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Global warming and artificial shorelines reshape seashore biogeography

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Abstract

Aim: Rapid anthropogenic warming coupled with changes in land use is altering the distributions of species, with consequences for ecosystem functioning and services. It is crucial to evaluate species range shifts based on understanding of the interaction of temperature with non-climatic factors such as habitat availability and dispersal potential. Here, we aim to investigate roles of environmental temperature, habitat availability and population connectivity on the distributions of hard-shore intertidal animals. We further examine potential roles of extensive artificial seawall construction in enabling poleward expansion of species in China, thus reshaping coastal biogeography.

Location: Chinese coast.

Time period: 2013–2017.

Major taxa studied: Intertidal invertebrates.

Methods: We took an integrative approach encompassing distributional ecology, thermal physiology, molecular genetics, heat budget modelling and larval dispersal to elucidate how interacting multiple drivers, including temperature, habitat availability and larval dispersal, determine distributions of hard-shore invertebrates, focusing on what sets their range edges at a boundary between biogeographic provinces.

Results: Our results untangle the complex interactions of global climate change with the impacts of regional scale coastal development. Temperature, larval transport and habitat availability are the major proximate factors controlling the range limits of coastal marine species. The artificial shorelines provide suitable habitats for hard-shore species on the Yangtze River Delta, and minimum temperature in winter is an important factor setting the new northern range limit of these hard-shore species along the Chinese coast.

Main conclusions: In the face of global warming and global sprawl of marine hard infrastructure, species distributions, community structures and biogeographic patterns are experiencing dramatic changes. The combined influence of multiple human stressors including climate change and artificial shorelines can be evaluated by using

a multidisciplinary framework, including ecological distribution, physiological sensitivity of species to these stressors, and the role of dispersal in maintaining population connectivity.

1 | INTRODUCTION

Anthropogenic global warming and habitat transformation have jointly led to shifts in species distributions, changes in community structure, and, potentially, rearrangement of biogeographic provinces (Nowakowski et al., 2018; Pereira et al., 2010; Vitousek, Mooney, Lubchenco, & Melillo, 1997). Untangling the interactions of these factors is challenging, yet vital in order to forecast future ecological responses. By far the most common approach used in generating predictions has been to quantify the current environmental conditions present at existing range boundaries, and then to extrapolate these presumed limiting factors to future modelled environmental conditions. Mainly statistical (Araújo & Peterson, 2012; Pagel et al., 2014; Stuart-Smith, Edgar, Barrett, Kininmonth, & Bates, 2015) but also mechanistic (Kearney & Porter, 2009; Poloczanska, Hawkins, Southward, & Burrows, 2008; Thomas & Bacher, 2018) approaches have been attempted. A key attribute of these methods has been the assumption that the physiological tolerance of a species to environmental (usually climatic) conditions ultimately sets its distribution limits (i.e., its fundamental niche space), and therefore any amelioration (e.g., at a poleward range edge) or worsening (e.g., at an equatorial range edge) will result in a range shift (Deutsch et al., 2008; Harris et al., 2018; Sunday et al., 2014). It has also been shown, however, that non-climatic factors such as ocean currents or the absence of suitable habitat for settlement can serve as barriers to dispersal and thus determine range edges (Cannizzo, Dixon, & Griffen, 2018; Dong, Huang, Wang, Li, & Wang, 2016; Gaylord & Gaines, 2000; Keith, Herbert, Norton, Hawkins, & Newton, 2011; Kimura & Weiss, 1964). Models that fail to incorporate these limiting factors can lead to either over- or under-projections of biogeographic shifts. The limitations of traditional modelling approaches take on new significance in an era when both the formation of new barriers to dispersal as well as the creation of new habitat (e.g., seawalls) are proliferating. A comprehensive mechanistic framework that causally links biogeographic distribution of species and their thermal physiology, for understanding the combined effect of global warming and habitat modification is still lacking. Perhaps nowhere is a need for such a framework as evident as in coastal marine systems.

With high connectivity in the marine ecosystem (Cowen & Sponaugle, 2009), marine organisms with pelagic larvae are often assumed to more fully occupy the extent of latitudes allowed by their thermal tolerance limits than are many terrestrial animals with more limited modes of dispersal (Kinlan & Gaines, 2003); consequently,

some marine species have been observed to rapidly extend their poleward range boundaries and contract their equatorward boundaries with climate warming (Sunday, Bates, & Dulvy, 2012). The fingerprint of warming on these economically and ecologically important ecosystems is already evident (Heron, Maynard, Van Hooidonk, & Eakin, 2016; Hoegh-Guldberg & Bruno, 2010; Pecl et al., 2017), and current global marine diversity patterns are expected to continue changing rapidly in response to ocean warming (Harley et al., 2006; Molinos et al., 2016; Sunday et al., 2012). However, most of the world's coastline is warming at rates that can exhibit high spatial and temporal heterogeneity, and changes are occurring not just at range boundaries but also well within species ranges (Burrows et al., 2011; Helmuth et al., 2002; Lima & Wethey, 2012; Oey, Chang, Chang, Lin, & Xu, 2013; Sevellec & Drijfhout, 2018). Concurrently, with increasing coastal development (e.g., industry, transportation, aquaculture, residential use, tourism and coastal defence), more and more artificial structures are being built along coastlines world-wide (Bulleri & Chapman, 2010; Dong et al., 2016; Huang, Wang, & Dong, 2015). These proliferating artificial hard substrata change local and regional biodiversity primarily through the provision of new habitat (Firth et al., 2016). They also facilitate the establishment and spread of both native and exotic species, leading to changes of long-standing distributional boundaries (Bishop et al., 2017; Cannizzo et al., 2018). With both climate change and emergence of new hard substrata bridging habitat gaps and increasing connectivity, animals inhabiting intertidal areas can rapidly occupy new hard-shore habitats at locations where conditions are within the species' thermal tolerance range. Once established, populations on these habitat patches can serve as critical 'stepping stones', enabling further colonization at other sites beyond the limits of present-day larval dispersal (Hannah et al., 2014). Importantly, and in contrast to most heuristic models, range edges can expand rapidly via these mechanisms. These range boundary shifts and assemblage composition changes will consequently reshape coastal biogeography, potentially at the level of biogeographic province.

