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Molluscs of an intertidal soft-sediment area in China: Does overfishing explain a high density but low diversity community that benefits staging shorebirds?

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ABSTRACT

The Yellow Sea is a key staging ground for shorebirds that migrate from Australasia to the Arctic each spring. A lot of attention has been paid to the impact of habitat loss due to land reclamation on shorebird survival, but any effects of overfishing of coastal resources are unclear. In this study, the abundance of molluscs in the intertidal mudflats of northern Bohai Bay on the Chinese Yellow Sea was investigated in 2008–2014 from the perspective of their importance as food for northward migrating shorebirds, especially Red Knots *Calidris canutus*. Numerically contributing 96% to the numbers of 17 species found in spring 2008, the bivalve *Potamocorbula laevis* (the staple food of Red Knots and other shorebirds) dominated the intertidal mollusc community. In the spring of 2008–2014, the densities of *P. laevis* were surprisingly high, varying between 3900 and 41,000 individuals/m^2 at distinctly small sizes (average shell lengths of 1.1 to 4.8 mm), and thus reaching some of the highest densities of marine bivalves recorded worldwide and providing good food for shorebirds. The distribution of *P. laevis* was associated with relatively soft sediments in close proximity to the recently built seawalls. A monthly sampling programme showed steep seasonal changes in abundance and size. *P. laevis* were nearly absent in winter, each year settling on the intertidal mudflats anew. Peak densities were reached in spring, when 0-age *P. laevis* were 1–3 mm long. The findings point to a highly unusual demographic structure of the species, suggesting that some interfering factors are at play. We hypothesise that the current dominance of young *P. laevis* in Bohai Bay reflects the combined pressures of a nearly complete active removal of adult populations from mid-summer to autumn for shrimp farming (this clearing of adults may offer space for recruitment during the next spring) and low numbers of epibenthic predators of bivalves, such as shrimps and crabs, due to persistent overfishing in recent decades (allowing freshly settled juveniles to reach high densities). To the best of our knowledge, the idea that overfishing of competing marine mesopredators benefits staging shorebirds, at least in the short term, is novel; it now needs further experimental and comparative scrutiny. The long-term effects of overfishing on benthic communities of the mudflats need further investigation.

1. Introduction

Estuarine intertidal habitats are the most productive areas on Earth (McLusky, 1989; Little, 2000; Castro and Huber, 2005). They combine rich nutrient conditions (resupplied with every high tide) with ample sunlight (during the daytime low water periods), which leads to abundant primary production, often in the form of diatoms. This is fed upon by secondary producers such as bivalves and gastropods (Mollusca) (Peterson et al., 1985; Dame, 2012). Such 'grazing' macrozobenthic animals in turn are eaten by species at higher trophic levels, usually including fish and crabs during high tide, and shorebirds during the times that the sediments are exposed at low tide (Seitz et al., 2001; Gray and Elliott, 2009).

The distribution of molluscs is a function of these predation pressures, along with several external factors including sediment characteristics and wave action (Gosling, 2003; Dame, 2012). Quite recently in evolutionary terms, there has been overexploitation by human population, which has caused major losses of biodiversity in estuarine and coastal ecosystems worldwide (Ellis et al., 2000; Lotze et al., 2006). Human pressures can fundamentally change the structure and function of ecosystems (Jackson et al., 2001; Worm et al., 2006; Defeo et al.,

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2009). For instance, benthic communities of intertidal mudflats worldwide are threatened by bottom-dredging forms of fishery (Jackson et al., 2001; Piersma et al., 2001; Atkinson et al., 2005; van Gils et al., 2006), activities which may have serious downstream effects on the predators of benthic invertebrates (Shepherd and Boates, 1999; Atkinson et al., 2003; Verhulst et al., 2004; van Gils et al., 2006). The loss of coastal ecosystem values is a persistent problem worldwide, especially in rapidly developing countries (Lotze et al., 2006; Worm et al., 2009; MacKinnon et al., 2012; Ma et al., 2014; Murray et al., 2014).

The coasts of the Yellow Sea, at least historically, offered the largest continuous system of intertidal mudflats in the world (Healy et al., 2002). The coastal wetlands contained a rich biodiversity and are key stopover sites each spring for millions of migratory waterbirds in the East Asian–Australian Flyway (Barter, 2002; MacKinnon et al., 2012). These intertidal foreshores are used by high densities of humans as well (CIESIN, 2005). Bottom-dwelling life such as polychaete worms, bivalves, gastropods and crustaceans are harvested all around the Yellow Sea (Melville et al., in press). There is evidence that these fisheries have changed the coastal ecosystem: overfishing has caused major declines of several benthic species, harvests by suction pumps resulted in damage of non-target benthic species, mudflats were poisoned by pesticide used for clearing unwanted organisms before industrially reared spat seeded in the mudflats, and waterbirds were disturbed by massive harvesters in intertidal areas (Lin and Yuan, 2005; Feng and Ma, 2012; MacKinnon et al., 2012; Melville et al., in press). Thus, besides the effects of habitat loss by the remarkably fast land claims (MacKinnon et al., 2012; Murray et al., 2014; Piersma et al., 2015), the effects of fisheries on waterbirds along the Yellow Sea coast are also of concern but little studied.

Bohai Bay, located in northwest of the Yellow Sea, is a staging area supporting half a million migrant shorebirds every year (Barter, 2002; Barter et al., 2003; Yang et al., 2011). On these mudflats molluscs comprise an important food for the waterbirds (Yang et al., 2013). This resource support several important shorebird species, e.g. Red Knots (*Calidris canutus*), Curlew Sandpipers (*C. ferruginea*) and Great Knots (*C. tenuirostris*), in the East Asian–Australian Flyway during their refuelling stage in the Yellow Sea (Yang et al., 2011, 2013). Their presence goes together with heavy fisheries in the mudflats and offshore along Bohai Bay (HPDLR, 2007; Zhao et al., 2008; Jin, 2014).

In this study, we set out a seven-year investigation on molluscs and factors in northern Bohai Bay to test if there is any effect of fisheries on molluscs in the intertidal mudflats. As there is a knowledge gap on intertidal molluscs in the western Yellow Sea in terms of shorebird food conditions (Zhang and Hu, 2005; HPDLR, 2007; Wang et al., 2011; Cai et al., 2014), the aim of this study is to investigate the changes in density and distribution of molluscs. We examined the distribution of bivalves and gastropods in northern Bohai Bay in 2008–2014, monitored from the perspective of their role as a food resource for shorebirds.

