Northward shift of a biogeographical barrier on China’s coast

Li-sha Hu\textsuperscript{1} | Yun-wei Dong\textsuperscript{1,2}

\textsuperscript{1}Key Laboratory of Mariculture of Ministry of Education, Fisheries College, Ocean University of China, Qingdao, China
\textsuperscript{2}Function Laboratory for Marine Fisheries Science and Food Production Processes, Qingdao National Laboratory for Marine Science and Technology, Qingdao, China

Correspondence
Yun-wei Dong, Key Laboratory of Mariculture of Ministry of Education, Fisheries College, Ocean University of China, Qingdao 266003, China.
Email: dongyw@ouc.edu.cn

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Abstract
Aim: Understanding the formation and maintenance of biogeographical breaks is fundamental for developing analyses related to biodiversity and conservation. Biogeographical patterns along China’s coast are changing dramatically in the face of climate change and alterations in land-use. In this paper, we sought to clarify the mechanisms responsible for the formation and maintenance of a biogeographical barrier on China’s coast.

Location: Coastline of northern China.

Methods: We have reviewed literature related to biogeographical and phylogeographical patterns of intertidal macrobenthos along the coast of Jiangsu Province and adjacent areas, summarized the distribution patterns and biogeographical breakers. We have also reviewed literature about the processes and drivers on coastal biogeographical breaks, to clarify the mechanisms acting to the northward shift of the biogeographical break.

Results: The Yangtze (Changjiang) River Estuary Biogeographical Barrier (YREBB) at 30°–31°N, which serves as a coastal biogeographical boundary for the Cold Temperate Northwest Pacific Province and the Warm Temperate Northwest Pacific Province for marine species, has moved northward to \(\sim33°–34°\)N due to the changes in habitat continuity, oceanographic circulation and climate factors. Consequently, a new biogeographic barrier for intertidal macrobenthos, the Subei Biogeographical Barrier (SBB) on the central coast of Jiangsu Province, has emerged.

Main conclusions: The formation and maintenance of the SBB are closely related to the larval dispersal potential, larval settlement success and post-settlement population establishment, all of which have been profoundly influenced by anthropogenic environmental changes. The northward shift of the YREBB and the appearance of the SBB provide an excellent model system for investigating the impacts of climate change and land-use change on coastal biogeographic patterning and for clarifying the mechanisms underlying the formation and maintenance of biogeographical barriers in the face of the unprecedented environmental changes.

KEYWORDS
biogeographical break, biogeographical pattern, climate change, intertidal macrobenthos, larval dispersal, seascape transformation
1 | INTRODUCTION

Biogeographical breaks, defined as regions where multiple species reach their ranges limit simultaneously, can lead to changes in species composition and species richness, and thus are important for the formation and maintenance of biogeographical patterns (Costello et al., 2017; Spalding et al., 2007). Great uncertainty remains about the roles of climate change and human land-use activities in the formation and maintenance of biogeographical barriers (Ayre & Rosser, 2021; Waters, 2008).

Along China’s coast, the Yangtze (Changjiang) River Estuary (30°–31°N) has been regarded as a break that separates the North Pacific Temperate Biotic Region (Cold Temperate Northwest Pacific Province) and the Indo-West Pacific Warm-water Biotic Region (Warm Temperate Northwest Pacific Province; Liu, 2013; Spalding et al., 2007). The formation of this biogeographical barrier has been attributed to complex interactions among historic events, Yangtze River Diluted Water, coastal circulation patterns, climatic factors and substrate types (Cheng et al., 2020; Dong et al., 2012; He et al., 2010; Ni et al., 2017; Qu et al., 2021; Wang et al., 2015).

In the last decades, the biogeographical barrier for some intertidal macrobenthos has moved northward to ~33°–34°N and has formed a new biogeographical barrier, the Subei Biogeographical Barrier (SBB). Mechanisms promoting the northward shift of the biogeographical barrier are mainly associated with oceanographic features, seascape transformation and climatic factors (Dong et al., 2016; Wang et al., 2020). These abiotic changes can consequently affect larval dispersal, larval settlement and post-settlement survival of the marine macrobenthos (Cowen & Sponaugle, 2009; D’Aloia et al., 2015; O’Connor et al., 2007; Sassa et al., 2006; Wilson et al., 2018). The northward shift of the biogeographical barrier and the formation of the SBB reveal the changes of species distribution limits and biogeographical patterning in the context of climate change and human land-use activities.

