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RESEARCH ARTICLE

How migratory shorebirds selectively exploit prey at a staging site dominated by a single prey species

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ABSTRACT

Competition intensity depends on the number of competitors and the amount of resources available. Coexistence of potential competitors can be enabled through niche differentiation or high resource availability. Using diet analysis, we investigated which of these 2 mechanisms was in play for coexisting shorebirds at a major staging site in the northern Yellow Sea, China, during northward migration in 2011 and 2012. Competition for food at this site is expected to be intense, with an estimated 250,000 migratory shorebirds gathering annually to refuel over a short period. Great Knots (*Calidris tenuirostris*), Eurasian Oystercatchers (*Haematopus ostralegus osculans*), and Red Knots (*C. canutus*) selected mostly the bivalve *Potamocorbula laevis*, whereas Bar-tailed Godwits (*Limosa lapponica*) had a broader diet and showed selection for polychaetes, even though most of their biomass intake was of *P. laevis*. Although all of these shorebirds fed on *P. laevis*, they showed different size selection and used different feeding methods. Bar-tailed Godwits, Great Knots, and Red Knots mainly swallowed *P. laevis* whole and preferred medium-sized *P. laevis* with relatively high ratios of flesh content to shell mass. By contrast, Eurasian Oystercatchers stabbed open *P. laevis*, ingested only the flesh, and preferred large *P. laevis* that provided the highest energetic return per prey taken. Despite evidence of niche differentiation in prey selection, the diets between the numerically dominant Bar-tailed Godwits and Great Knots overlapped substantially. Their coexistence seems to be enabled by high resource availability rather than niche separation.

Keywords: community pattern, East Asian–Australasian Flyway, foraging ecology, waders

Cómo las aves playeras migratorias aprovechan selectivamente las presas en lugares de parada migratoria dominados por una sola especie de presa

RESUMEN

La intensidad de la competencia depende del número de competidores y de la cantidad de recursos disponibles. La coexistencia de potenciales competidores puede ser posible mediante la diferenciación de nichos o de la alta disponibilidad de recursos. Usando análisis de dieta investigamos cuáles de estos dos mecanismos estaban en juego para permitir la coexistencia de aves playeras en un sitio importante de parada migratoria en el norte del mar Amarillo, China, durante la migración hacia el norte en 2011 y 2012. Se espera que la competencia por alimento en este sitio sea intensa, pues se estima que 250000 aves playeras migratorias se reunen cada año por un corto periodo para alimentarse. *Calidris tenuirostris*, *Haematopus ostralegus osculans* y *C. canutus* seleccionaron principalmente al bivalvo *Potamocorbula laevis*, mientras que *Limosa lapponica* tuvo una dieta más amplia y seleccionó poliquetos aunque la mayoría de su consumo de biomasa fue de *P. laevis*, Aunque todas estas aves playeras se alimentaron de *P. laevis*, las aves seleccionaron diferentes tamaños y usaron diferentes métodos de alimentación. *L. lapponica*, *C. tenuirostris* y *C. canutus* principalmente tragaron enteros los individuos de *P. laevis* y prefirieron animales con un contenido relativamente alto de carne en relación con su concha. En contraste, *H. o. osculans* abría las conchas de *P. laevis* con su pico, sólo consumía la carne y prefería individuos grandes que le dieran la mayor recompensa energética por presa consumida. A pesar de la evidencia a favor de la diferenciación de nicho en la selección de las presas, las dietas de la especie numerosa *L. lapponica* y de *C. tenuirostris* tuvieron una superposición sustancial. Su coexistencia parece ser permitida por la alta disponibilidad de recursos en vez de por la separación de nichos.

Palabras clave: aves vadeadoras, ecología de alimentación, patrones en comunidades, vía migratoria de Asia-Australasia Oriental

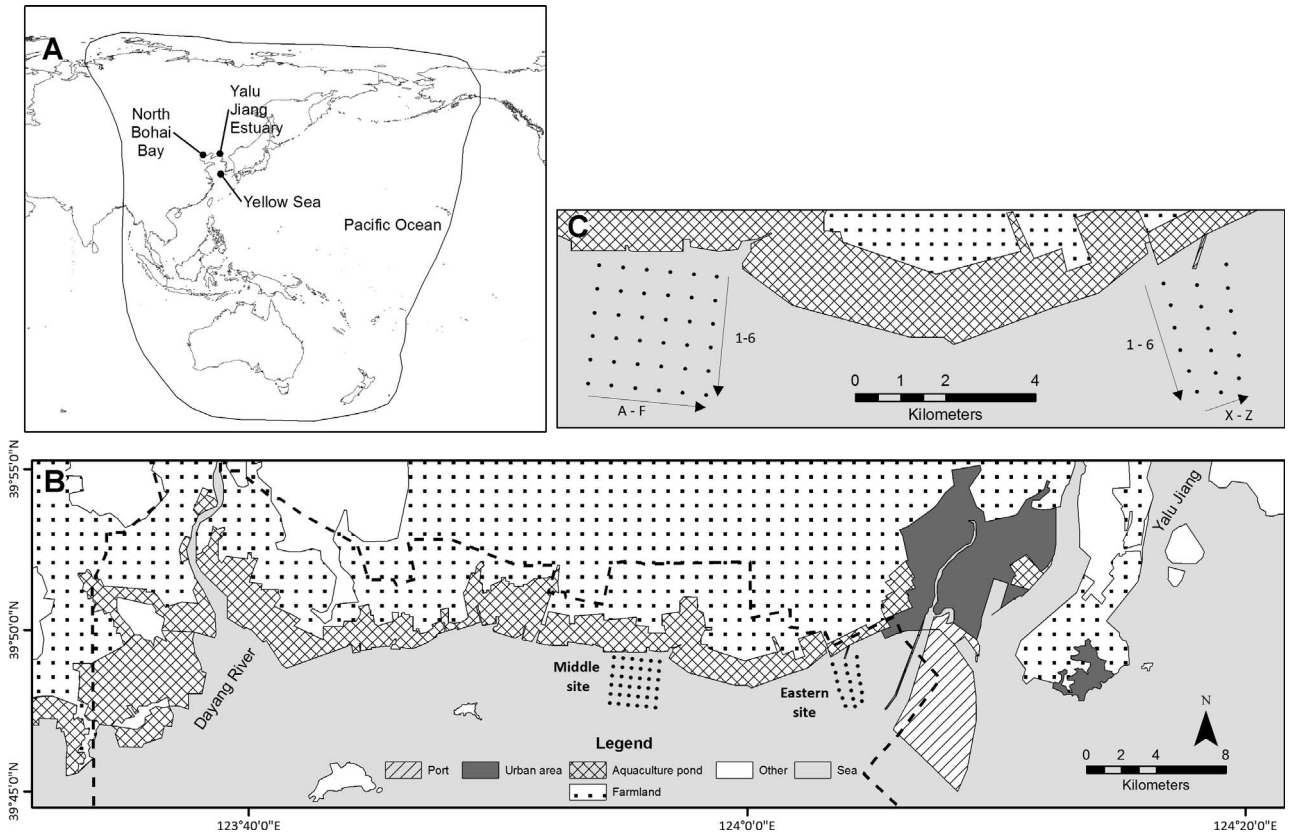

FIGURE 1. Maps showing the study area in China. (**A**) Boundary of the East Asian–Australasian Flyway. (**B**) The Dandong Yalu Jiang Estuary Wetland National Nature Reserve (area within dashed line). (**C**) The sampling stations in the middle (left) and eastern (right) sites.