2. Methods

2.1. Study area

The study area is located in the coast of Luannan County, Hebei Province, China (Fig. 1) and borders three fishing villages which are now separated from the sea because of previous land reclamations: Beipu, Nanpu and Zuidong (39°1–8′ N, 118°9–21′E). It also includes an actively exploited oilfield (Jidong Nanpu Oilfield) with three artificial islands in the intertidal and subtidal area (two of them presented in Fig. 1, one of which connects with land by a dike). The tidal area is limited by a seawall which was constructed at mid tide in the 1950s to enable the development of what are now among the largest salt works in the world.

Bohai Bay has a semi-diurnal tide and average tidal amplitude is 2.5 m (HPDLR, 2007). The remaining tidal mudflats of study area are 1–4 km wide at low tide and are completely submerged 2 h before high tide. The area has a typical temperate continental climate with cold, dry winters and hot, humid summers. The average temperature is −4 °C in January and 26 °C in July (HPDLR, 2007). The tidal area remains frozen normally between December and February. The local sea surface salinity is 33 ‰ in May and 31 ‰ in August (HPDLR, 2007). For more details of study area, see Rogers et al. (2010) and Yang et al. (2011).

There are two types of shellfish harvests on the intertidal mudflats in the study area. (1) The fishing of the bulk food for White Shrimp (*Litopenaeus vannamei*) raised in the adjacent saltpans. Local fishermen remove all bivalves over 2–3 mm long that occur in the top 2 cm layer of the sediment with suction devices from small fishing vessels (ca. 10 m length). The device consists of engine, pump, pipes and sieve. At high tide, pumping the water from the surface of the mudflats removes the upper layer of mud into the sieve on the boat to collect bivalves. The mud is disturbed to a depth of less than 4 cm. The harvest of White Shrimp-feed is carried out every summer and autumn, after northward migrants leave Bohai Bay, on the mudflats north of the offshore road to the oil island of Jidong Nanpu Oilfield (Fig. 1), and this activity has been ongoing for decades (J.C. Yang pers. Comm.). A similar harvest was carried out in the westernmost part of the mudflats between Nanpu and Zuidong until 2009 (Fig. 1). (2) The fishing of edible clams. For the collection of the edible clams, mainly *Mactra quadrangularis* over 2–3 cm long, fishermen pump the mudflats by suckers powered by engines on floating platforms (2–3 m diameter air-filled tyres). These are operated during outgoing and incoming tides by fishermen standing in seawater. Siphoning edible clams was adopted in 2009, and replaced the traditional digging by hand. It occurs on the mudflats between Zuidong and the sampling transects of this study in southern Beipu (Fig. 1). On the mudflats south to the offshore road to the oil island of Jidong Nanpu Oilfield, 15–20 engines have been active year-round except for midwinter, while 6–10 engines were active between March and May (i.e. during the staging of northward migrants) on the mudflats north to the offshore road. Leaving 5–10 cm-depth tracks after harvest, the disturbance of edible clam harvest appear more destructive for the surface sediments than that of White Shrimp's feed harvest. As we were not interested in quantifying the immediate effects of this fishery, we sampled areas where White Shrimp-feed were harvested, but did not sample areas where large edible clams were harvested. Although transects in Zuidong and Nanpu were in the edible-clam-harvest area in 2009 and one of transects in Nanpu was partly in the edible-clam-harvest area in 2013 and 2014 (Fig. 1), we sampled these transects in spring when fishing did not affect them.

2.2. Invertebrate sampling

2.2.1. Annual/spring sampling

In early and late spring 2008 benthic samples were collected at northern Beipu and Zuidong to investigate mollusc densities and sizes during the northward migration of shorebird migrants. Each site consisted of 4 transects 250 m apart on a grid running from the seawall to the low water line (Fig. 1). At each station, one sediment core of 1/56 m^2 to a depth of 20 cm was taken and sieved over a 1 mm mesh. To distinguish surface-living molluscs (i.e. prey accessible to probing shorebird predators) from deeper-living ones, the top 4 cm was sieved separately (see van Gils et al., 2009). Because gastropods were expected to occur in higher densities, they were sampled by a smaller core (1/267 m^2) to a depth of 4 cm and over a finer mesh (0.5 mm).

In early and late spring 2009 sampling sites were extended to S. Beipu and Nanpu, with 4 transects respectively (Fig. 1). The sampling method was changed to only take the top layer of the 1/56 m^2 core for bivalves with the small core from 2009, as in 2008 we established that all individuals of the numerically dominant bivalve species *Potamocorbula laevis* occurred in the top layer that is accessible to Red Knots (see Zwarts and Blomert, 1992).

Unfortunately, we had to reduce the number of sampling stations in 2010–2014 because of the reclamations of mudflats at Zuidong and