2 | DATA COLLECTION AND ANALYSIS

2.1 | Biogeographical and phylogeographical references search

To investigate the spatiotemporal changes of community structures and population genetic patterns of intertidal macrobenthos, literature related to biogeographical and phylogeographical patterns of intertidal macrobenthos along the coast of Jiangsu Province and adjacent areas has been searched and downloaded from Web of Science and Google scholar using the following general query:

\[ TS = \text{‘species name’ or ‘genus name’} \text{ AND TS=} \text{‘China’ life history’ or ‘China’ life character’ or ‘China’ larva dispersal’ or ‘China’ larva settle’ or ‘China’ larva post-settle’ or ‘China’ post-settle’ establish’ or ‘China’ population establish’}. \text{ (TS denotes a search for ‘Topic,’ * is a regular expression used to match all words including that string of characters).} \]

2.2 | Species life history references collection

To clarify the environmental factors controlling the shift of the biogeographical break, literature was search using the following general query:

\[ TS = \text{‘species name’ or ‘genus name’} \text{ AND TS=} \text{‘China’ life history’ or ‘China’ life character’ or ‘China’ larva dispersal’ or ‘China’ larva settle’ or ‘China’ larva post-settle’ or ‘China’ post-settle’ establish’ or ‘China’ population establish’}. \text{ (TS denotes a search for ‘Topic,’ * is a regular expression used to match all words including that string of characters).} \]

3 | BIOGEOGRAPHICAL PATTERN TRANSFORMATION IN THE YANGTZE RIVER DELTA

3.1 | Coastal biogeographical pattern and biogeographical barriers

Coastal biogeographical patterns are characterized by varying areas, ranging from regional scales to the global ocean (Costello et al., 2017; Liu, 2013; Spalding et al., 2007). The classification of these patterns is helpful in many ways, notably for development of marine reserves and assessment of biodiversity (Costello et al., 2017; Spalding et al., 2007). Coastal biogeographical barriers are ubiquitous across the globe. For instance, on the southeast coast of Australia, a biogeographical barrier called the Southeast Australian Biogeographic Barrier (SEABB) occurs, which plays an important role in shaping species distribution and phylogeographic patterns (Ayre et al., 2009; Ayre & Rosser, 2021; Waters, 2008). Similar biogeographical barriers occur in the southeast Pacific on the northern coast of Peru (Barahona et al., 2019), the west coast of the United States (Burton, 1998; Palumbi, 1996; Taylor & Hobbie, 2006), the east coast of North America (Pappalardo et al., 2015), the Atlantic–Mediterranean coast (El Ayari et al., 2019), and the coast of China (Dong et al., 2012; Liu, 2013). These barriers are not hard and fast, however, but shift when environmental changes occur. Thus, under the influences of climate change and human activities that modify shorelines, many species have managed to cross these biogeographical barriers and enter regions in which they formerly were rare, if not absent altogether (Adams et al., 2014; Bulleri & Airoldi, 2005; Dong et al., 2016; Miller et al., 2013; Wang et al., 2020).

3.2 | Yangtze River Estuary Biogeographical Barrier (YREBB)

Along China’s coast, the YRE has been regarded as a coastal biogeographical boundary separating two ecological provinces for marine species, the Cold Temperate Northwest Pacific Province and the Warm Temperate Northwest Pacific Province (Dong et al., 2012; Liu, 2013; Ni et al., 2017; Xu et al., 2020; Yan et al., 2019). Previous
studies that examined marine bivalves (Li et al., 2020; Ni et al., 2014, 2015), gastropods (Dong et al., 2012; Qu et al., 2021; Wang et al., 2016; Zhao et al., 2017), crustaceans (Cheng et al., 2020; Han et al., 2015), polyplacophorans (Ni et al., 2020) and macroalgae (Cheang et al., 2010; Ni et al., 2020) have indicated the barrier impacts of the YERBB on species biogeographic and phylogeographic patterns. The formation of the YERBB is closely related to habitat continuity, historical events, oceanographic features and climate factors (Figure 2).

3.2.1 | Habitat continuity

Habitat continuity is an important driver shaping the biogeographic boundaries of species (Buonomo et al., 2017; Fenberg & Rivadeneira, 2019; Fraser et al., 2012; Platts et al., 2019). For example, along the eastern Pacific rocky shore, habitat continuity is a top predictor of biogeographic structure and the richness gradient of gastropods. In the extratropical regions rocky shore habitat continuity is low, species turnover is relatively low, emphasizing the importance of habitat continuity on biogeographical patterns and processes (Fenberg & Rivadeneira, 2019).