INTRODUCTION

Animal migration has been described as a primary adaptation to exploit periodic and temporary resources (Harrington et al. 2002, Alerstam et al. 2003, Dingle and Drake 2007). Most shorebirds migrate (Warnock et al. 2002), and some are long-distance transoceanic and transcontinental migrants that require high-quality staging sites where they refuel before continuing their journeys (Atkinson et al. 2007, Choi et al. 2009, Warnock 2010, Battley et al. 2012, Hua et al. 2013). Along the East Asian–Australasian Flyway (EAAF), migratory shorebirds have a broad distribution in their nonbreeding and breeding areas, but a much narrower range during their stopovers in East Asia. Intense competition for limited resources is expected at staging sites, given the relatively high concentration of shorebirds, limited time for refueling, and limited resources (Skagen and Oman 1996, Newton 2008). This is particularly true in the Yellow Sea, which is located at the heart of the funnel-shaped landmass of the EAAF (Figure 1A). However, little is known about the feeding ecology of shorebirds during stopover along the EAAF, which hinders our understanding of why they select certain places and how they are supported by the resources present.

The degree of competition among predators depends on both their number and the amount of food available. The mechanisms for coexistence of potential competitors in a stable environment include superabundant food resources (Holmes and Pitelka 1968) and niche differentiation, in which differences in selection of prey species or size minimize dietary overlap (Zwarts and Ens 1999, Scheiffarth 2001). Shorebirds are ideal subjects to test this principle because they often forage in mixed flocks (Piersma et al. 1996) and their diets can be quantified through direct observation and fecal dropping analysis (Dekinga and Piersma 1993). Many studies have demonstrated prey selection or prey-size preference in shorebirds, but the focus has often been on single species (Zwarts and Blomert 1992, Moreira 1994, Piersma et al. 1994, Tulp and de Goeij 1994, Zwarts et al. 1996), missing a community perspective of how closely related predators coexist. In studies that have taken a community approach, results have been inconsistent. There was little evidence of niche differentiation in prey size in shorebirds in inland wetlands of North America during migration stopovers (Davis and Smith 2001). By contrast, different prey or prey-size selection among shorebirds was found in coexisting shorebirds during southward migration stopovers in Nor-

way (Lifjeld 1984) and during the nonbreeding period in the Netherlands (Zwarts and Ens 1999) and Australia (Dorsey 1981). Differences in reported prey selection are probably attributable, in part, to the different body sizes or bill lengths of shorebirds, with larger predators generally taking larger prey that are often buried deeper in the sediment (Zwarts and Ens 1999).

Here, we evaluate the degree of dietary overlap in the dominant shorebird species during northward migration at Dandong Yalu Jiang Estuary Wetland National Nature Reserve in the northern Yellow Sea, China. This is one of the most important stopover sites for shorebirds in Asia, with an estimated 250,000 shorebirds using the site during northward migration (Riegen et al. 2014), including 66,000 Bar-tailed Godwits (*Limosa lapponica*) and 44,000 Great Knots (*Calidris tenuirostris*; Choi et al. 2015). Given that the diets of the main species overlap in general terms—bivalves are taken by Eurasian Oystercatchers (*H. ostralegus osculans*), Great Knots, and Bar-tailed Godwits, and polychaete worms by Eurasian Oystercatchers and Bar-tailed Godwits (Supplemental Material Appendix A1)—there is considerable potential for competition among these species. We hypothesized that the coexisting shorebirds would show evidence of niche differentiation to reduce levels of competition, with Bar-tailed Godwits and Eurasian Oystercatchers having broader diets dominated by polychaetes whereas Great Knots and Red Knots (*C. canutus*) feed mostly on bivalves. We also explored some of the key properties of the bivalve *Potamocorbula laevis* that make it an especially important prey item for shorebirds at Yalu Jiang.

METHODS

Study Area

The Dandong Yalu Jiang Estuary Wetland National Nature Reserve (39°40′–39°58′N, 123°34′–124°07′E) is located west of the Yalu Jiang estuary, on the Chinese side of the China–North Korea border (Figure 1). The reserve was established in 1987 and designated as a National Nature Reserve in 1997 to conserve the coastal wetland ecosystem and wildlife (Yan 2008). More than 250 species of birds have been recorded, with ≥29 species listed as "Threatened" on the IUCN Red List (Yan 2008, IUCN 2012). The reserve and surrounding area is estimated to support 250,000 shorebirds during northward migration (Riegen et al. 2014), is recognized as an "Important Bird Area" (BirdLife International 2009), and supports internationally important numbers of 24 species of waterbirds (Bai et al. 2015).

The reserve extends ~70 km along the coast and comprises mainly bare intertidal mudflat and small, scattered patches of *Phragmites*-dominated saltmarsh on the seaward side of the seawall (only on the upper tidal flats on either side of the Dayang River), with aquaculture ponds and paddy fields on the landward side—a typical coastal landscape of the Chinese coast (Barter 2002, Ma et al. 2009, Yang et al. 2011, Li et al. 2013, Choi et al. 2014b). The sea freezes in winter and the ice melts in March. The extent of tidal flat exposed during ebb tide varies from ~4 km from the seawall in the middle and west of the reserve, to ~5 km from the seawall in the east (Figure 1).

Benthos sampling and focal bird observations were carried out in a grid in the middle of the reserve between March and May in 2011 and 2012. These areas were chosen because large numbers of foraging shorebirds were present on them during northward migration (Riegen et al. 2014, Choi et al. 2015; Figure 1C).

Study Species

The shorebird species of main interest in our study were the Bar-tailed Godwit, Great Knot, and Eurasian Oystercatcher. They were chosen because they forage in similar areas in high densities, may compete for the same prey, and use the reserve as their most important staging site during northward migration (averaging 19,000 [*L. l. menzbieri*] and 49,000 [*L. l. baueri*] Bar-tailed Godwits, 44,000 Great Knots and 2,400 Eurasian Oystercatchers during the peak of their northward migration between 2010 and 2012; Melville et al. 2014, Choi et al. 2015). Bar-tailed Godwits and Great Knots comprise >50% of the total shorebirds in the study area (Riegen et al. 2014: figure 3.24 and table 3.6). Attention was also paid to Red Knots, which were present in small numbers in 2012. All of the study species have a cosmopolitan distribution except the Great Knot, which is endemic to the EAAF (Piersma et al. 1996). Bar-tailed Godwits tend to be generalist feeders, taking a variety of benthos such as bivalves, crustaceans, and cumaceans, but predominantly polychaetes on the nonbreeding grounds (Piersma 1982, Piersma et al. 1993, McCaffery and Gill 2001, Scheiffarth 2001, Zharikov and Skilleter 2002, Duijns et al. 2013). By contrast, Great Knots and Red Knots are more specialized on bivalves, although other prey such as polychaetes, crustaceans, gastropods, and rhizomes are also taken occasionally (Dekinga and Piersma 1993, Piersma et al. 1993, Tulp and de Goeij 1994, Zhang et al. 2011, Yang et al. 2013, van Gils et al. 2016). Like Bar-tailed Godwits, Eurasian Oystercatchers seem to have a broad diet; they have been seen feeding on mollusks, crustaceans, polychaetes, and, occasionally, insects and fish (Melville et al. 2014).