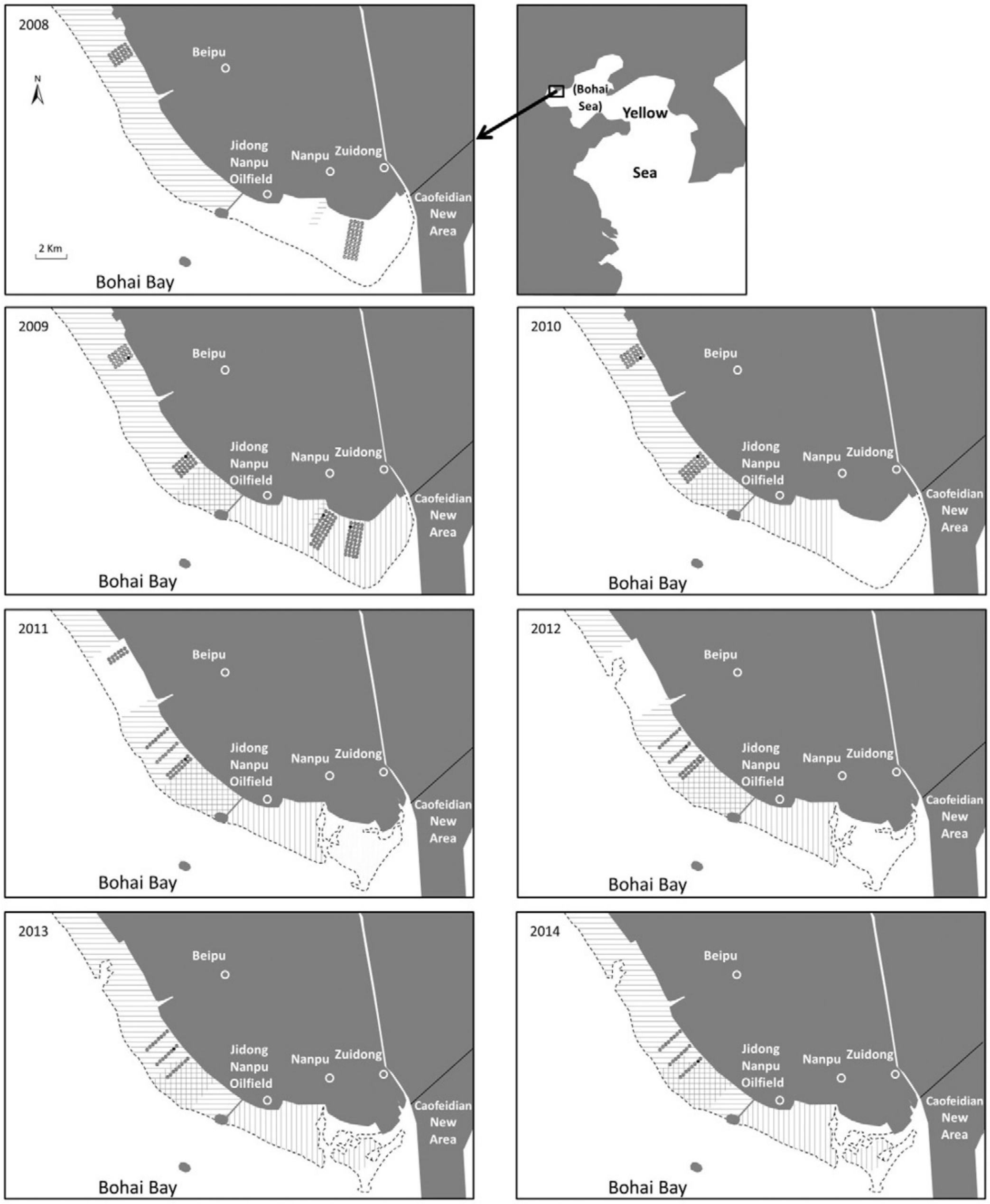

Fig. 1. Map of the study sites situated in northern Bohai Bay, the Yellow Sea: Beipu, Nanpu and Zuidong. Benthic and sediment sampling stations (grey dot) along transects and monthly benthic sampling stations (black dot) in 2008–2014 are shown. Grey area represents land, area between dash line and land is tidal mudflats exposed at spring low tides, which lost with time due to land reclamation (e.g. at Zuidong and Nanpu, a ca. 10 km^2 area of intertidal mudflats became embanked or was pumped away coincidentally leading to the loss of filled-in adjacent salt works in 2010–2012), and white area indicates sea water and river. All land is salt works expect three villages, oilfield, Caofeidian New Area, and claimed salt works between Zuidong and Nanpu in 2010–2014. The intertidal areas with harvest of edible clams and the bulk food for White Shrimp are presented in vertical and horizontal lines, respectively. These two types of shellfisheries overlapped in some areas.

Nanpu in 2010–2012 and at N. Beipu in 2011–2012, and the harvest of edible clam moving to our sampling area at S. Beipu from 2011 (Fig. 1). For partial replacement we established two transects at S. Beipu from 2011 (Fig. 1). The transects were sampled in early and late spring in 2010–2011, in early, middle and late spring in 2012, in middle spring in 2013–2014 (for more details of sampling, see Table A.1). Throughout, we did sample the areas actually used by foraging shorebirds.

All molluscs retained on the sieve were put in plastic bags and stored at −20 °C (Bocher et al., 2007; Kraan et al., 2009). In the laboratory, species, size (to the nearest mm) and number were determined (following the standard methods of e.g. Piersma et al., 1993a; van Gils et al., 2005b; Kraan et al., 2009).

2.2.2. Monthly sampling

To monitor the changes in density and size of *P. laevis*, monthly benthic samples were collected at stations of 500 m away from the seawall at the four study sites in 2009 (Fig. 1, Table A.2). Having established that the harvest of the bulk food for White Shrimp wiped out most of the molluscs in top layer of mudflats in autumn, from 2010 we took the benthic samples at monthly intervals only in spring and summer. As the reasons mentioned above, we took monthly samples at N. & S. Beipu in 2010, and only S. Beipu since 2011, which means that in 2011–2014 the monthly data of *P. laevis* was collected from only one station. We switched the sampling stations to the north transect at S. Beipu in 2012–2013 (for more details of sampling, see Table A.1). Ten cores of 1/56 m^2 to a depth 4 cm were taken in a subjectively random way over a fixed 100 m^2 area at each station for each month. Cores were sieved over a 1 mm mesh. The molluscs were stored at −20 °C and measured in the laboratory as described above.

2.3. Sediment sampling

Sediment samples were collected at the stations along transects at study sites in spring 2009–2014 (Fig. 1, Table A.1). At each station a sediment sample was taken with a 5 cm diameter core to a depth of 4 cm and stored frozen at −20 °C. At NIOZ Royal Netherlands Institute for Sea Research median particle size and the percentage silt (fraction <63 μm) of sediments were determined using a Coulter LS 230 particle size analyser. Particle sizes in the range of 0.04–2000 μm were measured using laser diffraction. Particles were treated following the procedure described by van der Bergh et al. (2003) and measured in the Coulter Counter.

2.4. Data analysis

We tested sediments among sites or over years and densities of *P. laevis* among sites or over years for significant variance using one-way ANOVA. We tested the difference in sediments at one site in two years using t-test. We also tested the relationship between densities of *P. laevis* and median grain size of sediments in 2009 using GLM. All analysis was performed using SYSTAT13 (Systat Software Inc.).

3. Results

3.1. Sediment characteristics

The grain sizes of sediments at four study sites were significantly spatially variable in 2009 ($F_{3,118} = 105.69$, $P < 0.001$, Table 1). The sediments at N. Beipu were silty (median grain size >4 μm and <63 μm) and those at S. Beipu, Nanpu and Zuidong were mixtures of silt and very fine sand (grain size >63 μm and <125 μm). The sediments at N. Beipu were coarser in 2011 than 2009 ($t = 8.06$, d.f. = 33, $P < 0.001$). At S. Beipu the sediments were the finest in 2009 and became coarser afterwards but were not significantly different between 2010 and 2014 ($F_{3,116} = 1.3$, $P = 0.28$). According to the grain size analysis, 82% of the stations with silty sediments (the number of silty stations is 114) were located within 1 km of the seawall.