The unprecedented coastal development and increasing warming along the Chinese coastline provide an excellent opportunity to study how climate change and habitat modification, two of the most important contemporary anthropogenic drivers, interact to change coastal biodiversity, ecosystem functioning and biogeographic patterns. The Yangtze River Mouth is regarded as a biogeographic barrier and is the boundary of two ecological provinces, the Cold Temperate Northwest Pacific and the Warm Temperate Northwest

Pacific provinces (Spalding et al., 2007). Climate, available suitable habitat and Yangtze River discharge have been deemed to be main causes of this barrier, coupled with historical events during glacial cycles (Dong et al., 2012; Ni, Kern, Dong, Li, & Park, 2017; Wang, Tsang, & Dong, 2015). Due to the shortage of appropriate substrate on Yangtze River Delta, rocky intertidal species are largely precluded from settling on the shore from the Yangtze River Mouth (*c.* 30° N) to Lianyugang, Jiangsu (*c.* 34.5° N) (Huang, 2008; Wang, Qian, Wang, & Guo, 2013; Zhang, Qi, Zhang, & Ma, 1963; Zhao, Li, Kong, & Yu, 2017). Over 60% of the Chinese shoreline has been modified due to land reclamation and other activities involving coastal construction (Hou et al., 2016; Ma et al., 2014). These hard artificial structures along the shoreline have transformed many natural muddy tidal-flats to a relatively homogeneous 'grey' artificial shoreline in the last few decades (Hou et al., 2016). The limited ecological and genetic data that exist reveal that these new artificial hard substrata can facilitate the poleward migration of hard-shore species (Dong et al., 2016). To mechanistically explore the impacts of coastal development and increasing warming on the biogeographic pattern of intertidal species, in the present study, we took an integrative approach encompassing distributional ecology, biophysics, thermal physiology, molecular genetics and larval dispersal to achieve the following purposes. First, by using distributional ecology and phylogeographic studies we wished to determine whether the construction of artificial shorelines, as suitable habitats for rocky intertidal species, can alter the species distribution and biogeographic pattern of intertidal macrobenthos along the Chinese coastline. Second, by using hydrodynamic model simulation and metabarcoding we tested whether larvae of southern intertidal species can go northwards beyond the Yangtze River Mouth, the former biogeographic barrier. Third, by using biophysics and physiological measurements, we examined whether temperature is a limiting factor for setting the northern range limit of hard-shore species that are absent in the natural muddy tidal-flats, but settle on and colonize artificial structures. Our work provides strong evidence that these artificial structures help set range limits for these species and, more broadly, alter a boundary between biogeographic provinces.

2 | MATERIALS AND METHODS

2.1 | Assemblage surveys and analyses

To investigate spatio-temporal changes in community structure on artificial and rocky shores, nine field surveys of intertidal macrobenthos were performed at 17 locations along the Chinese coastline from 2013 to 2017 (Figure 1 and Supporting Information Table S1). Among these 17 locations, two of them are natural rocky shores, namely Lianyungang (LYG) and Shenjiawan (SJW), and the others are artificial shorelines. At each location, species searches were conducted along at least 100 m of shore at each location for 1 hr during low tides, and presence/absence data were recorded. The rocky shore species compositions of invertebrates, including mobile, sessile and sedentary macrobenthic species of Gastropoda, Bivalvia, Polyplacophora and Cirripedia (body size > 0.5 cm) were recorded. Non-metric multidimensional scaling (nMDS) and cluster analysis based on Bray–Curtis similarity of presence/absence data were
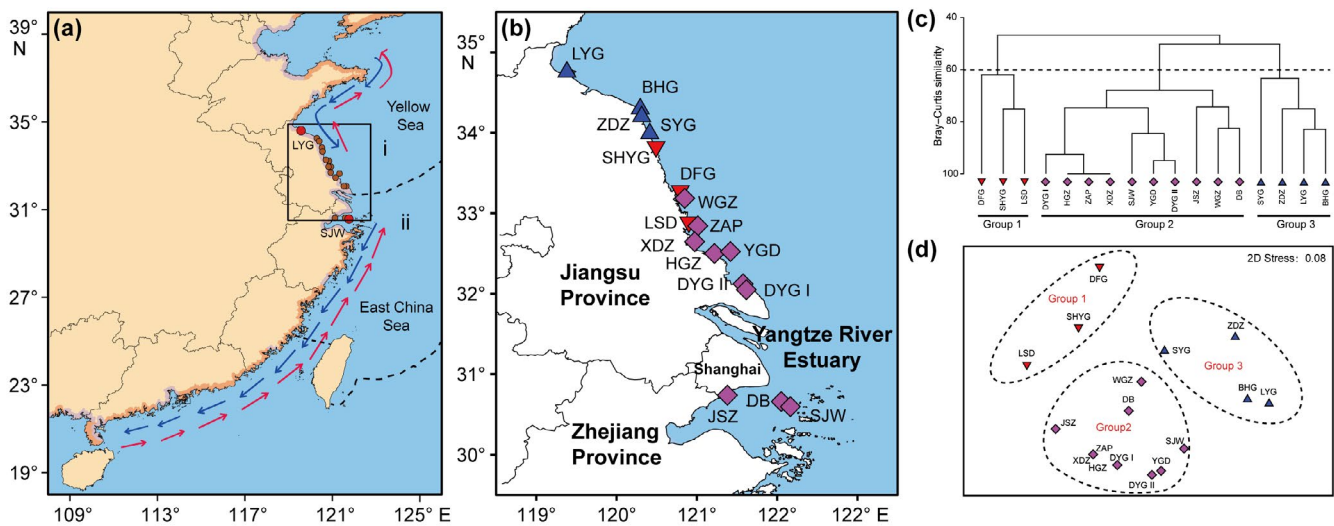