Benthos Sampling

We set up a 9 km^2 (3 × 3 km) grid at the middle site and divided it into 36 grid cells of 0.25 km^2 (0.5 × 0.5 km) (Figure 1C). Benthos were sampled at the center of each cell once a month between March and May in 2011 and 2012 (a total of 6 times). Another grid with 18 cells from

the eastern site was included in 2012 (each cell was sampled once a month between March and May), but the benthos data obtained were used only in analyzing the burrowing depth of different prey types. In total, 270 benthic core samples were collected. The first sampling was done soon after ice melt and before the peak arrival of migratory shorebirds, and the last sampling was carried out at the end of the migratory period (Choi et al. 2015). One benthos core sample (diameter = 15.5 cm, area = 0.019 m^2, depth = 30 cm) was taken at each sampling station. The top (5 cm) and the bottom (25 cm) layers were sieved separately in the field through a 0.5-mm sieve. All soft-bodied organisms were kept in 70% ethanol, or soaked in 5% formalin for ≥72 hr before being placed in 70% ethanol. Hard-bodied organisms were kept frozen until further analysis. All organisms were identified to the finest practicable taxonomic level using a dissecting microscope. In general, polychaetes were identified to family level, and mollusks and crustaceans to species or genus. Some soft-bodied organisms were broken during collection, but measurements of these specimens were still taken and recorded, with specific notes on whether they contained the head, tail, or body segment.

A subset of benthos, collected from sampling stations and opportunistically, was used to determine the size–biomass relationship (ash-free dry mass; hereafter AFDM). Dry mass was obtained by drying the samples at 60°C for 60 hr, and the ash mass was obtained by incinerating at 560°C for 5 hr. All masses were weighed to the nearest 0.0001 g, and the difference between dry mass and ash mass was the AFDM. Regressions between AFDM and a body-size measure were carried out for each taxonomic group, and the results were used to estimate the AFDM for those samples that were not incinerated, allowing us to calculate the taxonomic-group-specific biomass densities. Flesh was separated from the shell before drying for all bivalves, and only the AFDM from flesh was used to relate different sizes to AFDM. The exception was bivalves shorter than 3 mm, which were too small to separate; AFDM from both flesh and shell were used to give the AFDM for the corresponding size class. Because of its importance in the diet of shorebirds, the size-specific AFDM of *P. laevis* was investigated separately for each month in 2012 (March, April, and May, considered early-, mid-, and late-season, respectively). These relationships between body size and AFDM in different prey types were then used to estimate the total AFDM of different prey types available in different months and years, as well as the biomass intake rates of shorebirds.

Some *P. laevis* were collected from north Bohai Bay (39°04′08″N, 118°12′10″E, ~500 km west of Yalu Jiang) opportunistically in May 2012, and these were processed in the same way described above, to provide information on potential differences in the flesh content of this important prey for shorebirds at different stopover sites (Yang et al. 2013).

Focal Sampling of Shorebirds

Shorebird focal observations were conducted within the benthos sampling grid at the middle site between March and May in 2011 and 2012 (97 observations were made of Bar-tailed Godwits between March and May in 2010, but these data were used only in analyzing the handling time per prey item). A focal bird was chosen randomly from a flock of foraging birds and watched for 5 min, using a 20–60× telescope. All observations were carried out by C.-Y.C. and D.S.M., with regular exchanges on any abnormal findings, and an effort was made to alternate observations between Great Knots and male and female Bar-tailed Godwits, to minimize sampling bias. Individually marked birds were noted to minimize repeated sampling, which was further minimized by the large number of birds in the reserve in relation to the numbers sampled (932 Bar-tailed Godwits in 3 yr, 322 Great Knots in 2 yr). Observations were initiated for actively foraging birds only, but the observation continued even if the focal bird stopped foraging during an observation bout. In 2012, large numbers of Eurasian Oystercatchers were present in the study site, and observations were made of this species (n = 43) and also of Red Knot (n = 18) (though the latter was uncommon).

Before the start of each 5 min observation bout, the date, time, estimated location (based on the benthos grid map), breeding plumage score of the focal bird (Piersma and Jukema 1993), and number of conspecifics within 50 m were noted. During each observation bout, activities and events such as pecks, probes, prey items swallowed, and interference with other birds were recorded on a digital voice recorder (for a detailed explanation of different behaviors, see Supplemental Material Appendix A2). The digital sound files were then transcribed using JWatcher 1.0 (Blumstein et al. 2006), which allowed us to quantify the amount of time a bird spent on different activities. Swallowed prey items were categorized into 8 groups, namely bivalve (except razor clam), crab, gastropod, ghost shrimp, razor clam, polychaete, sea anemone, and unknown. Bivalve prey were further divided into "whole" (bivalve prey were swallowed whole) and "flesh" (only the flesh was taken; in 2012 many bivalves were gaping on the surface, and shorebirds could access the flesh without having to open the shells). It was sometimes impossible to see ghost shrimps and small worms when they were taken, but the behavior of predators when consuming these was quite distinctive, and their consumption could be confirmed by inspection of fecal droppings afterward, as well as by knowledge of benthos within the grid cell. Small polychaetes were likely to have been taken if prey items were repeatedly pulled out and swallowed from the same

TABLE 1. Numerical intake rates (prey per minute) of 4 shorebird species at Dandong Yalu Jiang Estuary Wetland National Nature Reserve, China, based on focal observations. Abbreviations: BAGO = Bar-tailed Godwit, GRKN = Great Knot, EUOY = Eurasian Oystercatcher, and REKN = Red Knot.

Year	Species (sex)	Sample size	Bivalve	Sea anemone	Polychaete	Gastropod	Crab	Ghost shrimp
2011	BAGO (all)	77	11.5 ± 11.97	0.01 ± 0.05	0.44 ± 0.7			0.23 ± 0.81
	BAGO (female)	36	8.86 ± 10.98		0.37 ± 0.51			0.28 ± 0.95
	BAGO (male)	35	13.67 ± 12.18	0.01 ± 0.07	0.47 ± 0.83			0.21 ± 0.71
	GRKN	37	6.93 ± 7.13		0.01 ± 0.03			
2012	BAGO (all)	181	1.81 ± 2.13	0.01 ± 0.06	0.6 ± 1.02		0.01	0.06 ± 0.24
	BAGO (female)	84	1.32 ± 1.75	0.02 ± 0.06	0.6 ± 0.95			0.08 ± 0.29
	BAGO (male)	90	2.16 ± 2.32	0.01 ± 0.07	0.56 ± 1.02		0.02	0.04 ± 0.19
	GRKN	172	1.61 ± 1.09			0.01 ± 0.06	0.02	
	EUOY	40	4.41 ± 2.74			0.02 ± 0.08		
	REKN	14	1.65 ± 0.85					

hole (capitellid and maldanid polychaetes were the most commonly broken taxa during benthos sampling). In addition, the motion of pulling a polychaete out was also slower, and exhibited tension, compared to when the prey was a ghost shrimp. Any swallowed prey item that was not seen or deduced with confidence was recorded as unknown.

Dietary Assessment and Prey-size Selection

Diet composition was determined from swallowed prey items recorded during focal observations in all 4 shorebird species. The relationship between the body size and AFDM of prey (see previous section) provided an estimate of AFDM per prey item swallowed. The average AFDM per prey item sampled per year for gastropods, shrimps, crabs, and sea anemones was treated as the AFDM obtained when a focal bird swallowed any of these 4 prey types. More precise AFDM estimates were obtained when birds took polychaetes and bivalves (dominated by *P. laevis*).

Data for different polychaete groups were pooled to obtain an overall AFDM–size relationship formula because it was impossible to identify polychaete species from focal bird observations. The size of polychaetes taken by focal individuals was divided into short, medium, and long, depending on its length in relation to the bill length of the focal bird (Supplemental Material Appendix A3). The average bill lengths of the different shorebird groups were obtained from banding records at the study area (Z. Ma personal observation). Therefore, different AFDM values for polychaetes could be obtained, depending on the shorebird group and year.