3.2. Molluscs distribution

A total of eight bivalve species and nine gastropod species occurred during the first assessment in 2008 (Table 2). At the two sites the mollusc assemblage was numerically dominated by *P. laevis* (96% of the total density), which occurred in the top 4 cm of the sediment. At Beipu densities of *P. laevis* were much higher than at Zuidong. In June the *P. laevis* was larger than in April, but the total density was lower. Densities of *P. laevis* at Zuidong increased from April to June, while those of *P. laevis* at Beipu declined. Among the five bivalve species occurring in April at Beipu, with lengths of 1–3 mm long and small proportions of 4–10 mm sized individuals, *P. laevis* were the smallest and in two age cohorts (0-age and 1-age) (Fig. 2). At Beipu all *M. quadrangularis* and *Moerella iridescens* were also small (1–7 mm long and 1–3 mm long, respectively). With animals up to 30 mm and 18 mm respectively, at Zuidong *M. quadrangularis* and *M. iridescens* seemed to show three age cohorts. Considering that Red Knots can only forage on small items (shell length < 20 mm) that occur in the top 4-cm of sediment (Zwarts and Wanink, 1989; Zwarts and Blomert, 1992; Piersma et al., 1993b), all molluscs at Beipu were harvestable, while 98.5% of total individuals at Zuidong were harvestable, due to the fact that half of big *M. iridescens* (>8 mm long) were in the bottom layer and all uningestible *M. quadrangularis* (>20 mm long) in the top layer.

Although the peak densities of *P. laevis* were significantly different between all sites in the spring of 2008–2014 ($F_{12,277} = 6.80$, $P < 0.001$, Fig. 3), they were always higher than 3900 ind/m^2 (ranging tenfold between 3,943 ind/m^2 and 41,113 ind/m^2) with average shell length from 1.1 to 4.8 mm (0-age), except a density of 1,285 ind/m^2 (0-age) at Zuidong in 2008. In all years *P. laevis* occurred in the highest densities within 1 km from the seawall (Fig. 4). The relationship between *P. laevis* and median grain size of sediment would indicate that they preferred to settle in the relatively muddy areas (Fig. 5).

3.3. Seasonal changes in P. laevis

The pattern of seasonal change in *P. laevis* at the stations 500 m away from the seawall is shown in Fig. 6. In February 2009 there were low densities of 0-age *P. laevis* at N. & S. Beipu, low densities of larger 1-age individuals at Zuidong, and high densities of what were mainly 1-age individuals of at Nanpu. In the ensuing months *P. laevis* settled at all sites, while the 1-age individuals rapidly declined. Densities of *P. laevis* peaked in May (over 15,000 ind/m^2 with average shell length 2.0–2.2 mm at all sites). The peak densities of *P. laevis* were significantly different between the four sites ($F_{336} = 11.4$, $P < 0.001$); at N. & S. Beipu densities were higher than that at the other two sites (N. & S. Beipu: $F_{118} = 0.97$, $P = 0.34$; Nanpu & Zuidong: $F_{118} = 0.32$, $P = 0.58$). Densities of *P. laevis* declined dramatically from May (the peak of shorebird staging) to June (the end of shorebird staging). From June densities continued to decline and reached zero in September at N. Beipu and in October at S. Beipu. At Zuidong the densities of 1,200 ind/m^2 were maintained in November and December. At all sites shell length increased constantly from spring to winter (Fig. 6). At S. Beipu *P. laevis* grew from 1 mm in February to 6 mm in September and from 1 mm in April to 6 mm in December at Zuidong.

In the spring and summer of 2010–2014, the density changes of *P. laevis* at Beipu followed the same pattern of 2009, i.e. densities peaked in May with average shell length 2.0–2.8 mm from smaller ones (1.0–1.6 mm) in early spring, except density peaked in June at S. Beipu in 2010 (Fig. 6). Peak densities at S. Beipu were significant different between 2009 and 2014 ($F_{553} = 6.01$, $P < 0.001$) with the lowest of 5,650 ind/m^2 in 2011 and the highest of 85,042 ind/m^2 in 2010.

4. Discussion

In this study, we found a surprisingly high density of molluscs of predominately small individuals in the intertidal mudflats of northern Bohai Bay. The community is dominated by the first cohorts of a single bivalve species, *P. laevis*. In fact, based on our reading, these densities may well be among the highest bivalve-densities recorded in intertidal areas worldwide (cf. Cranford et al., 1985; Martinia and Morrison, 1987; Sun, 1988; Jensen, 1992; González et al., 1996; Pepping et al., 1999;

Table 1
The average median grain size with range and mud fraction (% particles <63 μm) of sediment along transects at northern Beipu (BPN), southern Beipu (BPS), Nanpu (NP) and Zuidong (ZD).

Year	Site	Median grain size (μm ± SD)	Range (μm)	Mud fraction (%)	Sample number
2009	BPN	16.6 ± 8.2	7.5–32.3	94	24
	BPS	49.2 ± 20.8	19.0–104.3	64	24
	NP	83.0 ± 18.9	56.0–99.8	31	38
	ZD	75.4 ± 10.4	56.1–122.3	35	36
2010	BPS	70.0 ± 28.3	22.8–115.2	47	32
2011	BPN	86.3 ± 41.3	25.4–117.3	37	12
	BPS	78.9 ± 36.2	16.9–122.7	43	32
2012	BPS	68.4 ± 22.7	32.4–103.4	48	32
2013	BPS	65.1 ± 21.7	28.1–97.9	50	24
2014	BPS	70.0 ± 24.2	30.3–113.5	45	24

Table 2
Average density (AD) and the percentage of all mollusc species (Per), frequency of occurrence (Occ) of these species, average shell length of bivalves or shell height of gastropods (SL/SH) and size range of each species along transects at northern Beipu (BPN) and Zuidong (ZD) in April and June 2008. n is the number of individuals.