The muddy tidal flat habitat is a dominant coastline feature on the north region of the Yangtze River Estuary up to the northern shoreline of Jiangsu Province (~35°N). The absence of exposed natural rocky shore habitat has impeded mass settlement of rocky intertidal species in the Yangtze River Delta (Dong et al., 2016; Wang et al., 2018, 2020; Zhao et al., 2017). Discontinuity of habitat type, as in the absence of hard substrate in muddy tidal flats, plays an important role in the genetic differentiation among populations and for the formation of biogeographical barriers (Brown, 1995; Connell & Irving, 2008; Riginos & Nachman, 2001). With the construction of hard artificial structures in last decades along the coastline in Jiangsu Province (30.75°–35.3°N), the natural muddy shore seascape has been changed dramatically; many regions now are characterized by seawalls, breakwaters and other artificial hard shores. These artificial hard surfaces serve as stepping stones that promote larval settlement by rocky shore species, and thereby affect the biogeographical pattern (Wang et al., 2020).

3.2.2 | Historical events

Pleistocene glacial-interglacial cycles have led to changes of marginal sea level and these have influenced vicariance of marine species (Marko et al., 2010). With sea level dropping during the last glacial maximum (LGM), the East China Sea (ECS) was reduced to the Okinawa Trough and the South China Sea (SCS) became a semi-enclosed gulf. These glacial refuges were important for species persistence during the LGM (Shen et al., 2011). With the rising sea levels that followed the LGM, a northward migration from these refuges occurred, which has potential impacts on current species distributions and biogeographical patterns (Cheng & Sha, 2017; Dong et al., 2012; Ni et al., 2017).

3.2.3 | Oceanographic circulation

Oceanographic circulation is another important factor shaping current coastal biogeographical and phylogeographical patterns (Blanchette et al., 2008; Gosnell et al., 2014; Spalding et al., 2012; Wang et al., 2016). Oceanographic discontinuity can impede dispersal of marine larvae and prompt the formation of biogeographical breaks.

The coastline of China comprises four marginal seas, including Bohai Sea (BS), the Yellow Sea (YS), the ECS and the SCS (Figure 1), and is influenced by three major oceanographic systems: the Kuroshio Current and its branches, the Coastal Currents and Diluted Water (Liu, 2013; Williams et al., 2019). In YS and ECS, the water circulation is mainly wind-driven, leading to the strength and direction of oceanographic circulations highly variable seasonally (Williams et al., 2019). These coastal current systems influenced the present population genetic patterns and biogeographical histories of marine species, and delimitated the biogeographical boundary for marine species (Ni et al., 2014; Wang et al., 2016). The Kuroshio Current and its branch currents connect the SCS, ECS, YS and the Sea of Japan (Lie & Cho, 2016; Sassa et al., 2006). The Yangtze River Diluted Water has significant effects on the physical, chemical and biological environments around the Yangtze River Estuary (Lin et al., 2002), and has been proposed as a physical barrier critical for determining the coastal biogeographical pattern (Dong et al., 2012; Wang et al., 2015).

3.2.4 | Climate factors

Climate factors, particularly temperature, are often assumed to be the primary abiotic drivers that limit species distributions (Harley et al., 2006; Spence & Tingley, 2020). Ocean temperature can also lead to a direct and predictable influence on population connectivity, as the duration of the larval period and survival have strong correlations with ambient temperature (O’Connor et al., 2007). After settlement, ambient temperature can also determine population dynamics through influencing organisms’ reproduction, development, growth and survival (O’Connor et al., 2007; Punzón et al., 2021; Wang et al., 2018).

3.3 | Subei biogeographical barrier (SBB)

The biogeographical break for coastal species at the Yangtze River Estuary has been weakened since the 1950s (Xu et al., 2020). Mounting evidence from biogeographical and phylogeographical studies indicates that a new biogeographical break, the SBB, is emerging around 33°–34°N (Cheng & Sha, 2017; Dong et al., 2016; Li, Li, et al., 2021; Wang et al., 2018, 2020; Figure 2).

At the species level, some southern species have expanded their leading edges northward to ~33°–34°N (Wang et al., 2018, 2020; Xu & Zhang, 2011). For example, the warm water sea urchin Schizaster
lacunosus has extended its northern distribution range limit to ~34°N (personal communication, Yong Xu) in the YS during the period from 1958 to 2016 (Xu et al., 2020). Some intertidal macrobenthos, like Nerita yoldii (Wang et al., 2018) and Crassostrea sikamea (Wang et al., 2020), have moved northward to ~33°– 34°N (Figure 3).

Based on molecular markers, a clear phylogeographical break appeared around 33°–34°N for widely distributed coastal macrobenthos (Figure 3). In addition, with mitochondrial cytochrome oxidase subunit I (mtDNA COI) and nuclear ribosomal internal transcribed spacer (nrDNA ITS), Cheng and Sha (2017) found that the southern genetic lineage and northern genetic lineage of the Japanese mantis shrimp Oratosquilla oratoria were sympatric in their distribution ranges, with the southern Yellow Sea as an overlapped zone (Cheng & Sha, 2017).

