencing larval dispersal and recruitment (Largier, 2003)—as in the case of low current velocity around an island that contributed to high levels of local recruitment in the coral Heliopora coerulea (Harri & Kayanne, 2003). In our present study, the larval dispersal and thus population connectivity of N. yoldii might similarly be affected by the changed hydrodynamic conditions.

Previous studies have shown that the biogeographic and phylogeographic boundary for intertidal species around the Yangtze River Estuary may be the Yangtze River discharge, the coastal seawater temperature discrepancy across the mouth of the river, and/or habitat availability (Yu et al., 2014; Wang et al., 2015; Dong et al., 2012, 2016; Ni et al., 2014, 2017). The Yangtze River (the fifth largest river in the world) reaches its maximum discharge in spring and summer in the mouth of the river. The Yangtze River has shown a clear trend of increase over the last 50 years, with an annual average discharge of 10,227–2297 m³/s (Li, 2013). The relatively lower SST to the north of the Yangtze River (3–9°C in winter and 24–27°C in summer) compared to south of the river (10–20°C in winter and 27–30°C in summer) might affect the settlement and development of N. yoldii juveniles in this region. For areas both north and south of the Yangtze River, SST has shown a clear trend of increase over the last 50 years, with greater warming in autumn and winter (Bao & Ren, 2014). The recent increase in SST might have provided an appropriate thermal environment for the colonization of N. yoldii in the north of the river.

In summary, our study shows that N. yoldii can rapidly colonize the newly built artificial substrates along the Jiangsu coastline, indicating that habitat availability (in this case probably in combination with increasing SST) is one of the most important factors limiting the northward expansion of rocky intertidal species. SST in the marginal seas of China has increased significantly over the past 140 years and the potential for northward expansion of marine species is increasing for southern species with high dispersal capabilities. The construction of the new ‘Great Wall’ along the Chinese coast provides suitable habitats for the settlement of intertidal rocky-shore species, potentially promoting dispersal and gene flow across the biogeographic and phylogeographic barrier around the Yangtze River Estuary (Huang et al., 2015; Dong et al., 2016).

This, therefore, barrier may eventually disappear under the combined effects of climate change and human activity. Considering the limitations of our study (based on only the single mitochondrial COI gene), we suggest additional data from other species and more genes will give insight into the process of how newly built hard substrates and rising seawater temperatures affect northward range expansion of intertidal species.

ACKNOWLEDGEMENTS

This work was supported by grants from National Natural Science Foundation of China (41476115, 41776135), National Basic Research Program of China (2013CB956004) and Nature Science funds for Distinguished Young Scholars of Fujian Province, China (2017J07003). We would like to thank Colin Little for preparing the manuscript, and Associate Editor Peter Marko and two anonymous referees for helpful suggestions.

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