FIGURE 1 Field survey locations and assemblage structure of rocky shore species. (a) Field survey locations; the dashed lines are the boundaries of marine ecoregions: (i) the Cold Temperate Northwest Pacific and (ii) the Warm Temperate Northwest Pacific. In autumn and winter, the China Coastal Current (CCC, blue arrows) flows from north to south along the China coast, and in spring and summer, the CCC (red arrows) flows northwards into the East China Sea. (b) Partially enlarged map of panel a, abbreviations: LYG, Lianyungang; BHG, Binghaigang; ZDZ, Zhendongzha; SYG, Shuangyanggang; SHYG, Shuangyanggang; DFG, Dafenggang; WGZ, Wanggangzha; LSD, Liangduo South Dam; ZAP, Zhonganpeng; XDZ, Xindongzhen; YGD, Yangguang Island; HGZ, Huangangzhen; DYG II, Dayanggang II; DYG I, Dayanggang I; JSZ, Jinshanzui; DB, Donghai Bridge; SJW, Shenjiawan. Cluster analysis (c) and non-metric multidimensional scaling analysis (d) for community structure of rocky shore species based on Bray–Curtis similarity of presence/absence data. Different shapes of points indicate different groups in panels b, c, d

used to visualize the pattern of assemblages using PRIMER v. 7 (Clarke, Somerfield, & Gorley, 2008).

2.2 | Biogeographic and phylogeographic patterns

To analyse the change in the northern distribution range limits of southern species and populations with or without coastal artificial structures, the presence of two southern species (the snail *Nerita yoldii* and the oyster *Crassostrea sikamea*) at the 17 locations along the Chinese coastline were continuously recorded during the nine field surveys from 2013 to 2017 to track their northern distribution edges (Figure 1). As two southern species, the northern distribution range limit of *N. yoldii* and *C. sikamea* occurred to the south of the Yangtze River Mouth before the construction of artificial shorelines on the Yangtze River Delta (Huang, 2008; Wang et al., 2013; Zhang et al., 1963). Thus, by tracking their distribution range shift, it is possible to discover the impacts of artificial shorelines on the biogeographic patterns of southern rocky shore species.

In investigating the phylogeographic pattern of ubiquitously distributed species along the Chinese coastline, it is important to know the impacts of artificial shorelines on the genetic structures of widely distributed species. The barnacle *Fistulobalanus albicostatus* is a dominant species on both natural rocky shores and artificial hard shores along the whole Chinese coastline. In the present study, its population genetic structure was analysed using the mitochondrial *cytochrome oxidase I* (*COI*) gene. Barnacles were collected from Lianyungang (LYG), Binhaigang (BHG), Shuangyanggang (SYG), Wanggangzha (WGZ), Zhonganpeng (ZAP), Dayanggang II (DYG II) and Jiantiao (JT) (Figure 1, Supporting Information Table S1). A total of 145 sequences of *COI* (GenBank accession numbers: MH782278–MH782422) from 7 populations were amplified and sequenced using LCO1490 and HCO2198 (Folmer, Black, Hoeh, Lutz, & Vrijenhoek, 1994). PCR reactions were conducted following the protocol described in Dong et al. (2016). Sequencing was tested in both forward and reverse directions and sequences were assembled and manually inspected for ambiguities using DNAMAN7 software (Lynnon BioSoft, Quebec, Canada). Other *COI* sequences of three common species on the hard shore along the Chinese coastline, *Siphonaria japonica*, *Littorina brevicula* and *Littoraria sinensis*, were downloaded from GenBank (Dong et al., 2016, GenBank accession numbers: KP195742–KP196013, KP196014–KP196241, KP196242–KP196327; Wang et al., 2015, GenBank accession numbers: KF716505–KF716747).

A simulated annealing approach implemented in SAMOVA v. 2.0 (Dupanloup, Schneider, & Excoffier, 2002) was used for a varying number of groups (*K*) to define groups of populations that were phylogeographically homogeneous and maximally differentiated from each other. The analysis was run for two to seven groups (five simulations repeated for each *K*), with 1,000 permutations. Then the grouping associated with the highest variance among groups (F_{CT}) (i.e., the best number of groups and the best population configuration) was selected. Based on the results of groupings defined by SAMOVA, a hierarchical analysis of molecular variance (AMOVA) using ARLEQUIN v.

3.5 (Excoffier, Smouse, & Quattro, 1992) was conducted, to test for the phylogeographic separations of the four species, which are widely distributed along the Chinese coastline.

2.3 | Simulation of larval dispersal

To simulate larval dispersal to test whether the larvae of southern species can go northwards beyond the Yangtze River Mouth and to discover the seasons in which larvae of southern species can move further northward, we used the results of an operational hydrodynamic model to predict the dispersal of pelagic larvae from different areas along the coasts of the East China Sea and the Yellow Sea. The operational hydrodynamic model is based on the Regional Ocean Modeling System (ROMS; Haidvogel et al., 2000; Shchepetkin & McWilliams, 2005), and the modelling domain covers the Northwestern Pacific Ocean with curvilinear grids. It can simulate currents throughout the water column (30 layers) with a spatial resolution ranging from approximately 45 km at the open boundary to about 3.0 km along the Chinese coast. For details of the operational model please refer to previous studies (Chen, Jiang, Liu, & Gong, 2017; Liao, Oey, Yan, Li, & Jiang, 2018; Lin, Yan, Jiang, & Zhang, 2016). Based on the model results, a drift trajectory program was developed to simulate the trajectories of larvae as passive particles. Simulations were run starting from 57 locations (Supporting Information Table S2) at four distinct times: 15 January (winter), 14 April (spring), 11 July (summer) and 6 November (autumn) 2017. The number of simulative passive particles from each location and starting time was 200. Based on the pelagic larval durations (PLD) of common intertidal rocky shore species (Supporting Information Table S3), we chose a simulation time of 30 days with a step size of 1 hr.