Species	April					June				
	AD (ind/m^2) and per (%)		Occ (%)		SL/SH (mm ± SD) and size range (mm)	AD (ind/m^2) and Per (%)		Occ (%)		SL/SH (mm ± SD) and size range (mm)
	BPN	ZD	BPN	ZD		BPN	ZD	BPN	ZD	
Potamocorbula laevis	23,868 (99.4)	770 (60.4)	100	15	2.03 ± 0.12 (1–10) n = 10,779	10,316 (96)	1,285 (78.1)	100	25	2.91 ± 0.10 (1–9) n = 5,155
Mactra quadrangularis	30 (0.1)	224 (17.6)	29	35	7.22 ± 3.97 (1–30) n = 173	7 (0.1)	176 (10.7)	9	28	18.93 ± 2.72 (4–28) n = 129
Moerella iridescens	7 (0.03)	185 (14.5)	8	45	3.41 ± 2.79 (1–18) n = 135	5 (0.05)	41 (2.5)	9	43	10.55 ± 3.56 (2–18) n = 31
Theora fragilis	35 (0.1)	–	29	–	4.80 ± 2.10 (1–10) n = 15	10 (0.1)	–	9	–	4.25 ± 0.74 (3–5) n = 4
Musculus senhousei	2 (0.01)	1 (0.1)	4	3	1.50 ± 0.50 (1–2) n = 2	–	1 (0.1)	–	3	4 (4) n = 1
Mactra chinensis	–	–	–	–	–	–	1 (0.1)	–	3	2 (2) n = 1
Meretrix Meretrix	–	–	–	–	–	–	1 (0.1)	–	3	36 (36) n = 1
Solen gouldi	–	–	–	–	–	–	1 (0.1)	–	3	20 (20) n = 1
Stenothyra glabra	78 (0.3)	7 (0.5)	8	3	2.25 ± 0.28 (2–3) n = 8	325 (3)	27 (1.6)	13	3	2.53 ± 0.30 (1–3) n = 32
Umbonium thomasi	–	67 (5.3)	–	10	7.90 ± 0.80 (7–10) n = 10	–	73 (4.5)	–	18	8.36 ± 0.98 (6–10) n = 11
Nassarius succinctus	–	7 (0.5)	–	3	19 (19) n = 1	58 (0.5)	–	17	–	10.60 ± 3.13 (7–16) n = 5
Nassarius variciferus	–	7 (0.5)	–	3	19 (19) n = 1	–	–	–	–	–
Terebra koreana	–	7 (0.5)	–	3	12 (12) n = 1	–	13 (0.8)	–	5	12 ± 2 (10–14) n = 2
Mitrella bella	–	–	–	–	–	–	13 (0.8)	–	5	11 ± 1 (10–12) n = 2
Nassarius festiva	–	–	–	–	–	12 (0.1)	7 (0.4)	4	3	5 ± 1 (4–6) n = 2
Bullacta exarata	–	–	–	–	–	12 (0.1)	–	4	–	10 (10) n = 1
Rapana venosa	–	–	–	–	–	–	7 (0.4)	–	3	14 (14) n = 1
Total	24,020 (100)	1,275 (100)	–	–	–	10,745 (100)	1,646 (100)	–	–	–

Bocher et al., 2007; Compton et al., 2008; Honkoop et al., 2008; Nourinezhad et al., 2013; Ahmed Salem et al., 2014).

In our study, *P. laevis* started to grow in early spring and reached peak densities in May. Despite the variation between years, spatfall of *P. laevis* was high and predictable enough to support tens of thousands of specialized mollusc-predators such as Red Knots, which use the Bohai Bay as their most important staging ground during northward migration in the East Asian–Australian Flyway (Yang et al., 2011; H.Y. Yang unpublished data). Remarkably, although the classic criteria for prey quality (the meat to shell mass ratios, van Gils et al., 2005a) was not at its seasonal peak when Red Knots occur in northern Bohai Bay, they do find ample and high quality food because of the small size and crushability of small *P. laevis* (Yang et al., 2013). In the study years, 24,000–66,000 Red Knots, 8,000–40,000 Curlew Sandpipers and 1,000–10,000 Great Knots fed on molluscs when they staged in the study area between April and June during the long-distance migration from Australasia to the Arctic (Bamford et al., 2008; Yang et al., 2011; H.Y. Yang unpublished data). In most of the years, the densities of *P. laevis* declined towards the end of the spring staging period, suggesting that the predation pressure by avian predators could affect the