Among *P. laevis*, mean sizes taken by different shorebird groups were estimated from droppings and prey remains. These were collected on an opportunistic basis from places where birds were seen foraging for ≥30 min, and the samples from each foraging period were often pooled into one bag (sample sizes are presented in Table 1). Droppings from different species were distinguished mostly on the basis of the size of the dropping and the footprints near the dropping. Eurasian Oystercatchers are larger than Bar-tailed Godwits, and they seldom foraged in the same area at the same time. Great Knots are intermediate in size between Bar-tailed Godwits and Red Knots, but Red Knots were much less common (~100 birds) than Great Knots (44,000). Consequently, we collected very few droppings from Red Knots, and all of these were collected soon after a focal bird was observed defecating. Droppings collected in the field were kept frozen and later oven dried at 60°C for ~2 days before analysis. Samples were sorted under an Olympus SZX7 dissecting microscope. Identifiable prey items retained in the droppings were grouped into different taxonomic categories based on jaws of polychaetes, hinges of bivalves, whorls of gastropods, and pereopods of ghost shrimps and crabs. We counted 4 jaws as equal to a single individual *Glycera chirori* (because most of the jaws found in droppings were *G. chirori*, which has 4 jaws per individual) and 6 "plier-shaped" pereopods as one ghost shrimp (because most of the ghost shrimps have 3 pairs of pereopods that are plier-shaped). The size range of *P. laevis* taken by shorebirds was assessed through dropping analysis and collection of prey remains. For shorebirds that swallowed *P. laevis* whole, hinges (measured either by a graticule in the eyepiece or by using the image analysis software cellSens; Olympus, Tokyo, Japan) in droppings were used to estimate the length of the ingested shell by regressing shell length on height of left hinge ($n = 371$, $R^2 = 0.96$). For shorebirds that took only the flesh out of *P. laevis* without swallowing the shell, the size of *P. laevis* taken was estimated by measuring the lengths of *P. laevis* left on the mudflat surface after feeding.

The proportion of different size classes obtained each month, based on droppings, were fitted into the AFDM–size relationship formula to estimate month-specific AFDM per *P. laevis* for each size class for April and May in both

years, corresponding to the focal observation periods. The monthly weighted average AFDM values of 2 size classes (<10 or ≥10 mm) taken by Bar-tailed Godwits and both knots were then estimated. This gave us the biomass contribution of young and adult *P. laevis* to the diets of different shorebird groups at different times. When only the flesh of *P. laevis* was taken, the AFDM was extrapolated by fitting the average size (based on prey remains) to the AFDM–size relationship, but the AFDM was then multiplied by the average proportion of flesh taken, which was estimated by ashing the *P. laevis* remains left over by different shorebird groups. The *P. laevis* remains from Great Knots and Red Knots could not be collected, so we assumed these to be the same as for Dunlin (*C. alpina*), a species of similar bill length that we were able to collect fed-upon shells from ($n = 107$ shells). The relationships between AFDM and body size in different benthos groups are summarized in Supplemental Material Appendix A3. For unidentified prey items, the overall average AFDM per individual benthic item collected in that particular period was used.

Data Analysis

Food selection. Food selection by shorebirds was calculated using compositional analysis, which is an application of multivariate analysis of variance on discrete variables (Aebischer et al. 1993, Manly et al. 2002). Individual shorebirds observed during focal observations were treated as replicates, and only observations that lasted ≥2.5 min and for which all prey items were identified are included in this analysis.

Following Manly et al. (2002), d_i (the difference between the relative use and availability of prey i and j for the i^{th} individual bird) was calculated as

$$d_i = \log_e(o_{ui}/\pi_{ai}) - \log_e(o_{uj}/\pi_{aj})$$

where o_{ui} is the estimated proportion of prey type i used and π_{ai} is the available proportion of prey type i. Zero values in rare prey-type availability or use were replaced by 0.00001 when calculating d_i to allow logarithmic calculation to proceed (Aebischer et al. 1993, Warton and Hui 2011). Prey types that were unused were excluded in the analysis. Wilks's lambda test was used to test whether the mean vector of d (d_1, d_2, … d_{D-1}) was different from a vector of zeros, where D is the number of prey types available. The mean of d_i for all focal individuals would be significantly different from zero in the presence of prey selection. Significant results were followed by paired t-tests to compare the difference between prey types (Manly et al. 2002).

Size selection of *P. laevis*. In our investigation of *P. laevis* size selection among different shorebird species, prey use and availability were compared at the population level because droppings were pooled during collection (Manly et al. 2002: design 1). The selection ratio for *P. laevis* size class i in different shorebirds was calculated as

$$\hat{w}_i = \frac{u_i/u_+}{A_i/A_+}$$

where u_i/u_+ is the sample proportion of used *P. laevis* belonging to size class i, and A_i/A_+ is the proportion of available *P. laevis* in size class i. Manly's standardized selection ratio was calculated as

$$B_i = \hat{w}_i/(\sum_{i=1}^{I} \hat{w}_j)$$

where I is the total number of possible size classes. A selection ratio equal to $1/I$ denotes the absence of selection, a ratio larger than $1/I$ denotes selection, and a ratio less than $1/I$ denotes avoidance (Chesson 1978). Manly's standardized selection ratio gives an estimated probability that each *P. laevis* size class would be the next one selected if all the size classes were equally available to the birds, which allows direct comparison between size classes.

In addition to the descriptive approach using selection ratios, a chi-square goodness-of-fit test was adopted to test the null hypothesis of no difference between proportions of use and proportions available in all *P. laevis* size classes. The test was followed by Bailey's adjusted 95% confidence intervals (CIs) for the proportion of use when the null hypothesis was rejected. Bailey's CIs were used instead of other CIs because the former was less sensitive to small sample sizes and had lower error rates (Cherry 1996).

Prey quality, handling time, and efficiency. To assess the prey quality of individual *P. laevis* of different sizes, we used the formula $Q = d \times a \times \mathrm{AFDM_{flesh}} / \mathrm{DM_{shell}}$, where Q is the prey quality (defined as flesh-to-shell ratio, presented as kJ g^{-1} shell dry mass; van Gils et al. 2003), d is the energetic density of flesh (22 kJ g^{-1} AFDM; Zwarts and Wanink 1993), and a is the assimilation efficiency (0.8; Kersten and Piersma 1987).

Successful handling time is the duration of a handling process that leads to the swallowing of a prey item. We calculated the handling time from focal bird observations between 2010 and 2012 as the time elapsed between capturing a prey and swallowing it. In contrast to other researchers who calculated handling efficiency by taking into account negative handling time (handling that led to rejection of prey), we estimated the handling efficiency only for events in which the prey was successfully ingested. The handling efficiency (profitability) of different prey types for different shorebird groups was calculated using the ash-free dry mass gained per handling time (in seconds) (van de Kam et al. 2004). If the same prey type was taken more than once by a focal individual, the average handling time and efficiency for the particular prey type were used.

TABLE 2. Diet composition of 4 shorebird species, based on analyses of droppings collected in the field in Yalu Jiang coastal wetland in 2011 and 2012. Values are percentages (weighted average) of all identified prey items.

Prey type	Bar-tailed Godwit	Great Knot	Eurasian Oystercatcher	Red Knot
Potamocorbula laevis	64.57 ± 8.05	95.40 ± 9.77	0	100 ± 0
Other bivalve	1.22 ± 1.11	2.05 ± 1.43	50	0
Polychaete	4.02 ± 2.01	0.4 ± 0.64	50	0
Gastropod	0.25 ± 0.51	1.58 ± 1.26	0	0
Ghost shrimp	29.58 ± 5.45	0.08 ± 0.28	0	0
Crab	0.35 ± 0.59	0.49 ± 0.70	0	0
Number of pooled samples	16	37	1	5
Number of droppings	315	692	20	5
Number of individual prey items	1,808	1,962	2	20

TABLE 3. Frequency (percentage of total observations) of multiple prey species being taken by 4 shorebird species at Dandong Yalu Jiang Estuary Wetland National Nature Reserve, China, in 2011 and 2012, during 5 min intake-rate observations (after excluding cases with observation time <2.5 min, with unknown prey type, or with no prey item swallowed during the observation).