Community structure similarity of intertidal macrobenthos further confirmed the existence of the SBB. Cluster analyses based on Bray-Curtis similarity have showed that the intertidal communities can be clustered into three groups along the coast of Jiangsu.
patterns can be largely attributed to these environmental changes (Blanchette et al., 2008; Gaylord & Gaines, 2000; Gosnell et al., 2014; Pappalardo et al., 2015). The weakened YREBB and emerging SBB provide model systems for clarifying the impacts of environmental changes on the formation and maintenance of biogeographical breaks (Figure 5).

4.1 | Larval dispersal potential and oceanographic features

With high connectivity in the marine ecosystem, pelagic larval dispersal is the key process of population connectivity for species with biphasic life cycle (Cowen & Sponaugle, 2009; D’Aloia et al., 2015). Life history characters, such as reproductive mode, reproductive period, larval type and pelagic larval duration (PLD) can affect larvae dispersal potential (Table 1), and then determine whether the species can successfully migrate across biogeographical barriers (Ayre et al., 2009; Feary et al., 2014; Wilson et al., 2018). PLD is usually regarded as the most important trait influencing larvae dispersal distance and thus shaping population connectivity (Liggins et al., 2016; Wang et al., 2020). A previous study using the results of an operational hydrodynamic model has shown that along China’s coast, species with a relatively long PLD (>17 days) can disperse across the Yangtze River Estuary, and have high connectivity between southern and northern populations (Wang et al., 2020). A cold-water species Chthamalus challengeri widely distributes along China’s coast without a clear genetic break around the Yangtze River Estuary (Cheang et al., 2012; Liu et al., 2015), and the lack of genetic break of C. challengeri might attributed to its long PLD (Cheang et al., 2012).

Increasing evidence has shown that oceanographic features such as upwelling systems, fronts, moving convergences, eddies and counter currents provide conditions for larvae transport and can enhance population connectivity (Hidas et al., 2007). Significant changes of strength, direction and behaviour of the current systems combined with rapid climate change can have strong influence on the formation of distribution boundaries of marine species (Gaylord & Gaines, 2000; Hoegh-Guldberg & Bruno, 2010). Another factor is the El Niño–Southern Oscillation (ENSO) which drives oceanographic variability, as ENSO can relax the barrier effect of transition zones in areas of convergence of marine currents (Ayre et al., 2009).

The SBB is highly concordant with the Subei tide-induced Coastal Current (STCC). As Wu et al. (2018) indicated, subtidal transport in the inner Subei Coastal Water (SCW) is northward and exists from the Yangtze River Estuary all the way along the Subei Coast until reaching ~33.5°N (Figure 2). Tidal waves from the ECS and the northern Yellow Sea collide in coastal waters between 32.5° and 34°N (Wu et al., 2018), and the estuary of the Yangtze River, Doulong Port River, Xinyang Port River, Sheyang River, Old Yellow River and Guanhe River range from ~32° to 35°N (Zhu & Wu, 2018). These regional coastal circulations are

FIGURE 2 Transformation of the biogeographic pattern of intertidal Mollusca species. The boundary entitled “before northward shift” is the former biogeographical barrier. The boundary entitled “after northward shift” is the present biogeographical barrier after the northward distribution shift of macrobenthos in recent decades. YRDW, Yangtze River Diluted Water; STCC, Subei tide-induced Coastal Current; YSCC, Yellow Sea Coastal Current. SBB, Subei Biogeographic Barrier; YREBB, Yangtze River Estuary Biogeographical Barrier. 1, Guanhe River; 2, Old Yellow River; 3, Sheyang River. 4, Xinyang Port River; 5, Doulong Port River

provinces (Figure 4). The southern group includes most communities south of 33°N, and northern group includes communities north of 34°N (like intertidal community in Qingdao, Morton, 1990). Between 33° and 34°N, an intermediate group with both southern species and northern species exists as an ecotone (Dong et al., 2016; Wang et al., 2020). From 2013 to 2017, the intermediate group has been contracting. Based on data collected from 2013 to 2015, two communities (ZAP and XDZ) were classified to the intermediate group, whereas these two communities were classified to the southern group with data from 2013 to 2017 (Figure 4), implying that the southern group is moving northward.

4 | MECHANISMS ACTING TO THE NORTHWARD SHIFT OF BIOGEOGRAPHICAL BREAK

Biogeographical distributions of marine species are changing rapidly over the world in the context of global change and human activities like shoreline construction (Amarasekare & Simon, 2020; Pinsky et al., 2020), and the rearrangements of biogeographical
important factors affecting larval dispersal and shaping the distribution boundaries.