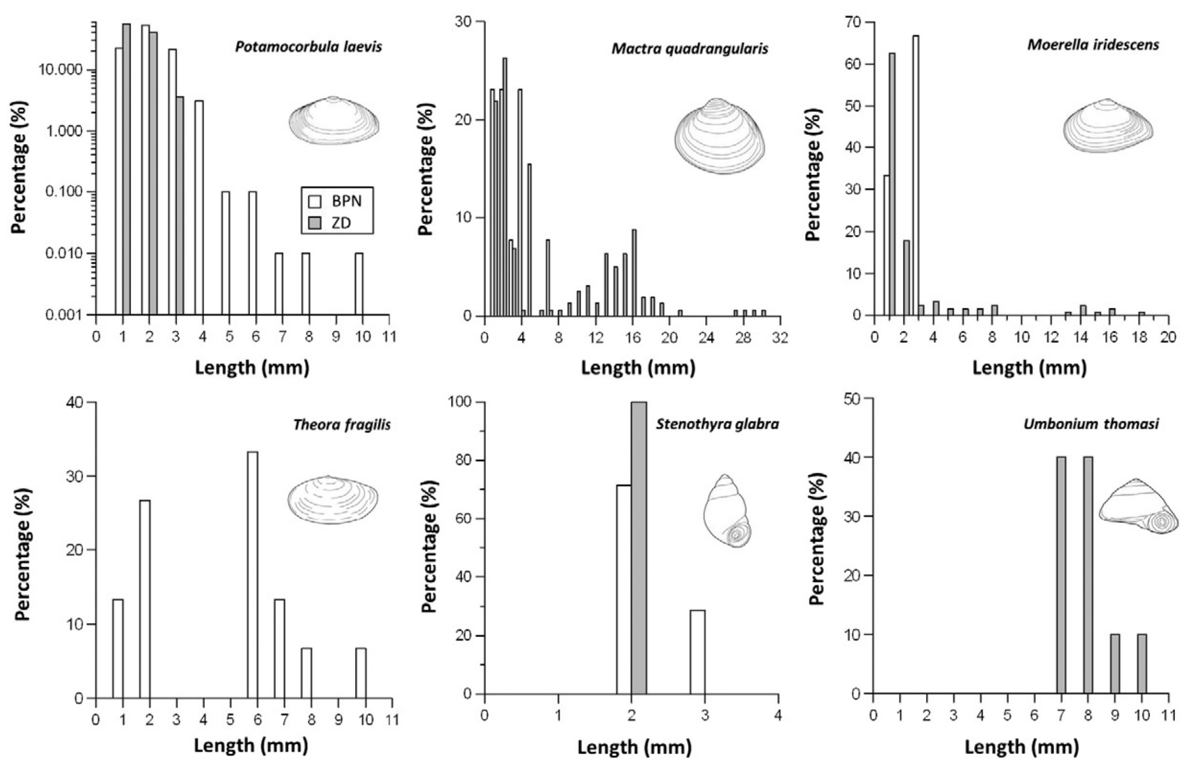

Fig. 2. Size distributions of six mollusc species at northern Beipu (BPN, white bar) and Zuidong (ZD, grey bar) in April 2008. Four other species with 100% at one size class, as sample number is one, were not shown: *Musculus senhousei* (100% of 1 mm at BP, 100% of 2 mm at ZD), *Nassarius succinctus* (100% of 19 mm at ZD), *Nassarius variciferus* (100% of 9 mm at ZD), *Terebra koreana* (100% of 2 mm at ZD).

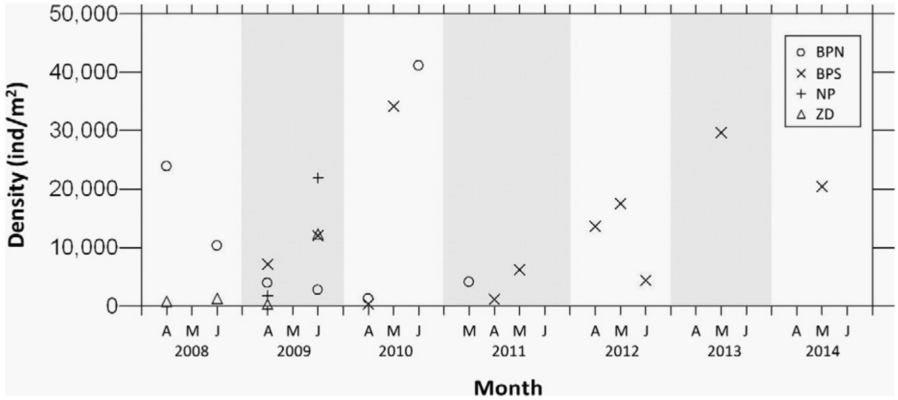

Fig. 3. Densities of *Potamocorbula laevis* (n = 122,091) along transects at northern Beipu (BPN), southern Beipu (BPS), Nanpu (NP) and Zuidong (ZD) in spring (March, April, May, June) in 2008–2014.

populations of bivalves. However, considering that there were still 2,600–85,000 ind/m^2 of *P. laevis* left in June in different years, the food stock is still remarkably high by the time the shorebirds have left for their Arctic breeding grounds.

Normally *P. laevis* can grow to 20 cm long and occur in 4 age cohorts (Wei and Guan, 1985b). However, the demographic structure is highly unusual in our study. Why do *P. laevis* have large recruitments in spring but always disappear in late autumn? We suspect that it is related to fishing activities. As we have seen, from July to October local fisherman harvest the top layer of the intertidal mudflats by sucking devices to collect *P. leaves*, which they use to feed White Shrimp farmed in the nearby saltpans. The baby White Shrimp are released into the saltpans in March and grow to 3–4 cm-long juveniles to be given *P. laevis* in July. Fishermen adjust the amount of caught *P. laevis* based on the need of the shrimp farm. Consequently, only few or no adult *P. laevis* survive the harvest. In rare cases, such as in 2009 at N. Beipu, red tide events in summer may be involved in the mortality of *P. laevis*. Elsewhere on the Chinese Yellow Sea, in an area with prawn cultures, the densities of young *P. laevis* without adult presence were as high as in northern Bohai Bay (Sun, 1988), while in areas with a high percentage of adults, the densities of *P. laevis* were much lower (Wei and Guan, 1985a; Choi et al., 2014). Experimental studies in northern Europe indicated that adult-juvenile competition significantly affects bivalve recruitment (Bonsdorff et al., 1986; Flach, 2003). A long term investigation in the White Sea also showed that significant abundance of bivalve juveniles often coincided with the rapid decline of a former dominant generation probably due to the available habitat in the mudflats (Gerasimova and Maximovich, 2013). Hence, we proposed that the 'adult free' mudflats could offer good habitat for the juvenile *P. laevis* to establish in spring.

Shrimps and crabs have been reported to be the main predators of juvenile bivalves in the intertidal areas in western and northern Europe (van der Veer et al., 1998; Flach, 2003; Dekker and Beukema, 2014). The recruitment success of bivalves has been correlated with the abundance of these predators (Beukema et al., 1998; Masski and Guillou, 1999; Strasser et al., 2003; Beukema and Dekker, 2005). Due to overfishing since 1950s in the Bohai Sea in China (see Fig. 1), the low-trophic-level fish and crustacean species replaced the harvest of mainly high-trophic-level fish species (Xu et al., 2010). Over the past twenty years this was followed by declines in the stocks and decreases in body size of the lower-trophic fish and crustaceans, as well as early mortality associated with advances in the age of sexual maturity of most of the species (HPDLR, 2007; Jin, 2014). Among the low-trophic-level species in the Bohai Sea, six species of crabs, shrimps, octopus and fishes are predators of bivalves and other four species of fishes and shrimps are predators of bivalve larvae (Deng et al., 1997; Yang, 2001a, 2001b; HPDLR, 2007; Song et al., 2013; Jin, 2014). There has been a steady decline in all of these species, especially the main predator of freshly settled bivalves,

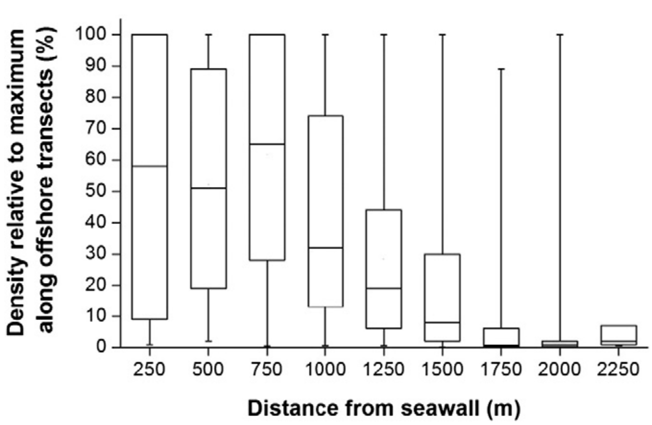

Fig. 4. Relative densities of *Potamocorbula laevis* (n = 122,091) with distance from seawall along transects at northern and southern Beipu, Nanpu and Zuidong in spring 2008–2014. The highest density within one transect during one sampling period is 100% and other densities along the same transect in same period are fractions of the maximum. Horizontal bars are median value; boxes indicate the range within which the central 50% of the value fall; bars represent extreme values.