2.4 | Larvae metabarcoding

To investigate whether the larvae of southern intertidal species can be found to the north of the Yangtze River Mouth, plankton samples were collected in August 2014 and June 2015 around the Yangtze River Mouth and Yellow Sea coast (Supporting Information Figure S1) using a plankton net (mesh size 0.155 μm) and were stored at −20 °C for metabarcoding analysis. DNA extraction and PCR amplification were carried out as described by Ding, Wang, and Dong (2018). A *COI* gene fragment from total genomic DNA was pyrosequenced on the Roche 454 GS FLX+ platform (Branford, CT) at Xiamen University. An improved quantitative insights into microbial ecology (QIIME) pipeline (Caporaso et al., 2010) was used to analyse the raw data. Firstly, sequences of primers and multiplex identifiers (MIDs) were removed from the raw 454 reads. Then, quality control, denoising and chimera removal were implemented by using the QIIME pipeline. Because of the lack of a reference sequences database for *COI*, the programs CROP (Hao, Jiang, & Chen, 2011) and SAP (Munch, Boomsma, Huelsenbeck, Willerslev, & Nielsen, 2008) were used for operational taxonomic unit (OTU) picking (at 97% similarity) and taxonomic assignment for the final species composition of zooplankton.

2.5 | Body temperature estimation and cold thermal-safety margins (cTSM) measurements

To test whether the minimum temperature in winter is a limiting factor restraining the northern range limit of rocky intertidal species, the cold thermal-safety margins (cTSM) were calculated by integrating body temperature and thermal tolerance. The snail *N. yoldii* is originally a southern-occurring species, but recently has extended its range northward in a stepwise manner (Wang et al., 2018), with a current northern range limit at *c.* 33° N.

Estimates of body temperature for *N. yoldii* from 1978 to 2017 were calculated using a heat budget model (Marshall, Rezende, Baharuddin, Choi, & Helmuth, 2015) modified for snails from a model originally developed for mussels (Helmuth et al., 2011). The model was tailored by changing the shape and size of the animal, and the amount of contact with the substratum to be specific for each snail species. Variables for the heat budget model, such as air temperature, wind speed and solar radiation, were extracted from National Oceanic and Atmospheric Administration (NOAA)'s Climate Forecast System Reanalysis (CFSR). CFSR provides global hourly environmental data with a geographic area of 0.3° × 0.3° pixels (Saha et al., 2010). Body temperature estimations for each species and location were summarized as 95th and 99th percentiles of minimum body temperature (T_{b_min}) from 1979 to 2017.

Snails (*N. yoldii*) were collected from five locations (Xiamen, XM; Dongtou, DT; Zhoushan, ZS; Dayanggang II, DYG II; Yangguang Island; YGD) along the Chinese coastline and acclimated at 16 °C under identical conditions for *c.* 6 months. In the laboratory, snails were washed in filtered seawater, allowed to emerge from their shells and attach to lidded Petri dishes and the substrata of the Petri dishes were then cooled down from 16 °C at a rate of 6 °C/hr using a THD-3030 water bath (Tianheng, Ningbo, China). A non-invasive method was used to measure individual heart rates (Chelazzi, Pirro, & Williams, 2001). Flatline temperature of cardiac performance (FLT_{cold}) is the minimum temperature at which cessation of heartbeat was first observed (*n* = 12 to *n* = 19). Minimum temperatures lethal for 50% of individuals (LT_{50}) of four populations (Xiamen, XM; Zhoushan, ZS; Dayanggang II, DYG II; Yangguang Island; YGD) were calculated. When temperature reached each designated temperature (−4, −6, −8, −10, −12 and −14 °C) using the method mentioned above, three parallel groups (five individuals in each group) were randomly taken out and allowed to recover at 16 °C for 7 days. The survival of each treatment group was examined, and LT_{50} of each population was calculated using Probit analysis (*n* = 3). One-way ANOVA was used to determine the difference in FLT_{cold} and LT_{50} among different populations using SPSS 20.0 (IBM Corp., Armonk, NY).

The cTSM for FLT_{cold} or LT_{50} are defined as:

$$cTSM = FLT_{cold} - T_{b\_min} \qquad (1)$$

or

$$cTSM = LT_{50} - T_{b\_min} \qquad (2)$$

where T_{b_min} is the minimum body temperature. When the cTSM < 0, animals can tolerate the low temperature in winter; when the cTSM > 0, animals are threatened by low temperatures under either FLT_{cold} or LT_{50}.

3 | RESULTS

3.1 | Community structural similarity

From 2013 to 2017, 21 species of macrobenthos, including molluscs and barnacles, were recorded at 17 locations from the Yangtze River Mouth to north of the Yangtze River Delta (Figure 1a and Supporting Information Table S1). Based on Bray–Curtis similarity of presence/absence data (Supporting Information Table S4), cluster analysis (Figure 1c) and nMDS plots (Figure 1d), we show that all 17 locations can be generally divided into three groups with 60% similarity. Because there was not hard substrate before the construction of artificial shorelines, hard-shore assemblages on the former muddy tidal-flats, from Donghai Bridge (DB) to Binhaigang (BHG), were absent until recent times. With the construction of sea defences on the muddy tidal-flats, three emergent assemblages on the artificial habitats in the middle of the Yangtze River Delta between latitudes of 33 to 34° N (SHYG, DFG and LSD) clustered together as group 1. Some assemblages on the artificial habitats up to latitude 33° N (WGZ) clustered together with a southern natural rocky shore assemblage (SJW) at 31° N as group 2. Three assemblages on the artificial shorelines at the northern Yangtze River Delta (SYG, ZDZ and BHG) clustered with the assemblage at the northern natural rocky shore (LYG) as group 3.

Due to a lack of appropriate habitats on the natural muddy tidal-flats in the Yangtze River Delta up until recent times, the historical northern distributional boundaries of *N. yoldii* and *C. sikamea* were around 30 to 31° N (Figure 2a). On the artificial hard shores in the Yangtze River Delta, these two southern species now are dominant species and their northern distribution range limits have moved further north to 33 to 34° N. During the period of our field survey, the distribution of *N. yoldii* showed a gradual expansion of its northward distribution. From 2014 to 2017, it expanded from 32°30.0' to 33°10.8' N, a distance of 80 km.

AMOVA results, based on the *COI* gene, showed that populations of *F. albicostatus* along the Chinese coast divide into two groups, a northern group and a southern group (Table 1). This is also true for the other three species, *S. japonica*, *Littorina brevicula* and *Littoraria sinensis* (Table 1). With the construction of artificial habitats, the northern boundary of the southern group for all four species moved across the Yangtze River Mouth to the artificial structures around 33° N (Figure 2b).