4.2 Larval settlement and seascape transformation

The characteristics of the sites that can be recognized and selected for settlement can influence post-settlement mortality and thereby determine biogeographical patterns (Bell et al., 2015; Harrington et al., 2004). Persistence of range expansion varies greatly among species, and most of the variation between species can be explained by differences in habitat availability and habitat specificity (Harrington et al., 2004; Platts et al., 2019).

The availability of suitable substrate for planktonic larval settlement can affect the success of metamorphosis from larvae into benthic juveniles (Cowen & Sponaugle, 2009). Construction of artificial hard structures is a vital factor contributing to the transformation of the biogeographic pattern around the Yangtze River Delta that has taken place in the last several decades. Over the past 70 years, about 3000 km² of tidal mudflats have been reclaimed using artificial hard structures along Jiangsu’s coastline (Zhang et al., 2013). These artificial hard structures, including seawalls, breakwaters, ripraps and other structures, provide appropriate substrates for rocky intertidal species to settle upon and thereby facilitate their northward distribution shift (Bishop et al., 2017; Strain et al., 2019; Bishop et al., 2017; Strain, Cumbo, et al., 2020; Wang et al., 2020).

Various abiotic and biotic cues on the substrate, such as surface texture/roughness and complexity (Coombes et al., 2015; Loke & Todd, 2016; Sedano et al., 2020) and chemical cues produced by conspecifics and microbial biofilms (Coombes et al., 2015; Ding et al., 2018; Pawlik, 1992), can influence the rate and patterns of larval supply and settlement (Ding et al., 2018; Hunt & Scheibling, 1997), and thereby the structuring of macrobenthic communities (Loke & Todd, 2016; Sedano et al., 2020; Strain, Steinberg, et al., 2020). Furthermore, the composition of the intertidal community on the artificial structures is also related to the environmental tolerances of the species living on the artificial structures (Ayre et al., 2009). Species that can withstand the harsh environment of the bare artificial structures, grow and reproduce in a variety of environments, and have huge numbers of eggs with high dispersal rates usually can occupy the artificial structures rapidly and display a broad range of distribution. For example, the snail *Littoraria sinensis* and the barnacle *Fistulobalanus albicostatus* rapidly occupied the habitats on the newly built seawalls in Zhonganpeng within
The rapid occupation of these new habitats promotes the northward distribution range extension of intertidal species.

4.3 Post-settlement establishment and global warming

A growing amount of evidence has suggested that post-settlement establishment plays a more important role in the maintenance of biogeographic breaks in the oceans than larval dispersal (Keith et al., 2015). Invertebrates usually exhibit high rates of post-settlement mortality, which are mainly due to the delay of metamorphosis, competition, predation, physiological stress (Hunt & Scheibling, 1997) and genetic inviability driven by genotype-environment interactions (Barahona et al., 2019; Plough et al., 2016). Importantly, the capacity of species to tolerate physiologically marginal conditions influences their ability to establish a viable population after successful dispersal (Keith et al., 2015) and the persistence of their present distribution ranges (Dong et al., 2015; Han et al., 2019). Along China’s coast, the most thermally vulnerable locations occur in the Yangtze River Delta, based on analyses using thermal safety margin as a proxy (Deutsch et al., 2008; Dong et al., 2017; Ma et al., 2021). Mapping of operative temperatures between 2010 and 2020, as calculated using heat budget models (Wethey et al., 2011), shows that the region between 32°N and 33°N is one of the hottest areas in summer along China’s coast, and this area can potentially act as a thermal barrier for intertidal species.
| Species               | Tidal height | Habitat exposure | Reproductive mode | Larval type | Pelagic larval duration | Reproductive period                                      | References                  |
|----------------------|-------------|------------------|-------------------|-------------|------------------------|----------------------------------------------------------|-----------------------------|
| *Littoraria sinensis*| H           | E                | I/BR              | PP          | 3–10 weeks             | Summer                                                   | Reid et al. (2010)          |
| *Littorina brevicula*| H           | M-S              | I/BR              | PP          | 9 days                 | December to April                                        | Son and Hong (1998)         |
| *Patelloida pygmaea* | M           | E                | Pelagic development | PP         | >60 days               | July to August (Korea); February to August (Hong Kong)   | Anderson (1965)             |
| *Reishia clavigera*  | M-L         | M                | I/EM              | PP          | >60 days               | July to August (Korea); February to August (Hong Kong)   | Lee (1999)                  |
| *Nerita yoldii*      | M           | M-S              | I/EM              | PL          | ~1 month               | April                                                    | Yeung (2006)                |
| *Siphonaria japonica*| M           | E                | I/BR              | >7 days     |                        | March to July (Japan); February to May (Xiamen)          | Hirano and Inaba (1980)     |
| *Monodonta labio*    | M-L         | M                | Pelagic development | PP         |                        | July to September (Japan)                               | Lijima and Furota (1998)    |
| *Echinolittorina radiata* | Sp-H      | E                | I/BR              | PP          | 3–4 weeks              |                                                                 | Reid (1989)                 |
| *Cellana toreuma*    | M-L         | E                | E/BS              | PL          | 4–18 days in congeners | June to September (north Zhejiang, China)                | Anderson (1962)             |
| *Crassostrea gigas*  | M-L         | E                | E/BS              | PP          | >17 days               | April to August                                          | Rose et al. (2006)          |
| *Crassostrea sikamea*| M           | E                | E/BS              | PP          | >17 days               | July to October                                          | Rose et al. (2006)          |
| *Xenostrobus atratus*| M           | M                | E/BS              | PP          | Pelagic development    | Pelagic development                                      | Reid (1998)                 |
| *Mytilus galloprovincialis* | M         | M                | E/BS              | PP          | Pelagic development    | Throughout the year (Spain)                             | Cáceres-Martínez et al. (1993) |
| *Fistulobalanus albicostatus* | M   | E                | I/EM              | PP          | 5–7 days               | July to October (Japan)                                 | Chang et al. (2017)         |
| *Chthamalus challengeri* | H-M      | E                | I/BR              | PP          |                        |                                                          | Egan and Anderson (1989)    |
| *Amphibalanus reticulatus* | M       | E                | I/BR              | PP          |                        | Throughout the year (tropical)                           | Satheesh and Wesley (2009)  |