	Bar-tailed Godwit					
Number of prey types taken	Female (n = 275)	Male (n = 308)	Unsexed (n = 25)	Great Knot (n = 228)	Eurasian Oystercatcher (n = 41)	Red Knot (n = 15)
1	68	66.2	64	96.9	97.6	100
2	30.2	30.2	36	3.1	2.4	0
3	1.8	2.9	0	0	0	0
4	0	0.6	0	0	0	0

TABLE 4. Prey species selection by shorebird groups on northward migration at Dandong Yalu Jiang Estuary Wetland National Nature Reserve, China, in 2011 and 2012. The ranking of 6 prey types was based on 5 min focal bird observation (sample size in parentheses) and ash-free dry mass of prey. Prey types that were not taken by a species were excluded from analysis. Rank orders were based on the mean d_i values across the focal birds observed, with the highest rank at the top and lowest rank at the bottom. Different superscripts indicate significant differences between prey types (paired t-tests, $P < 0.05$). Abbreviations: Biv = bivalve, Cra = crab, Gas = gastropod, Gho = ghost shrimp, Pol = polychaete, and Sea = sea anemone.

	Bar-tailed Godwit					
Species	Overall (258)	Male (125)	Female (120)	Great Knot (210)	Eurasian Oystercatcher (40)	Red Knot (14)
Rank order	Pol [a] Biv [b] Gho [b] Cra [c] Sea [d]	Biv [a] Pol [a,b] Gho [b] Cra [c] Sea [d]	Pol [a] Gho [b] Biv [b] Sea [c]	Biv [a] Cra [b] Pol [c] Gas [d]	Biv [a] Gas [b]	Biv
Wilks's lambda	0.294	0.226	0.416	0.048	0.333	NA
P value	<0.001	<0.001	<0.001	<0.001	<0.001	NA

Over 1,200 observations were made, and all data from focal observations were used to estimate handling time and profitability, but only those that lasted ≥2.5 min were used in estimating the frequency of multiple prey species. Moreover, cases lasting ≥2.5 min and with all prey identified were used in prey selection and numerical intake-rate analyses. Similarly, only the observations with total foraging time of ≥2.5 min and with all prey identified were used to estimate the biomass intake rate. All analyses were performed with Microsoft Excel. A significance level of 0.05 was used for all statistical tests (2-tailed). Results are presented as means ± SD unless stated otherwise.

RESULTS

Prey Selection

Observations of foraging individuals and analysis of droppings confirmed that the bivalve *P. laevis* was the dominant prey item in the diet of Bar-tailed Godwits, Great Knots, Eurasian Oystercatchers, and Red Knots (Tables 1 and 2), constituting 73–99% of the identified prey items during standardized observations (95–99% of prey swallowed by the knots and Eurasian Oystercatchers were identified; for Bar-tailed Godwits, 68% were identified). Individual Great Knots and Eurasian Oystercatchers typically fed upon just a single prey type during a 5 min

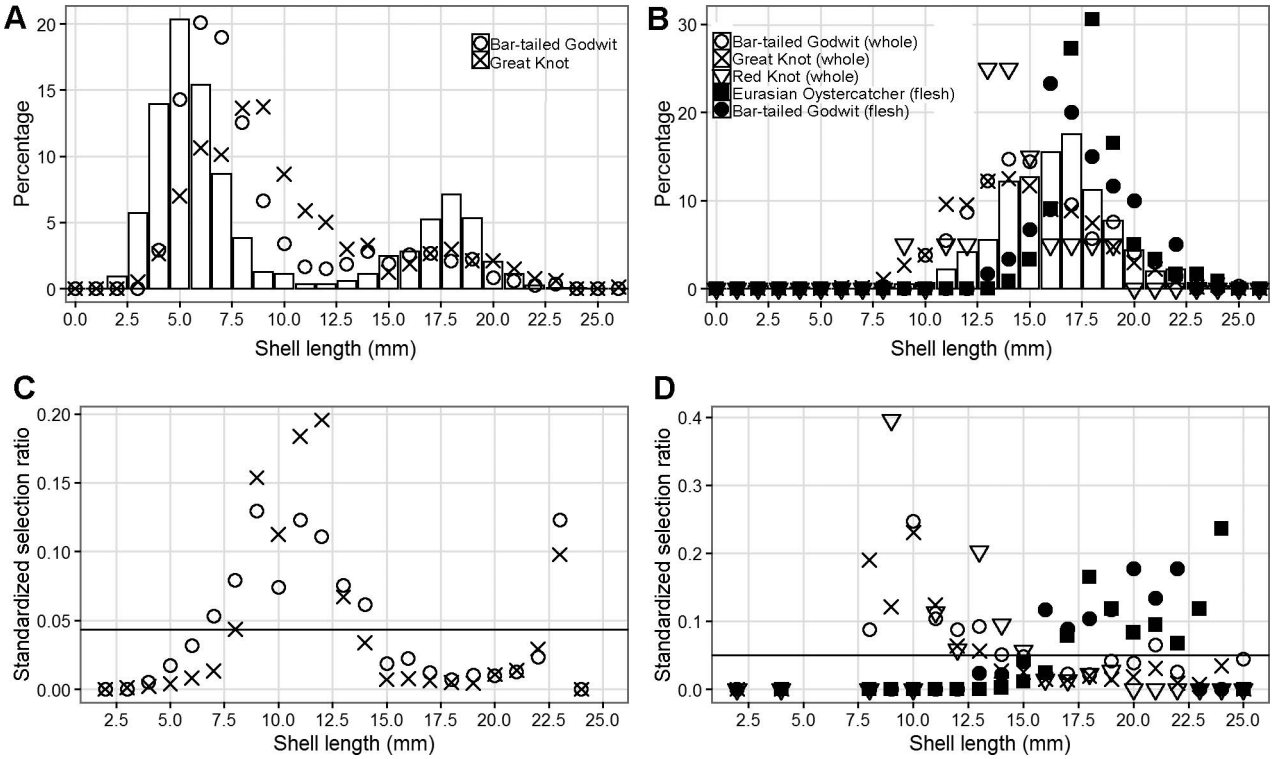

FIGURE 2. Selection of different-sized bivalve *Potamocorbula laevis* by groups of shorebirds at Dandong Yalu Jiang Estuary Wetland National Nature Reserve in 2011 and 2012. The proportions of different-sized *P. laevis* available and taken in 2011 and 2012 are shown in **A** and **B**, respectively; white bars represent availability. Standardized selection ratios of different-sized *P. laevis* in 2011 and 2012 are shown in **C** and **D**. The expected values of random feeding were 0.04 in 2011 and 0.05 in 2012, as represented by the horizontal lines.

observation period, whereas Bar-tailed Godwits more frequently fed upon multiple prey species (Table 3). Bar-tailed Godwits and both knot species swallowed *P. laevis* whole, whereas Eurasian Oystercatchers pried open the valves and extracted the flesh. The different feeding method used by Eurasian Oystercatchers was also reflected in the 20 droppings collected, in which only 2 polychaete jaws and 1 bivalve hinge were found. Occasionally, Bar-tailed Godwits also fed from shells gaping on the surface.