3.2 | Larvae dispersal across the Yangtze River barrier

For the intertidal species that reproduce in spring and summer to the south of the Yangtze River Mouth (area C), larvae with PLDs > 17 days can go beyond the Yangtze River Mouth and reach the coast of the Yangtze River Delta (Figure 3a–d and Supporting Information Figure S2). For the intertidal species on the artificial habitat at the Yangtze River Delta (area B), their larvae can move further north to
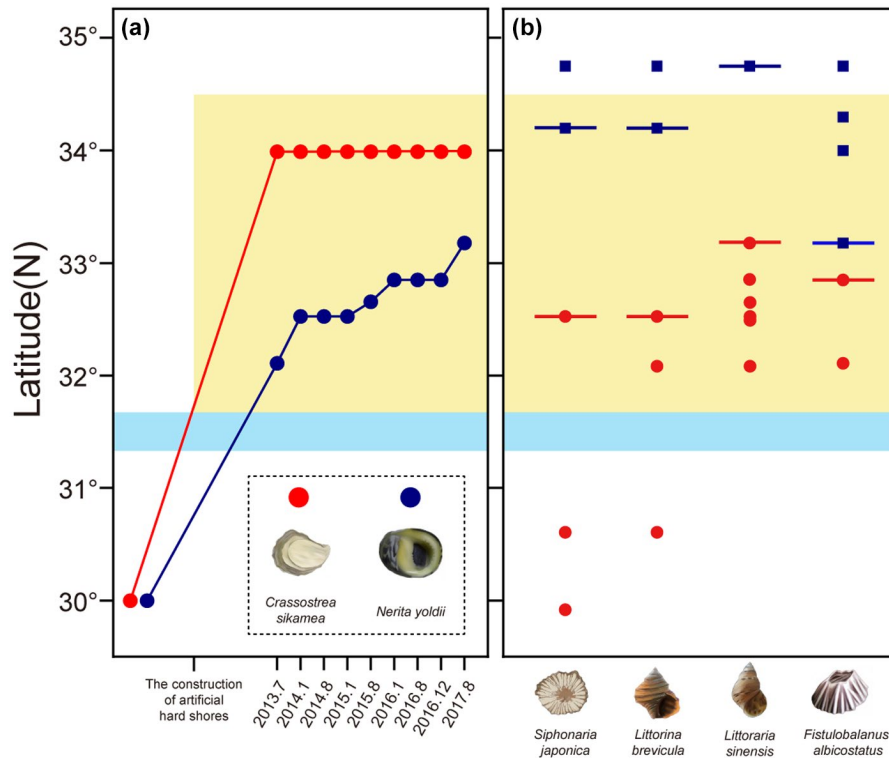
FIGURE 2 Biogeographic and phylogeographic patterns of rocky shore species influenced by artificial coastal structures. (a) The changes in the northern distribution range limits of southern species, *Nerita yoldii* and *Crassostrea sikamea*, based on data from nine field surveys from July 2013 to August 2017. The range limits of these two species before the construction of artificial hard shores were obtained from previous studies (Huang, 2008; Wang et al., 2013; Zhang et al., 1963). (b) The distribution range limits of the southern group (red lines) and the northern group (blue lines) of widespread species with coastal artificial structures; the red circles and blue squares represent the southern populations and northern populations of each species from 30 to 35° N, respectively, based on the results of analysis of molecular variance (AMOVA) (Table 1). The shadings around 31° 30′ indicate the Yangtze River Mouth. The shadings from 31° 30 to 34° 30′ N indicate the area of coastal artificial structures
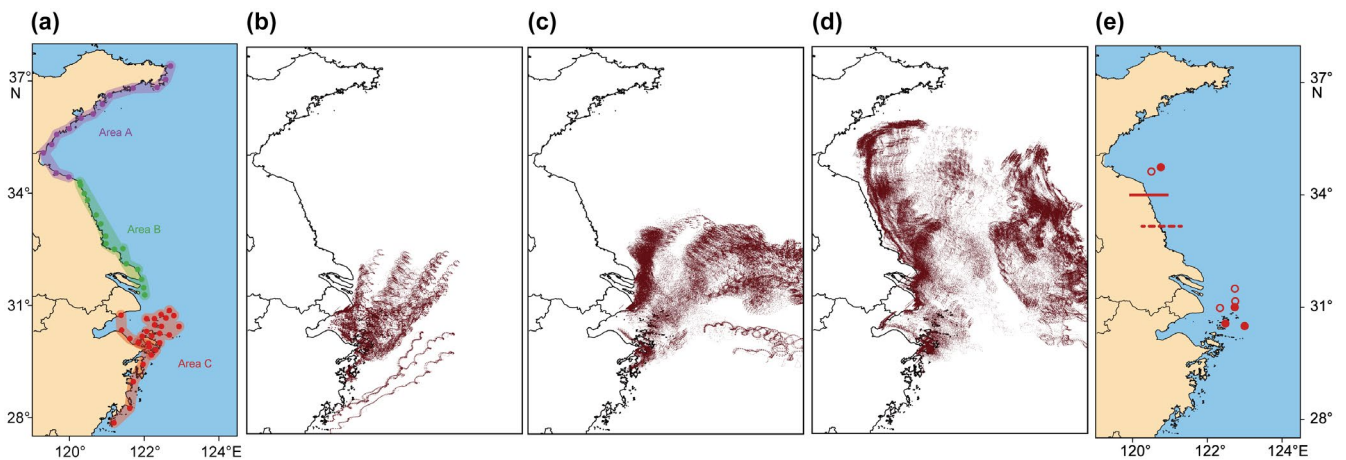

FIGURE 3 The results of larval dispersal simulations and detection of intertidal species' larvae in aquatic communities. (a) Starting locations of the larval dispersal simulations. The dispersive trajectory of larvae with different pelagic larval durations [(b) 1–7 days, (c) 8–17 days, (d) 18–30 days] from area C in summer. (e) The distribution of *Nerita yoldii* (open circles) and *Crassostrea sikamea* (sold circles) larvae and the northern distribution range limits of adult *N. yoldii* (dash line) and *C. sikamea* (solid line)

the north China rocky shore (area A) in spring and summer (Supporting Information Figure S2), and move southward to areas south of the Yangtze River Mouth (PLD > 17 days) in autumn and winter (Supporting Information Figure S2).

