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# The Northward Migration Stopover Ecology of Bar-tailed Godwits and Great Knots in the Yalu Jiang Estuary National Nature Reserve, China

A thesis presented in partial fulfilment of the requirements for the degree of

Doctor of Philosophy in Ecology Massey University Palmerston North, New Zealand

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January 2015

To my family and friends,

whose understanding, patience and continual selfless support have allowed me to soar with the birds

#### Abstract

Stopover ecology is the scientific study of the behaviour of migrants, the interrelationships among migrants, and between migrants and their environment, at stopping sites. Many shorebird species are long-distance migrants and require high quality stopping sites to rest and refuel during migration. The suitability of a stopping site depends mostly on food availability, level of competition, and predation or disturbance pressure. Events at stopover may not only affect migration performance, but also the subsequent reproduction or survival, and therefore become the limiting factor for the population sizes of migrants. The stopping sites in the Yellow Sea along the East Asian-Australasian Flyway are used extensively by long-distance migratory shorebirds along the flyway, but very little is known about the stopover ecology of these birds. Moreover, the stopping sites within the Yellow Sea region are under serious threats; some of them are being lost before their importance to shorebirds is fully understood.

In this thesis, my aim was to study the stopover ecology of Bar-tailed Godwits *Limosa lapponica* and Great Knots *Calidris tenuirostris* at an important stopping site in the northern Yellow Sea, the Yalu Jiang coastal wetland, during northward migration between 2010 and 2012. I estimated the number of these shorebirds transiting and their passage dates using repeated counts incorporated with Thompson's modelling approach. I described the type, abundance and characteristics of their benthos resources by benthos sampling. I investigated their dietary compositions, foraging patterns and mechanisms of coexistence by behaviour scans, focal bird observations and faecal dropping analysis. Finally, I studied their predation impact on their main bivalve prey, *Potamocorbula laevis*, using exclosures.

My results indicated that at least 42% of the East Asian-Australasian Flyway's northward migrating *L. l. baueri* godwits, 19% of *L. l. menzbieri* godwits, and 22% of the Great Knots used Yalu Jiang coastal wetland, thereby indicating the importance of the study area to these species. Polychaetes and bivalves numerically dominated the benthic communities, while one bivalve species, *P. laevis*, constituted more than three quarters of total macrobenthic biomass during the study period. Great Knots, Red Knots *Calidris canutus* and Far Eastern Oystercatchers *Haematopus ostralegus osculans* selected mostly the bivalve *P. laevis* while Bar-tailed Godwits had a broader diet and selected mostly polychaetes, even though most of their intake was of *P. laevis*. Moreover, the size of *P. laevis* preferred by godwits and Great Knots overlapped. Their coexistence seems to be enabled by high resource availability rather than niche separation. The different dietary

selections between godwits and knots possibly led to different foraging patterns on the tidal flats. There was clear behavioural evidence that a digestive bottleneck existed in the bivalve-feeding shorebirds. Such digestive constraints of hard-shelled prey, decreased prey quality (amount of energy per dry mass of shell taken), and increased handling and searching time were potential reasons behind a decline in total biomass intake rate in godwits and Great Knots from 2011 to 2012, despite similar numerical and biomass density of their main prey in both years. Finally, there was evidence that predation by shorebirds had a significant impact on the number of *P. laevis* in one of the years studied.

My thesis showed the importance of Yalu Jiang coastal wetland to Bar-tailed Godwits and Great Knots during northward migration. These two species competed for the same bivalve prey and their coexistence in the years of study was enhanced by ample food resources rather than niche differentiation. The lack of young *P. laevis* recruitment in the final year of study and the significant predation impact detected indicated a potential decline in food resources after my study. Long-term monitoring will reveal how these species respond to the changes in prey availability. My study provided important scientific information on the numbers of birds using Yalu Jiang coastal wetland, their prey resource availability, their dietary compositions, and behaviours that are crucial for their conservation management in the reserve and potentially in other stopping sites in the Yellow Sea.

### PREFACE

Ecology is the science which says what everyone knows in language that no one understands. (Elton 1927)

This quote captured precisely how I saw scientific research when I was in the planning stage of my project. Scientific stories on popular science magazines are often well written and capture readers' attention successfully. In contrast, a PhD thesis on the same topic can sometimes be so difficult to understand that it easily deter even the most enthusiastic readers. I remember reading the PhD thesis written by one of the most influential scientists in my field and I kept falling asleep time after time. It was not until I had done all my fieldwork, laboratory measurements, and statistical analyses that I was finally able to appreciate and relate my work to that brilliant scientist's. The most enjoyable way to read ecological research work is perhaps through reading some ecology textbooks that are not only easy to read, but also provide a more general perspective that allows readers to grasp the significance of such work.