Note: E, exposed shores; M, moderately exposed shores; S, sheltered; R, rock pools; L, low-intertidal; M, mid-intertidal; H, high-intertidal; Sp: Splash zone; I/BR, internal fertilization/eggs brooded; I/EM, internal fertilization/egg mass; E/EM, external fertilization/egg mass; E/BS, external fertilization/gametes broadcast spawn; PP, planktonic planktotrophic; PL, planktonic lecithotrophic; CJ, crawling juveniles; BL, benthic lecithotrophic.
The low temperatures in winter can also impede the northward shift of southern species and contribute to the formation of the SBB. Northern distributional boundaries of larvae of two southern species, *N. yoldii* and *C. sikamea*, could be found at 34.5°N, which is beyond the current northern distributional limit of adults at ~33°N and ~34°N, respectively. This can be explained by low temperatures during winter that reach the species’ thermal tolerance limits, and thus define their current distributional boundaries (Wang et al., 2020). In the process of colonization by *N. yoldii* to the north of the Yangtze River Estuary, some specific haplotypes have been filtered out (Wang et al., 2018), and a clear phylogeographical break may consequently have formed (Kawecki, 2008).

The thermal plasticity of intertidal macrobenthos varies greatly at different spatiotemporal scales in the face of global warming and increasing occurrences of heat wave (Li, Tan, et al., 2021; Zhang et al., 2021). Structural complexity of the habitat could provide microhabitat for intertidal species as “thermal refugia,” and micro-scale physiological thermal tolerance can play an important role in determining whether species could survive in the face of extreme events (Li, Tan, et al., 2021; Lima et al., 2016). The accumulation of micro-scale physiological variations could enhance the macro-scale thermal resilience of intertidal species (Dong et al., 2017; Strain, Cumbo, et al., 2020), and thereby influence species distributional shifts affected by climate change (Bates et al., 2018; Li, Tan, et al., 2021; Liao et al., 2021; Schils & Wilson, 2006). At different time-scales, heat hardening can work synchronously with seasonal acclimatization to increase resistance of raze clam *Sinonovacula constricta* to high temperatures (Zhang et al., 2020, 2021).

5 | PERSPECTIVES

The biogeographical pattern of intertidal species has been experiencing dramatic transformation along China’s coast, and the vanishing YREBB and emerging SBB are closely related to the changes of oceanographic features, seascape transformation and climatic factors. These changes can affect the formation and maintenance of the biogeographical barrier during the period of larval dispersal, larval settlement and post-settlement establishment. For further clarifying the underlying mechanisms responsible for the formation and maintenance of a biogeographical barrier, using SBB as a model system, the following monitoring and experimental studies should be carried out:

1. Continuously monitoring species distributions for clarifying the biogeographic patterns of coastal invertebrates over a long-time scale. For achieving this purpose, regular field surveys and in situ recording of environmental factors, such as temperature and salinity, and biological community in marine stations should be designed along China’s coast.

2. Regional oceanographic conditions are crucial dynamic processes shaping distribution boundaries, so knowledge of formation and maintenance mechanisms of oceanographic systems is crucial for understanding and predicting the distribution patterns of marine species. For example, the SBB is highly concordant with the STCC. However, integrative studies about biogeographical pattern and regional oceanography systems are still relatively rare, and demand more attention in future research.