Using a DNA barcoding technique with *COI* as the biomarker, *N. yoldii* and *C. sikamea* larvae were found in the Yellow Sea, 34.5° N, in August 2014 and June 2015, further confirming that larvae of southern species can reach the coastal region beyond the

TABLE 1 Results from analysis of molecular variance (AMOVA) in *Fistulobalanus albicostatus*, *Siphonaria japonica*, *Littoraria sinensis* and *Littorina brevicula*

Species	Among groups			Among locations within groups			Within locations		
	df	Φ_{CT}	%Var	df	Φ_{SC}	%Var	df	Φ_{ST}	%Var
F. albicostatus	1	8.03694*	80.55	5	−0.00537	−0.05	138	1.94615	19.50
S. japonica	1	1.09559***	29.75	10	−0.02019	−0.55	317	2.60697***	70.80
Littoraria sinensis	1	0.26965*	36.33	8	0.00659	0.89	262	0.46602***	62.78
Littorina brevicula	2	0.02210**	10.31	5	−0.00145	−0.68	220	0.19363***	92.42

Note: Φ_{CT}, Φ_{SC}, Φ_{ST} = total molecular variance among groups, among populations within groups, and among populations whatever the groups, respectively; %Var = proportion of this part of variance accounted for the total genetic variance. The grouping refers to the best SAMOVA population grouping: for *F. albicostatus*, South group (ZAP, DYG II, JT), North group (LYG, BHG, SYG, WGZ); for *S. japonica*, South group (YGD, SJW, ZS, XM, DS, HK, HAK), North group (WH, QD, RZ, LYG, ZDZ); for *Littoraria sinensis*, South group (WGZ, ZAP, XDZ, YGD, HGZ, DYG I, DT, XM), North group (QD, LYG); for *Littorina brevicula*, South group (YGD, DYG I, SJW, DT), North group (QD, LYG, ZDZ), Single group (WH). See Supporting Information Table S1 for locality abbreviations.
*p < .05; **p < .01; ***p < .001.

FIGURE 4 The cold thermal-safety margins (cTSM), which represent the difference between cold temperature tolerance (Flatline temperature of cardiac performance FLT_{cold} or Low temperatures lethal for 50% of individuals, LT_{50}) and minimum body temperature (T_{b_min}), for *Nerita yoldii* (a). Solid circles are cTSM for LT_{50}; hollow circles are cTSM for FLT_{cold}. The shaded region shows where species are threatened by low temperatures due to either FLT_{cold} or LT_{50}. The 95th (b) and 99th (c) percentiles of minimum body temperature (T_{b_min}) of *N. yoldii* at 30° N and 33° N
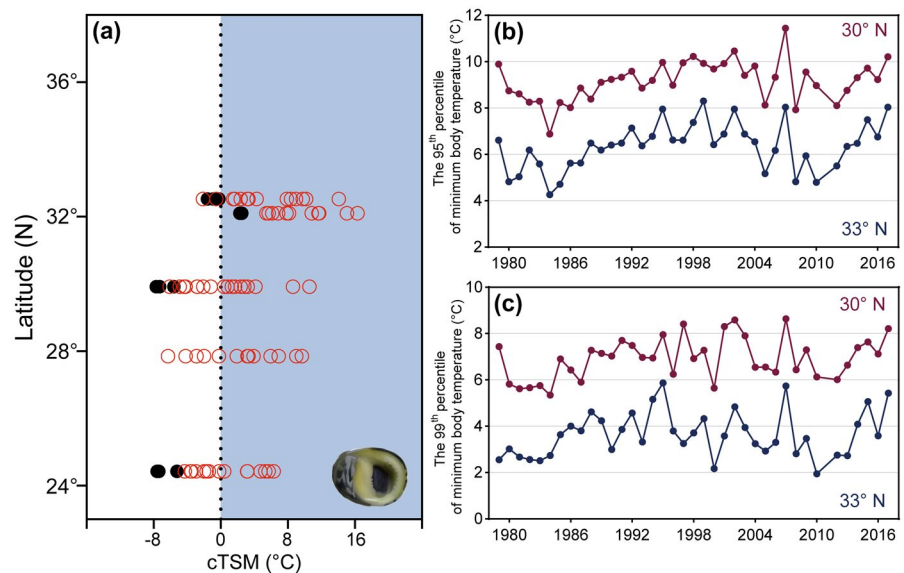
current northern distributional limit of adults at a latitude of *c.* 33 °N (Figure 3e). Results of taxonomic assignment are available through the Dryad data repository (https://doi.org/10.5061/dryad.34tmp g4fq), and all the metabarcoding data were deposited in GenBank (Sequence Read Archive accession: PRJNA559658).

3.3 | Body temperature estimation and cold thermal safety margin

Among different populations, *N. yoldii* showed no significant differences in either FLT_{cold} or LT_{50} (FLT_{cold}, $F_{(4, 70)}$ = 0.345, *p* = .846; LT_{50}, $F_{(3, 11)}$ = 0.133, *p* = .938; Figure 4). However, the cTSM results manifested the divergent dangers arising from cold stress among populations. High percentages of individuals were predicted to have survived cold stress during winter at sites from Xiamen (XM, *c.* 24° N; 52.94%), Southern China to Zhoushan (ZS, 30° N; 42.11%), south of the Yangtze River Mouth. However, hindcasts suggested that *N. yoldii* on the artificial structures at Dayanggang II (DYG II) and Yangguang Island (YGD) (both *c.* 32° N) suffered high mortality

(95–100%) during winter (Figure 4a). The minimum body temperature (T_{b_min}) at most locations increased from 1979 to 2017, especially at the Yangtze River Delta (30–35° N) (Supporting Information Figure S3; Figure 4b,c). Specifically, T_{b_min} at the Yangtze River Mouth, the original northern distribution limit around 30° N, and its current distribution range limit, around 33° N, clearly increased from 2010 to 2017 (Figure 4b,c). At 30° N, the 95th percentile of T_{b_min} of *N. yoldii* increased from 8.97 °C in 2010 to 10.21 °C in 2017; at 33° N, T_{b_min} increased from 4.80 °C in 2010 to 8.04 °C in 2017. The 99th percentiles of T_{b_min} also showed warming trends at both 30 and 33° N from 2010 to 2017.