Compositional analysis (taking prey biomass and availability into account) indicated that significant prey species selection was present in all focal shorebird species, with bivalves being selected over other prey by Great Knots, Eurasian Oystercatchers, and Red Knots, bivalves and polychaetes by male Bar-tailed Godwits, and polychaetes by female Bar-tailed Godwits (Table 4).

Size Selection in *P. laevis*

The size composition of *P. laevis* differed markedly between years, with 2 cohorts present in 2011 (Figure 2A) but only one in 2012 (Figure 2B), yet there was clear and consistent *P. laevis* size selection by different shorebird groups in both years. The density of young *P. laevis* decreased from an average of 567 m^{-2} in 2011 to 21 m^{-2} in 2012, while adults increased from an average of 337 m^{-2} to 781 m^{-2}. Knots and the Bar-tailed Godwits that swallowed *P. laevis* whole selected individuals mostly 7–14 mm long, based on the standardized selection ratio (Figure 2C), whereas the Bar-tailed Godwits and Eurasian Oystercatchers that fed only on the flesh of *P. laevis* preferred those with shell lengths of $\geq$15 mm (Figure 2D). Such selection for certain size classes based on standardized selection ratios was consistent with the results from statistical significance tests (95% CIs [Bailey] of taken vs. available proportions; see Supplemental Material Appendix A4).

Prey Properties

Vertical distribution. There was a clear difference in the vertical distribution of different prey types taken by shorebirds. Most of the biomass of bivalves and gastropods was found within the top 5 cm of the sediment surface (88% and 74%, respectively), whereas shrimps and Anthozoa were mainly distributed deeper than 5 cm (97% and 91%, respectively). The vertical distributions of polychaetes and crabs were more or less similar (57.7% and 42.4% within the top 5 cm, respectively). Among the bivalve prey taken by shorebirds, 30% were captured

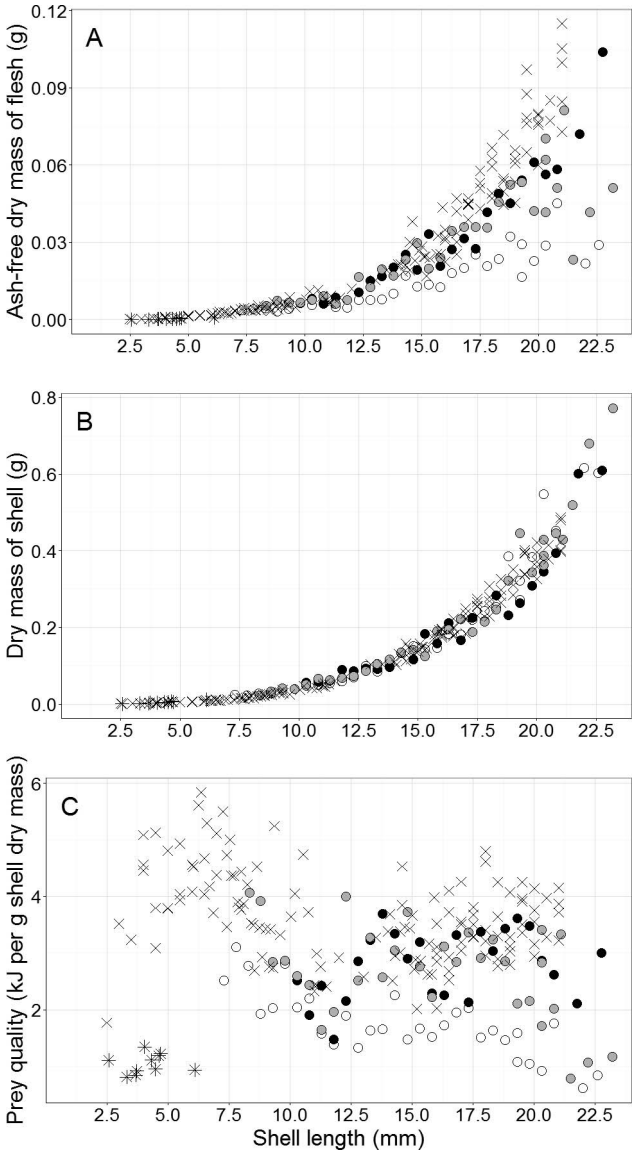

FIGURE 3. Changes in prey properties with shell length in the bivalve *Potamocorbula laevis*: (**A**) flesh mass, (**B**) shell mass, and (**C**) prey quality. Different symbols represent different sample locations and periods: X's denote Yalu Jiang coastal wetland in 2011; for the same location, open circles denote early 2012 (March), gray circles denote mid-2012 (April), and black circles denote late 2012 (May). Stars denote 68 individuals from north Bohai Bay (2012), which are included to show the contrast between study areas (some of these individuals were pooled together during incineration; otherwise the weight differences were not detectable, because of their very small weight).

through pecks and 66% through short probes ($n = 9{,}466$), indicating that most bivalve prey were available near the surface.

Prey quality. The AFDM per *P. laevis* increased with size and also within season across the monthly samples taken in 2012 (Figure 3A). However, because shell mass also increased similarly with length (Figure 3B), the prey quality (energy in relation to shall mass ingested) decreased to approximately 11–12 mm length, after which it remained roughly constant across larger sizes (Figure 3C). Because of the increase in AFDM through the season, the quality also increased from March to May (Figure 3C). The quality of *P. laevis* collected in north Bohai Bay (which were all ≤6 mm) was remarkably lower than that of *P. laevis* collected in Yalu Jiang coastal wetland (Figure 3C).

Handling time and efficiency. Handling time varied substantially between prey types. Bar-tailed Godwits took an average of 1–4.5 s to handle bivalve prey, ~6 s for a sea anemone or ghost shrimp, and 9 s to handle a long worm (Supplemental Material Appendix A5). They rarely spent more than 10 s handling a prey item. The 2 knot species had similar diets and took ~2 s to handle bivalves. Great Knots occasionally fed on gastropods and rarely on crabs, which took an average of 40 s to handle. Oystercatchers fed mostly on "healthy" bivalve flesh, which took an average of 5 s to handle. Like the Great Knots, Eurasian Oystercatchers occasionally fed on gastropods that took >40 s to handle. It was clear that the handling time required for bivalve prey was the shortest across prey types in all shorebird species.

Taking the amount of energy gain into consideration, the handling efficiency for bivalve prey was consistently high among all shorebird groups compared with that for other prey types (Supplemental Material Appendix A6). The handling efficiency for sea anemones and long polychaetes appeared to be even higher, but these prey were less common and the handling efficiencies between focal birds were highly variable.

The biomass intake rates of all shorebird groups were dominated by *P. laevis*, which comprised >90% of the total intake in both knot species and in Eurasian Oystercatchers (Table 5). The contribution of large *P. laevis* to total intake was consistent between years in all shorebird groups, despite total intake rates being substantially lower in 2012 (Table 5). The disappearance of small *P. laevis* in 2012 was, to an extent, replaced in Bar-tailed Godwits by the uptake of bivalve flesh from open shellfish.

DISCUSSION

Our results demonstrate a high degree of overlap in the diet of shorebirds during the northward migration staging period. Despite the subtle differences in their selection for prey type and preference for prey size among coexisting shorebirds, the numerically most abundant Bar-tailed Godwits and Great Knots relied heavily on similar size ranges of a single bivalve species. This indicates that the high food availability, rather than niche differentiation, explains the coexistence of the shorebird community during the 2 yr of the study.