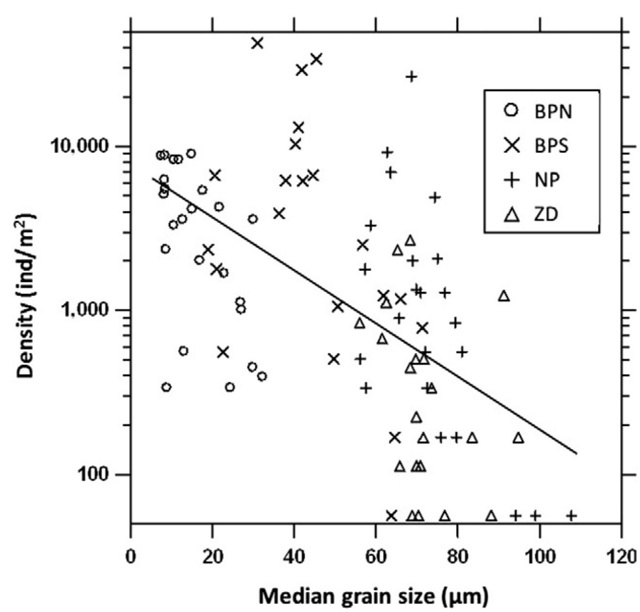

Fig. 5. Density of *Potamocorbula laevis* in relation to median grain size along transects at northern Beipu (BPN), southern Beipu (BPS), Nanpu (NP) and Zuidong (ZD) in April 2009. We fitted a semilogarithmic regression: log y = −0.016× + 3.87 (R^2 = 0.33, $P < 0.001$, N = 90).

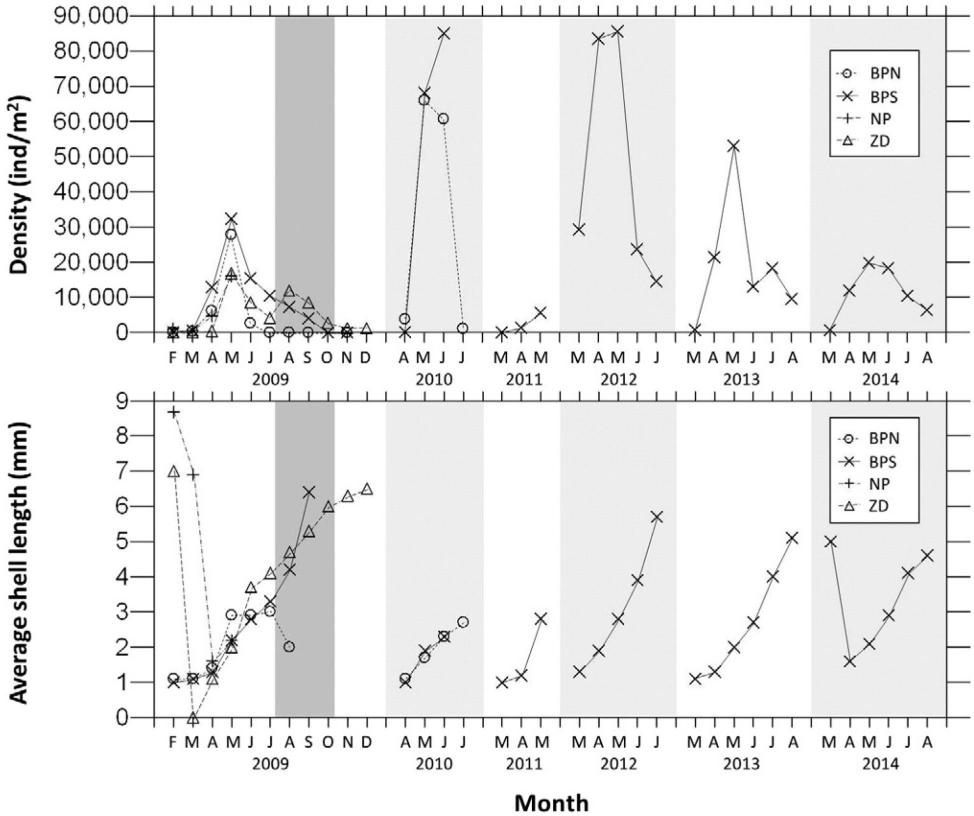

Fig. 6. Monthly changes of densities (above) and average shell length (below) of *Potamocorbula laevis* (n = 162,266) at northern Beipu (BPN), southern Beipu (BPS), Nanpu (NP) and Zuidong (ZD) in 2009–2014. The dark grey areas indicate the period in 2009 when *P. laevis* is fished to be fed to White Shrimp.

e.g. the catch *of Portunus trituberculatus* declined from 24 kg/h per cruise in August 1992 to 0.3 kg/h per cruise in August 2010, the catch *of Fenneropenaeus chinensis* declined from 11 kg/h per cruise in 1959 to 0.3 kg/h per cruise in August 2010, the catch *of Oratosquilla oratoria* declined from 6 kg/h per cruise in August 1992 to 0.6 kg/h per cruise August 2010 (HPDLR, 2007; Zhao et al., 2008; Jin, 2014). Among them the Chinese shrimp *F. chinensis*, a large migratory prawn, is a key crustacean predator of bivalves in the Yellow Sea region breeding in the intertidal areas in spring and for which the coastal Bohai Sea was one of the main breeding areas (Deng et al., 1990; Liu, 1990). They have been fished so intensively since the 1960s that they became commercially 'extinct' in the early 1990s and their wild population is endangered (Deng et al., 1990; Chen, 2002; Deng, 2003; Song and Yang, 2009). In view of the decline in predator abundances of bivalve larvae and spat, we propose that these decreases of epibenthic mesopredators now help juvenile *P. laevis* to reach high densities each spring.