3. Species’ response to global climate change has been verified to be largely determined by their physiological performance (Han et al., 2019; Liao et al., 2021). In order to accurately assess the impact of global climate change on the survival and distribution of intertidal macrobenthos, physiological tolerance of intertidal species at multiple spatiotemporal scales must be considered.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

PEER REVIEW

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All used data were downloaded from literature, and some have been restructured.

ORCID

Li-sha Hu https://orcid.org/0000-0003-4669-8654
Yun-we Dang https://orcid.org/0000-0003-4550-2322

REFERENCES

Adams, T. P., Miller, R. G., Aleynik, D., & Burrows, M. T. (2014). Offshore marine renewable energy devices as stepping stones across biogeographical boundaries. *Journal of Applied Ecology, 51*(2), 330–338. https://doi.org/10.1111/1365-2664.12207

Amarasekare, P., & Simon, M. W. (2020). Latitudinal directionality in ectotherm invasion success. *Proceedings: Biological Sciences, 287*(1920), 20191411. https://doi.org/10.1098/rspb.2019.1411

Anderson, D. T. (1962). The reproduction and early life histories of the gastropods *Bembicium auratum* (Quoy and Gaimard) (Fam Littorinidae), *Cellana tramoserica* (Sower) (Fam Patellidae) and *Melanerita melanotragus* (Smith) (Fam Neritidae). *Proceedings of the Linnean Society of New South Wales, 37*, 62–68.

Anderson, D. T. (1965). The reproduction and early life histories of the gastropods *Notoacmaea petterdi*, *Chiazacmaea flammea*, and *Patelloidea alticostata*. *Proceedings of the Linnean Society of New South Wales, 90*, 242–251.

Ayre, D. J., Minchinton, T. E., & Perrin, C. (2009). Does life history predict past and current connectivity for rocky intertidal invertebrates across a marine biogeographic barrier? *Molecular Ecology, 18*(9), 1887–1903. https://doi.org/10.1111/j.1365-294x.2009.04127.x