TABLE 5. Biomass intake rates (mg s^{-1} ash-free dry mass [AFDM]) of shorebird groups at Dandong Yalu Jiang Estuary Wetland National Nature Reserve, China, on various prey types, with percentage of total intake in parentheses. Abbreviations: BAGO = Bar-tailed Godwit, GRKN = Great Knot, EUOY = Eurasian Oystercatcher, and REKN = Red Knot.

Year	Species (sex)	Sample size	Total	Bivalve total	Bivalve (whole, small)	Bivalve (whole, large)	Bivalve (flesh)	Polychaete	Sea anemone	Gastropod	Crab	Shrimp
2011	BAGO (all)	74	1.99 ± 1.5	1.64 ± 1.71 (82)	0.44 ± 0.48 (22)	1.19 ± 1.3 (60)		0.28 ± 0.59 (14)	0.03 ± 0.2			0.04 ± 0.14
	BAGO (female)	34	1.73 ± 1.47	1.34 ± 1.68 (78)	0.34 ± 0.44 (20)	1 ± 1.31 (58)		0.33 ± 0.64 (19)				0.05 ± 0.16
	BAGO (male)	34	2.24 ± 1.49	1.9 ± 1.72 (85)	0.51 ± 0.49 (23)	1.39 ± 1.31 (62)		0.27 ± 0.59 (12)	0.05 ± 0.27			0.04 ± 0.12
	GRKN	29	1.8 ± 1.65	1.8 ± 1.65 (100)	0.3 ± 0.32 (17)	1.49 ± 1.34 (83)						
2012	BAGO (all)	170	1.01 ± 0.81	0.77 ± 0.88 (76)	0.01 ± 0.01 (1)	0.63 ± 0.81 (62)	0.13 ± 0.48	0.19 ± 0.38 (19)	0.04 ± 0.17		0 ± 0.01	0.01 ± 0.05
	BAGO (female)	79	0.91 ± 0.69	0.56 ± 0.73 (61)	0 ± 0.01 (1)	0.49 ± 0.66 (53)	0.07 ± 0.38	0.28 ± 0.47 (31)	0.05 ± 0.18			0.02 ± 0.07
	BAGO (male)	84	1.06 ± 0.89	0.92 ± 0.95 (87)	0.01 ± 0.01 (1)	0.71 ± 0.88 (68)	0.2 ± 0.57	0.1 ± 0.21 (9)	0.02 ± 0.17		0 ± 0.01	0.01 ± 0.04
	GRKN	128	0.81 ± 0.48	0.74 ± 0.48 (92)	0.01 ± 0.01 (1)	0.69 ± 0.47 (85)	0.04 ± 0.2			0.07 ± 0.31		
	REKN	10	0.73 ± 0.44	0.73 ± 0.44 (100)	0.01 ± 0 (1)	0.64 ± 0.36 (88)	0.08 ± 0.13					
	EUOY	38	2.7 ± 1.5	2.65 ± 1.55 (98)			2.65 ± 1.55			0.05 ± 0.19		

Food Selection

The bivalve *P. laevis* was the most important prey type for the coexisting shorebird species during their stopover. After taking availability into consideration, Great Knots, Eurasian Oystercatchers, and Red Knots showed strong selection for and fed almost exclusively on *P. laevis*, which was also an important food source for Bar-tailed Godwits. However, the Bar-tailed Godwits had a broader diet with selection for polychaetes. Female Bar-tailed Godwits selected polychaetes more than bivalves, but both of these prey were selected equally by males. Meanwhile, ghost shrimps had a higher selection ranking in female than in male Bar-tailed Godwits. The differences between the sexes may stem from the longer bills of females, which allow them to reach deeper when feeding on polychaetes and ghost shrimps (mean bill lengths at the study site were 84.7 ± 4.8 mm [$n = 51$] in males and 108.1 ± 7.3 mm [$n = 46$] in females; Z. Ma personal observation). The sex differences in prey selection among Bar-tailed Godwits observed here are similar to what has been reported for Bar-tailed Godwits in Europe, where male Bar-tailed Godwits on northward migration seemed to take more bivalves than females (Scheiffarth 2001)—though, because prey availability was not considered, different selection, per se, is not necessarily implied. In addition to the different food selection between species and sexes, the shorebird groups also differed in their prey-size preference, depending on the feeding strategies they used. When *P. laevis* was swallowed whole by Bar-tailed Godwits, Great Knots, and Red Knots, shell lengths of 5–15 mm were preferred; when only flesh was taken by Bar-tailed Godwits and Eurasian Oystercatchers, shell lengths of 15–20 mm were preferred.

Differences in prey-size selection within shorebird communities have been documented in worm-feeding shorebirds in Australia and Argentina, where small-sized shorebird species fed more on smaller polychaete worms than did larger coexisting shorebird species (Dorsey 1981, Martínez-Curci et al. 2015). Similarly, differences in bivalve size selection have been documented in Europe, where Red Knots, Eurasian Oystercatchers, and Eurasian Curlews (*Numenius arquata*) fed on different size classes of sand gaper (*Mya arenaria*; Zwarts and Ens 1999). Oystercatchers on Yalu Jiang coastal wetland had the longest handling time when taking flesh out of *P. laevis* compared to other shorebird groups, which may indicate that Eurasian Oystercatchers were the only group that actively opened up *P. laevis*, whereas other shorebird groups simply scavenged on individuals that were already gaping on the surface or swallowed *P. laevis* whole. The average handling time of 5 s was significantly less than that reported for bivalve-feeding Eurasian Oystercatchers in Europe, which spent ≥16 s when feeding on peppery furrow shell (*Scrobicularia plana*; Wanink and Zwarts 1985).

Why *P. laevis*?

Potamocorbula laevis is clearly the dominant dietary item across a suite of species at Yalu Jiang (Supplemental Material Appendix A1). This implies that it is accessible, detectable, ingestible, digestible, and profitable (van de Kam et al. 2004). Indeed, the general properties of *P. laevis* seem to meet all the requirements listed. They were mostly distributed within 5 cm of the surface, and their siphons left clear traces of holes on the surface of the sediment (C.-Y. Choi personal observation), making them both accessible and detectable for the shorebirds studied. The *P. laevis* in our study area seldom reached a length of >23 mm, which allowed most of them to be swallowed by even Red Knots (Tulp and de Goeij 1994), the smallest shorebird species in the present study. The force required to crush the shell of small *P. laevis* in Bohai Bay was found to be within the range of force required to crush other species of bivalves that were fed on by shorebirds in the Dutch Wadden Sea (Yang et al. 2011). The relatively short handling time with high energy gain compared to some other prey types made *P. laevis* a profitable prey for shorebirds. The short handling time also presumably lowers the chance of interference and kleptoparasitism (van Gils and Piersma 2004), both of which occurred commonly, not only between Bar-tailed Godwits and other species such as Black-headed Gulls (*Chroicocephalus ridibundus*) but among Bar-tailed Godwits themselves (Dann 1987, Boyle and Slaymaker 2010; C.-Y. Choi personal observation). Finally, they occurred in substantially higher densities (mean = 597 individuals m^{-2}; up to 11,270 m^{-2} in some areas) than other prey types (Choi et al. 2014a). This high density and accessibility probably explains why *P. laevis* was taken more than other potentially profitable prey such as sea anemone and long polychaetes.

The occurrence of *P. laevis* gaping on the sediment surface in 2012 was an unusual, and as yet unexplained, event. One possibility is that it was a consequence of environmental factors such as cold winter temperatures that can have an important influence on population dynamics of benthic animals (Beukema 1979, 1982); another is that the shellfish were suffering from parasitism or disease (Burdon et al. 2014). Regardless of the cause, the gaping *P. laevis* provided a supplementary food source for shorebirds in 2012, a year in which the prey quality and abundance of small individuals were substantially lower than in 2011. However, given that the "healthy" *P. laevis* were consistently selected in both years and only a small proportion of biomass intake came from surface-gaping *P. laevis* (at most, 13% in Bar-tailed Godwits in 2012; Supplemental Material Appendix A6), it is unlikely that the gaping *P. laevis* changed the prey selection of the shorebirds studied.