4 | DISCUSSION

Habitat availability, larval transport and temperature are important factors controlling the range limits of intertidal macrobenthos along the Chinese coastline. Our results further confirm the respective roles of these three variables in establishing species distributions in

the face of anthropogenic climate change and development-driven habitat modification (Bishop et al., 2017; Deutsch et al., 2008; O'Connor et al., 2007). These results are critical for predicting biogeographic ranges in a rapidly changing world, and for suggesting how human activities might need to be altered to ameliorate or adapt to these changes.

The effects of artificial shorelines in reshaping biogeographic patterns of intertidal macrobenthos, as indexed by community similarity and distribution of rocky shore species, are verified by data from the 5-year field survey. Due to a lack of appropriate habitats on the natural muddy tidal-flats in the Yangtze River Delta up until recent times, the original distribution boundaries of the hard-shore species we investigated lay to the south of the Yangtze River Mouth (about 30–31° N; Dong et al., 2012, 2016; Wang et al., 2015). All the assemblages of hard-shore species on the coastal artificial structures at the Yangtze River Delta have appeared during the past few decades in conjunction with the construction of structures made of concrete and rocks. With the construction of artificial hard shore, rocky intertidal species appeared on these structures. For example, seawalls in Zhonganpeng (ZAP) were built in July 2013, and there were no hard-shore macrobenthic species at that time. From 2014 to 2017, *Littoraria sinensis*, *Littorina brevicula*, *C. sikamea* and *F. albicostatus* became common species on the seawalls, indicating that the artificial structures were rapidly occupied by rocky intertidal species. In the present study, the community similarity index and the northward range shift of southern species (*N. yoldii* and *C. sikamea*) clearly show that the former biogeographic boundary between Cold Temperate Northwest Pacific and Warm Temperate Northwest Pacific provinces has been breached and a new boundary now exists approximately 200 km further northward along the shoreline. These results indicate that the appearance of new hard-surface habitats with the construction of coastal structures has facilitated the northward distributional shift for southern fauna.

Phylogeographic data also support the conjecture that the genetic boundary for the ubiquitously distributed species has moved further northward with the construction of artificial structures. Excluding the populations on the artificial hard shores on the Yangtze River Delta, a phylogeographic break lies at the Yangtze River Mouth for intertidal rocky shore species (e.g., *Cellana toreuma*, *Thais clavigera* and *S. japonica*; Dong et al., 2012; Ni et al., 2017; Wang et al., 2015). The construction of coastal structures also has modified the phylogeographic pattern of intertidal macrobenthos and the construction of artificial hard shores can assist southern haplotypes of widely distributed intertidal species to move across the Yangtze River Mouth. Therefore, both biogeographic and phylogeographic data support the appearance of a new boundary for hard-shore macrobenthic assemblages around 33° N.

Hydrodynamic simulation and DNA metabarcoding data showed that larvae of some southern species can go beyond the Yangtze River Mouth. In many marine invertebrates with complex life histories, their range boundaries may be delimited by effects on multiple life stages (Crickenberger & Wethey, 2018; Pandori & Sorte, 2019). The pelagic stage is the dominant stage for the exchange of

individuals among such marine populations (Cowen & Sponaugle, 2009). Life-history features and larval behaviour can interact with current regimes to make organisms more or less able to breach the dispersal barrier around the Yangtze River Mouth. Reproductive season, retention features and coastal processes play important roles in larval dispersal and settlement (Day, 2000). The results from high-resolution Regional Ocean Modeling System (ROMS) hydrodynamic modelling show clearly that pelagic larvae can move further northwards across the Yangtze River Month in spring and summer. As previous studies mentioned, there are some limitations of ROMS for simulating larval dispersal (Levin, 2006), and the impacts of larval behaviour were not considered in the simulations (Kim & Barth, 2011; Pfeiffer-Herbert, McManus, Raimondi, Chao, & Chai, 2007). Here, the main purpose of ROMS simulation is to test whether the larvae of southern fauna can go northwards beyond the Yangtze River Mouth and to identify the season in which larvae of southern species can move further northward. The DNA metabarcoding data confirmed that the pelagic larvae of southern species appeared in the Yellow Sea, north of the Yangtze River Mouth, with a PLD > 17 days. Thus, the oceanographic currents around the Yangtze River Mouth do not limit the northward dispersal of the larvae with a relatively long PLD, at least when the China Coastal Current flows northwards. It thus is pertinent to investigate other potential limiting factors, notably temperature, that could be important in resetting the northern range limit.

Low temperature in winter is an important factor for setting the new northern range limit of intertidal species along the Chinese coastline. A mechanistic understanding of the drivers of range limits is necessary to evaluate how distributions of species will likely shift with climate change. Physiologically based species distribution models (SDMs) incorporate the mechanistic links between the physiological traits of organisms and their environments, and potentially make more robust and confident predictions of species ranges under the environmental changes to come (Harris et al., 2018; Kearney & Porter, 2009). Tolerance of low temperatures is a plausible causal factor that determines the northern range limits of ectothermic species. Results of cTSM for *N. yoldii* showed that individuals at latitude of c. 33° N are currently threatened by low temperatures in winter, confirming that low temperature is a limiting factor for further northward range shift of this southern species. With further global warming, the latitude at which cTSM challenges first occur is likely to increase over time, allowing a further northward shift in distribution.