Ayre, D. J., & Rosser, N. (2021). Gene flow across a major biogeographic barrier is not increasing under climate change for the barnacle...
Xu, F. S., & Zhang, J. L. (2011). Characteristics of bivalve diversity in Wilson, S. K., Depcyznski, M., Fisher, R., Holmes, T. H., Noble, M. M., Brooks, P., Chan, B. K. K., Cheah, C. B., Chee, S. Y., Coutinho, R., Crowe, T., Davey, A., Firth, L. B., Fraser, C., ... Bishop, M. J. (2020). A global analysis of complexity–biodiversity relationships on marine artificial structures. Global Ecology and Biogeography, 30(1), 140–153. https://doi.org/10.1111/greb.13202
Taylor, M. S., & Hellberg, M. E. (2006). Comparative phylogeography in a genus of coral reef fishes: Biogeographic and genetic concordance in the Caribbean. Molecular Ecology, 15(3), 695–707. https://doi.org/10.1111/j.1365-294X.2006.02820.x
Wang, J., Gannanee, M., Shau-Huai, A. T., Majahid, A., & Dong, Y. W. (2016). Pleistocene events and present environmental factors have shaped the phylogeography of the intertidal limpet Cellana toreuma (Reeve, 1855) (Gastropoda: Nacellidae) in Southeast Asia and China. Journal of Molluscan Studies, 82(3), 378–390. https://doi.org/10.1093/mollus/ey071
Wang, J., Tsang, L. M., & Dong, Y. W. (2015). Causations of phylogeographic barrier of some rocky shore species along the Chinese coastline. BMC Evolutionary Biology, 15, 114. https://doi.org/10.1186/s12862-015-0387-0
Wang, J., Yan, H. Y., Cheng, Z. Y., Huang, X. W., Wang, W., Ding, M. W., & Dong, Y. W. (2018). Recent northward range extension of Nerita yoldii (Gastropoda: Neritidae) on artificial rocky shores in China. Journal of Molluscan Studies, 84(4), 345–353. https://doi.org/10.1093/mollus/eyy042
Wang, W., Wang, J., Choi, F. M. P., Ding, P., Li, X. X., Han, G. D., Ding, M. W., Guo, M. Q., Huang, X. W., Duan, W. X., Cheng, Z. Y., Chen, Z. Y., Hawkins, S. J., Jiang, Y. W., Helmuth, B., & Dong, Y. W. (2020). Global warming and artificial shorelines reshape seashore biogeography. Global Ecology and Biogeography, 29(2), 220–231. https://doi.org/10.1111/geb.13019
Waters, J. M. (2008). Marine biogeographical disjunction in temperate Australia: Historical landbridge, contemporary currents, or both? Diversity and Distributions, 14(4), 692–700. https://doi.org/10.1111/j.1472-4642.2008.00481.x
Wethey, D. S., Brin, L. D., Helmuth, B., & Mislan, K. (2011). Predicting intertidal organism temperatures with modified land surface models. Ecological Modelling, 222(19), 3568–3576. https://doi.org/10.1016/j.ecolmodel.2011.08.019
Williams, G. A., Chan, B. K. K., & Dong, Y. W. (2019). Rocky Shores of Mainland China, Taiwan and Hong Kong: Past, Present and Future. In S. J. Hawkins, K. Bohn, L. B. Firth, & G. A. Williams (Eds.), Interactions in the Marine Benthos: Global patterns and processes (Systematics Association Special Volume Series, pp. 360–390). Cambridge University Press. https://doi.org/10.1017/9781108232572.015
Wilson, S. K., Depczynski, M., Fisher, R., Holmes, T. H., Noble, M. M., Radford, B. T., Rule, M., Shedrawi, G., Tinkler, P., & Fulton, C. J. (2018). Climatic forcing and larval dispersal capabilities shape the replenishment of fishes and their habitat-forming biota on a tropical coral reef. Ecology and Evolution, 8(3), 1918–1928. https://doi.org/10.1002/ece3.3779
Wu, H., Gu, J. H., & Zhu, P. (2018). Winter counterwind transport in the inner Southwestern Yellow Sea. Journal of Geophysical Research-Oceans, 123(1), 411–436. https://doi.org/10.1002/2017jc013403
Xu, F. S., & Zhang, J. L. (2011). Characteristics of bivalve diversity in typical habitats of China seas. Biodiversity Science, 19(6), 716–722. https://doi.org/10.3724/SP.J.1003.2011.07158
Xu, Y., Sui, J. X., Ma, L., Li, X. Z., Wang, H. F., & Zhang, B. L. (2020). Temporal variation of macrobenthic community zonation over nearly 60 years and the effects of latitude and depth in the southern Yellow Sea and East China Sea. Science of the Total Environment, 739, 139760. https://doi.org/10.1016/j.scitotenv.2020.139760
Yan, J., Sui, J. X., Xu, Y., Li, X. Z., Wang, H. F., & Zhang, B. L. (2019). Major environmental variables related to north-south differences in the macrozoobenthic community in adjacent sea areas of the Yangtze River estuary, China. Ecological Indicators, 105, 70–81. https://doi.org/10.1016/j.ecolind.2019.05.056
Yeung, C. Y. (2006). The ecology of Nerita yoldii and N. albicilla on Hong Kong rocky shores. Thesis for the Degree of Ph.D. of The University of Hong Kong.
Zhang, W. Y., Storey, K. B., & Dong, Y. W. (2020). Adaptations to the mudflat: Insights from physiological and transcriptional responses to thermal stress in a burrowing bivalve Sinonovacula constricta. Science of the Total Environment, 710, 136280. https://doi.org/10.1016/j.scitotenv.2019.136280
Zhang, W. Y., Storey, K. B., Dong, Y. W., & Rezende, E. (2021). Synchronization of seasonal acclimatization and short-term heat hardening improves physiological resilience in a changing climate. Functional Ecology, 35(3), 686–695. https://doi.org/10.1111/1365-2435.13768
Zhang, X. X., Yan, C. Q., Xu, P., Dai, Y. X., Yan, W. B., Ding, X. R., Zhu, C. X., & Mei, D. D. (2013). Historical evolution of tidal flat reclamation in the Jiangsu coastal areas. Acta Geographica Sinica, 68(11), 1549–1558. https://doi.org/10.1002/11821/dbx20131010
Zhao, D., Li, Q., Kong, L. F., & Yu, H. (2017). Cryptic diversity of marine gastropod Monodonta labio (Trochidae): did the early Pleistocene glacial isolation and sea surface temperature gradient jointly drive diversification of sister species and/or subspecies in the Northwestern Pacific? Marine Ecology, 38(4), e12443. https://doi.org/10.1111/mae.12443
Zhu, P., & Wu, H. (2018). Origins and transports of the low-salinity coastal water in the southwestern Yellow Sea. Acta Oceanologica Sinica, 37(4), 1–11. https://doi.org/10.1007/s13131-018-1200-x

**BIOSKETCH**

Li-sha Hu’s research focuses on genetic adaptive strategies of intertidal molluscs to global warming and human activities. According to the genetic variations of different species or populations, and the correlation between environmental factors and genetic variations, to investigate the genetic adaptive mechanism of intertidal organisms.

Yun-wei Dong’s research focuses on the impact of climate change and human activities on the biogeography of intertidal species, and their physiological and ecological adaptation mechanisms. Which aims to interpretation the responses, temporal and spatial patterns and adaptation mechanisms of intertidal species to complex environmental conditions.

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