The highest concentrations of *P. laevis* occur within 1 km from the seawall in spring as do the fine sediments. Interestingly, this is also where the shallow siphoning of the top layer of the mud occurs every year. Thus, unlike the effect of the much deeper shellfish dredging in the Dutch Wadden Sea (Piersma et al., 2001), the sediments in northern Bohai Bay maintained high silt fractions with associated large spat fall of *P. laevis*. The lack of loss of fine sediments may relate to the pattern of sediment supply and deposition by the two big rivers with the highest average sediment deposition in China — the Yellow River and Luan River, the estuaries of which are located in western Bohai Sea, contributing sediments to the coastal areas in the Bohai Sea. The fact that the sediments became coarser at the study sites after 2009 may relate to a scraping off to sea by the sea ice in the 2009–2010 winter, which was the most severe in Bohai Bay for 30 years (Shi, 1987; Qiao et al., 2010; Yang et al., 2011).

The peak of spawning by *P. laevis* is in September in the Yellow Sea (Wei and Guan, 1985b; Liu and She, 2003), when there are still many grown individuals of 0-age (e.g. there were 4,049 and 8,518 ind/m^2 with 5–6 mm of average shell length at S. Beipu and Zuidong, respectively, in September 2009) with developed gonads maintain to spawn in the study area before the grown 0-age *P. laevis* were harvested entirely in October (H.Y. Yang pers. Obs.). It takes 30–40 days for larvae to develop into <0.5 mm-long juveniles, which settle in the mudflats in late autumn (Wei, 1984). In spring, with temperatures increase, these juveniles grow fast. Indeed, as food for cultured crustaceans, *P. laevis* used to be one of the main targets of fisheries in the intertidal areas along the coast of the Chinese Yellow Sea until the 1980s, after which it showed declines (Wei, 1984; Liu and She, 2003; HPDLR, 2007). In the study area, although the harvest of *P. laevis* is intensive, local fishermen try to keep the population alive by maintaining a certain fraction of bivalves during the harvest. Furthermore, *P. laevis* from Shandong Province in the southern Yellow Sea were brought in the Nanpu mudflats by 2009. Such exploitation of intertidal bivalves is a common practise in marine shellfish farms in China (Wang and Wang, 2008).

Nevertheless, on the mudflats south to the offshore road to the oil island of Jidong Nanpu Oilfield, the siphoning harvest of edible clams stopped in 2015 as there were no harvestable *M. quadrangularis* and few *Ruditapes philippinarum* (bivalves adapted to sandier mudflats) left after strong harvests over years. In spring 2015 the local fishermen started to seed baby *M. quadrangularis* on these mudflats (Y.C. Chan, H.B. Peng and A.L. Yang pers. comm.). As the harvest season of *M. quadrangularis* on the mudflats north to the offshore road is from March to May, we are worried about the effects of this fishery on the staging shorebirds. The study area is among the few remaining staging sites along the shores of Bohai Bay and indeed much of the Yellow Sea (Yang et al., 2011; Murray et al., 2014; Piersma et al., 2015). The flyway populations of Red Knots, which highly depend on the bivalves in the study area, may then face even more savage declines than they currently face (Yang et al., 2013; Piersma et al., 2015).

5. Conclusions

Our study found that the density of *P. laevis* is extremely high in spring — probably the highest marine bivalves recorded worldwide — in the mudflats of the Bohai Bay, on the Chinese Yellow Sea. This happens despite, or perhaps because of, the intensive siphoning for the bivalves in summer and autumn and the overfishing of the potential (meso-)predators of young spat including shrimps and prawns. We suggest that these pressures have combined to offer very good food conditions for several molluscivore shorebird migrants (Yang et al., 2011, 2013). To the best of our knowledge, the idea that overfishing of competing marine mesopredators benefits staging shorebirds is a novel hypothesis that now needs further scrutiny. The long-term effect of harvesting edible clams on the benthic community of the mudflats also needs further investigation. We suggest that a regulated fishery for *P. laevis* may benefit both humans and birds, while the harvest of edible clams needs to be regulated on strict terms in important intertidal waterbird habitats along the Yellow Sea.

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Appendix A

Table A.1
Sampling details of benthos along transects at northern Beipu (BPN), southern Beipu (BPS), Nanpu (NP) and Zuidong (ZD) in 2008–2014. Stations with * means taking sediment samples simultaneously.

Year	Site	Date	Number of transects	Number of stations sampled	Number of stations in each transect
2008	BPN	31 March–13 April	4	24	6
		3–7 June	4	23	6 or 5
	ZD	3–9 April	4	40	10
		5–6 June	4	40	10
2009	BPN	1–6 April	4	24*	6
		2–7 June	4	24	6
	BPS	31 March–5 April	4	24*	6
		4–5 June	4	24	6
	NP	2–8 April	4	38*	10 or 8
		1–11 June	4	34	10 or 8
	ZD	3 April	4	36*	9
		8–10 June	4	36	9
2010	BPN	4–5 April	4	24	6
		1–2 June	4	24	6
	BPS	2–3 April	4	32*	8
		28–30 May	2	16	8
2011	BPN	23 March	2	12*	6
	BPS	24 March–5 April	4	32*	8
		23–26 May	4	32	8
2012	BPS	11–14 April	4	32*	8
		5–7 May	3	24	8
		8–12 June	4	32	8
2013	BPS	1–3 May	3	24*	8
2014	BPS	1–6 May	3	24*	8

Table A.2
Sampling details of monthly *Potamocorbula laevis* at northern Beipu (BPN), southern Beipu (BPS), Nanpu (NP) and Zuidong (ZD) in 2009–2014.

Year	Site	Position	Month
2009	BPN	39°7.61′ N, 118°9.98′E	February–September, November
	BPS	39°4.16′ N, 118°12.22′E	February–November
	NP	39°1.93′ N, 118°18.4′E	February–May
	ZD	39°1.47′ N, 118°19.5′E	February–December
2010	BPN	39°7.61′ N, 118°9.98′E	April–July
	BPS	39°4.16′ N, 118°12.22′E	April–June
2011	BPS	39°4.16′ N, 118°12.22′E	March–May
2012	BPS	39°4.62′ N, 118°11.77′E	March–July
2013	BPS	39°4.62′ N, 118°11.77′E	March–August
2014	BPS	39°4.16′ N, 118°12.22′E	March–August

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