Why Medium-sized *P. laevis*?

Bar-tailed Godwits, Great Knots, and Red Knots showed a preference for medium-sized *P. laevis*, even though they took mostly small *P. laevis* when available (in 2011) and gained most of their energy from large *P. laevis* in both years of the study (Table 5). The long searching times that would be required for medium-sized *P. laevis* given their low abundances may explain the relatively low biomass intake of medium-sized *P. laevis* in Bar-tailed Godwits and both knot species. The apparent preference for the least abundant size classes seems paradoxical, but is likely explained by the relative profitability of the various size classes. Shorebirds that swallow prey whole are known to select high-quality prey (i.e. high meat-to-shell ratio; van Gils et al. 2005), and although flesh content of *P. laevis* increased with shell length (Figure 3A), so did shell mass (Figure 3B). The profitability (flesh:shell mass ratio) was highest for small sizes (~5 mm), then decreased to ~12.5 mm and was similar across larger sizes (Figure 3C). The selection of medium-sized shellfish (approximately 8–12 mm) therefore represents a balance between the increased biomass of flesh per shellfish and the processing burden of the larger and heavier shells. The fact that the smallest shellfish (~5 mm) were not taken in proportion to availability, despite their higher flesh:shell ratio, indicates that the relative prey quality alone did not determine size selection in these shorebirds. Other factors, such as processing capacity and handling time, should be taken into consideration to get a better understanding of prey selection.

Our finding that the upper prey-size limit is apparently related to prey quality is in contrast to other studies in which the upper prey-size limit was found to be set by accessibility (deeper burying depth in larger bivalves) or handling ability (gape size of the predators) (Baird et al. 1985, Zwarts and Wanink 1989). On the other hand, when birds preyed upon gaping shells—and, thus, did not have to process the hard shells—they preferred large *P. laevis* that contained higher energy content. It should also be noted that the mean arrival times of Bar-tailed Godwits and Great Knots were the end of March and early April, respectively (Choi et al. 2015), which was 2–3 wk after the first benthos sample was taken and which coincided with an increase in the quality of *P. laevis*.

The selection for different prey types and preference for different prey sizes in the coexisting shorebirds we studied fit with the expectation that individuals attempt to optimize their intake rate. However, such differences might also be inevitable when the morphology of these birds is considered. In addition to the different bill lengths already discussed, the fact that most *P. laevis* are equally accessible to all species seems to suggest that other limiting factors may be in play. Scolopacid shorebirds, including Red Knots and Bar-tailed Godwits, have been shown to have numerous sensory pits in their bill tips to detect hidden prey, which they can locate more efficiently than Eurasian Oystercatchers that lack these organs (Piersma et al. 1998, van de Kam et al. 2004, Cunningham et al. 2013). Shorebirds whose diets are predominantly hard-shelled (including Great and Red Knots) have significantly heavier gizzards for their body mass than species with mixed or soft diets (Battley and Piersma 2005), and gizzard size directly affects the ability to process shell material (van Gils et al. 2003). It is not surprising, then, that Great and Red Knots show such a preference for bivalves that are ingested whole. Bar-tailed Godwits often have a mixed diet of soft-bodied prey such as polychaetes and harder prey such as crabs and bivalves (Piersma 1982, Tulp and de Goeij 1994), and this was true of birds staging at Yalu Jiang. Females, in particular, showed selection for polychaetes and ghost shrimps, even though the bulk of their intake was from bivalves, which presumably reflects the abundance of bivalves during our study. Unlike Bar-tailed Godwits, Eurasian Oystercatchers fed solely on *P. laevis* despite the availability of polychaetes and ghost shrimps. This contrasts with the behavior of oystercatcher species reported elsewhere, in which foraging on polychaetes is relatively more frequent (Eurasian Oystercatcher [*Haematopus o. ostralegus*], Goss-Custard and Durell 1983; Pied Oystercatcher [*H. longirostris*] and Sooty Oystercatcher [*H. fuliginosus*], Lauro and Nol 1995). In Eurasian Oystercatchers, there is evidence that their bill tips may have a larger horny layer of keratin than in Bar-tailed Godwits and Red Knots (Piersma et al. 1998, Cunningham et al. 2013), which may make them more suited to opening the *P. laevis* and only ingesting the flesh, but less suited to detecting prey buried deep in the mud. This indicates that morphological differences could play an important role in the different selection for different prey types and preference for different prey sizes among the coexisting shorebirds.

It is interesting that the same prey type, *P. laevis*, is also an important prey for Red Knots (Yang et al. 2013), and probably for Curlew Sandpipers (*C. ferruginea*) and Great Knots that stage in north Bohai Bay during northward migration (Yang et al. 2016). The substantially lower quality of *P. laevis* in north Bohai Bay compared to those in Yalu Jiang warrants further investigation (Figure 3C). Long-term comparative studies in these 2 sites could provide insights into factors that may have shaped the selection for different stopping sites in shorebird species with similar diet.

Future Studies

Our results demonstrate prey niche partitioning in a coexisting shorebird community at a staging site during northward migration, but such partitioning alone could

not explain the coexistence of the numerically most abundant Bar-tailed Godwits and Great Knots. Their coexistence was enabled by high resource availability rather than by niche differentiation, as reflected by their similar prey-size preferences and biomass intake rates. Our finding is consistent with the hypothesis that competition for food in seasonally productive habitats (e.g., breeding grounds, northerly staging sites) has less influence on shorebird community patterns than in wintering grounds because food is often superabundant in the former but not in the latter (Colwell 2010). It is therefore important to control any commercial or unsustainable harvest of *P. laevis*, which is commonly harvested along the Chinese coast because it can be used to feed prawns in aquaculture and poultry and is also used to produce fertilizer (Wei 1984, Wei and Guan 1985, Yang et al. 2016). Studies on the life history and habits, especially natal dispersal, of *P. laevis*, and the contrasting flesh content between Yalu Jiang and north Bohai Bay, will assist in the development of a more thorough conservation plan for shorebirds in the Yellow Sea. Long-term monitoring on how shorebirds respond to changes in *P. laevis* abundance will be interesting and valuable for conservation management, especially for the knots and Eurasian Oystercatchers that rely heavily on *P. laevis*. Investigations on the foraging ecology of Red Knots and other shorebirds such as Far Eastern Curlews (*N. madagascariensis*), Eurasian Curlews, and Black-bellied Plovers (*Pluvialis squatarola*) will create a more complete picture of how these shorebirds coexist in this important staging site during their migration and of the possible role of competitive exclusion in shaping the differential use of staging grounds in Red Knots and Great Knots (Hua et al. 2015). Given the rapid intertidal habitat loss and degradation in the Yellow Sea (Murray et al. 2014, Melville et al. 2016), there is an urgent need to identify not only important staging sites, but also critical feeding areas within staging sites to prioritize conservation efforts.

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Ethics statement: Although no living vertebrates were collected during the study, we still strived to minimize disturbance of the birds when we were in the field.

Author contributions: C.-Y.C., P.F.B., M.A.P., and Z.M. designed the experiments and wrote the manuscript. C.-Y.C. and D.S.M. conducted fieldwork. C.-Y.C. and P.S. conducted laboratory work. C.-Y.C. analyzed the data.

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