Besides habitat availability, larval transport and temperature, there are multiple biotic and abiotic factors potentially affecting species distribution and then biogeographic patterning (Araújo & Peterson, 2012; Kearney & Porter, 2009). As previous studies have described, biotic interactions, including food sources (Bustamante et al., 1995; Ding et al., 2018; Notman, McGill, Hawkins, & Burrows, 2016), competition (Wethey, 2002) and predation (Matassa & Trussell, 2015; Miller, Matassa, & Trussell, 2014; Rilov, 2009), can affect the distribution of intertidal species. Microhabitat heterogeneity (Denny, Dowd, Bilir, & Mach, 2011; Dong et al., 2017), biogenic habitat (Jurgens & Gaylord, 2018; Wangkulangkul, Hawkins, &
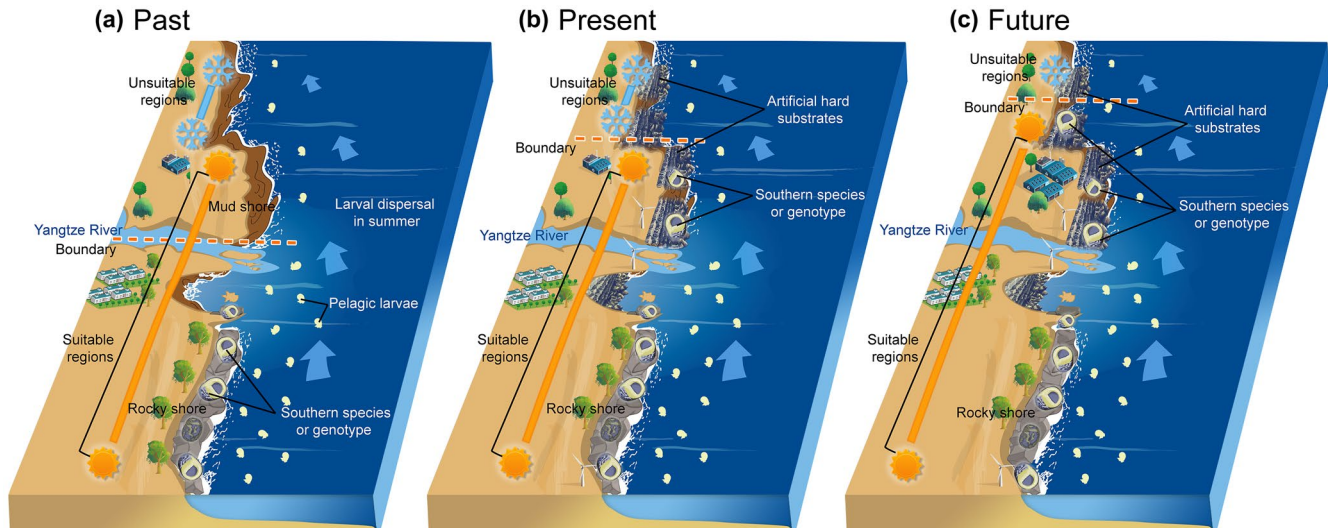
FIGURE 5 The processes whereby anthropogenic global warming and habitat transformation affect species distributions, community structure, and, potentially, shifting of biogeographic provinces. (a) Without artificial structures on the muddy shore, pelagic larvae of southern rocky intertidal species cannot settle and survive on the muddy shore north of the Yangtze River Mouth due to the lack of available substrata, even though some larvae can pass through the low salinity runoff. In the absence of hard structures, then, the boundary of the two eco-provinces lies in the Yangtze River Mouth. (b) With the construction of artificial structures on the muddy shores north of the Yangtze River Mouth, larvae can now settle and develop into adults on these artificial habitats; thus, the boundary of the two eco-provinces moves further north to around 33° N. The new northern limit of species distribution is related to the minimum body temperature in winter. The artificial structures on the muddy shore, serving as stepping stones, can promote the northward dispersal of larvae, but survival at higher latitudes may be limited by winter temperatures. (c) With the construction of the artificial infrastructures on muddy shores plus warming, it is reasonable to speculate that the boundary of the two eco-provinces will potentially move further north in future

Jenkins, 2016) and behavioural responses (Ng et al., 2017) are also important factors for determining species distribution shifts and biogeography along coastlines. In addition, climate change is likely to have profound influences on the strength, direction and behaviour of the world's major current systems (Bindoff et al., 2007). These changes to currents have the potential to strongly influence the distribution of marine ecosystems (Hoegh-Guldberg & Bruno, 2010).

With a higher pace of shifting climate in marine ecosystems (Burrows et al., 2011), temperature plays an increasingly important role in influencing reproductive output (Moore, Thompson, & Hawkins, 2011) and rates of larval development (O'Connor et al., 2007), as well as affecting the survival and reproduction of adults (Deutsch et al., 2008). Ocean temperature can change the duration of the larval period, influence larval dispersal distance and survival, and thus have a direct and predictable influence on population connectivity, community structure and regional-to-global scale patterns of biodiversity (O'Connor et al., 2007). For sessile adults, temperature can affect survival and reproduction in their benthic habitats (Morley, Batt, & Pinsky, 2017). Minimum temperature is an essential limiting factor restricting northwards shifts in distribution for the range shifting southern hard-shore species; the low temperature around 33° N sets a new 'red line' for their northern range limit (Figure 5), but this 'red line' may continue to shift to higher latitudes with on-going global change. In the face of global warming and human-caused habitat modifications, species distributions, community structures and biogeographic patterns are experiencing

unprecedented change due to the responses of organisms to the interactions of these global and local drivers. These ecological and biogeographic alterations are now seen to be occurring in both marine and terrestrial environments, and they pose critical challenges to the future of the biosphere in a world increasingly impacted by anthropogenic change.

CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

AUTHOR CONTRIBUTION

YD and BH designed the study; WW, JW, XL, GH, MD, XH, ZCheng, ZChen and YD carried out field surveys and larval sampling; YJ, PD

and MG performed simulation of larval dispersal; WW, XL, JW, GH and MD carried out laboratory experiments; FMPC and BH performed heat budget model temperature estimations; WW, JW, FMPC, XL, PD, SH, YD, BH, YJ and WD analysed and interpreted the data; YD, SJH, BH and WW led the writing, but all authors contributed to the writing.

DATA AVAILABILITY STATEMENT

The taxonomic assignment results of larval metabarcoding, the data on macrobenthic species in the nine field surveys, and the results of larval dispersal simulations are available through the Dryad data repository (https://doi.org/10.5061/dryad.34tmpg4fq). All metabarcoding data have been uploaded to GenBank (SRA accession: PRJNA559658).

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BIOSKETCH

Yun-wei Dong is mostly interested in macroecology and ecological physiology. His work mainly focuses on studying the impacts of climate change and human activities on the biogeography of intertidal species.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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