Perhaps the other reason why I kept falling asleep was because I had not finalised my research topic at that stage, which meant I did not have the right questions in mind before reading. There were a few potential projects that I might have undertaken. These included the stopover ecology of Bar-tailed Godwits at the Yalu Jiang coastal wetland, stopover ecology of Red Knots at the Gulf of Carpentaria, and the foraging ecology of Wrybills in New Zealand. These are all interesting topics but logistics were extremely difficult at the Gulf of Carpentaria and there were more crocodiles than people living there. Wrybills are adorable but there was more urgency to understand shorebirds' stopover ecology in the Yellow Sea that may contribute to the conservation of shorebirds that have been declining along the whole flyway. Before the start of my PhD project, only two stopping sites in the Yellow Sea (Chongming Dongtan and Bohai Bay) were studied and many stopping sites were shrinking rapidly due to coastal development. Yalu Jiang coastal wetland has been shown to support a significant proportion of shorebirds along the flyway, but we knew nothing about the basic questions such as the function of this place to shorebirds, what food resources are available to the birds, why is it so attractive to shorebirds and what are the threats in this site.

My adventures at the Yalu Jiang coastal wetland were an eye-opening experience, at least for me, who had only seen shorebirds in flocks of hundreds or a few thousand before visiting Yalu Jiang. This thesis will describe the life of some of the hundred thousand shorebirds during their one and a half month stopover at Yalu Jiang, using the language that most, if not everyone, understands (*hopefully*!).

#### ACKNOWLEDGEMENTS

First of all, I have to thank my supervisors Phil Battley, Murray Potter and Zhijun Ma for their patience and support throughout my five years of research. Phil's passion, knowledge and experiences on shorebirds provided very important guidance in my research. Murray's different research expertise and logical mind have improved my research planning, analysis and writing enormously. Dr Ma, my mentor in shorebird study, introduced me to this fascinating field of research ten years ago and has set the excellent work ethic for his students to follow. My research benefited tremendously from their constructive criticisms. I would not be able to follow the shorebirds and complete their annual cycle, from breeding grounds in Alaska, wintering grounds in New Zealand, and stopovers in China, without the support from my supervisors, as well as Richard Lanctot.

Before the start of my first field season, I benefited greatly from the knowledge of the study site shared by the Miranda Naturalists' Trust, especially Adrian Riegen and Keith Woodley, and also from local birdwatcher Qingquan Bai.

My research could not be completed without the help from David Melville, Qingquan Bai, Dezhong Xin, Hebo Peng, Ying Chen, Julia Melville, Peter Brakels, Parinya Sukkaewmanee, Xiaojing Gan, Ning Hua, Yingtai Cai, Xuan Zhang, Chungyu Chiang, Shihhan Hsu, staff from the Yalu Jiang Estuary National Nature Reserve, especially Na Jia and Guangming Zhang, and volunteers from the Miranda Naturalists' Trusts, in both field and laboratory work.

During my research planning, data sorting, data analysis and write-up, I benefited greatly from advices and feedback given by Wenliang Liu, Ken Rogers, Danny Rogers, Hongyan Yang, Ian Henderson, Dianne Brunton, Jim Briskie, Jan van Gils, Zutao Ouyang, Jesse Conklin, Nick Murray, Xiongzhao He, Hebo Peng, Theunis Piersma, Sjoerd Duijns, Alice Ewing, Heather Gibbs, Roger Standen and Clare Morton. I would also like to thank Jesse Conklin for sharing his figure, and Kayla Friedman and Malcolm Morgan for sharing the template used in this thesis.

I am also indebted to The Australasian Wader Studies Group, Chris Hassell and Danny Rogers in particular, the Ornithological Society of New Zealand, Qingquan Bai, for allowing me to examine their count data, Chris Hassell, Clare Morton and Rob Schuckard for allowing me to examine their colour-banding data, and Lee Tibbitts, Rob Gill and the US Geological Survey for allowing me to examine the satellite tracking data. My study in New Zealand was supported by the New Zealand International Doctoral Research Scholarships. I also received financial support from the Institute of Agriculture and Environment (formerly the Institute of Natural Resources), Massey University, Conservation Leadership Programme, Miranda Naturalists' Trust and The Ornithological Society of New Zealand, for field costs and to attend conferences and a short course.

Our current shorebird knowledge along this flyway benefited tremendously from dedicated volunteers and workers, including those no longer with us, Mark Barter and Heather Gibbs. Mark's early counting effort along the East China coast provided very important reference materials for monitoring and research work that follows.

On a more personal note, I am grateful to the inspiration and encouragement I got from my friends, many of them from the Miranda Naturalists' Trust and the Conservation Leadership Programme, in particular, David Melville, Adrian Riegen, Keith Woodley, Gillian Vaughn, Estella Lee, Yufang Gao, Simba Chan and Wah Guan Lim. Their selfless dedication and enthusiasm to conservation or their passions, often reminded me why I am doing what I am doing, especially during periods when I was drained by my research work and losing my head.

Would it be weird to be grateful to the Mother Nature? Not only for supporting our lives but also creating the wonderful world for us to study.

Finally, I would like to thank my family – my parents for sending me to Australia, where I discovered my lifelong passion, giving me the freedom to follow my heart and providing the support and shelter whenever I need; my wife for her patience, understanding, inspiration and 'light of wisdom' that allows even the innocents to shine. I would not be where I am today without them.

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# **Chapter 1. INTRODUCTION: STOPOVER** ECOLOGY

#### **1.1 Animal migration**

Animal migration is the periodic movements of individual organisms to and from a given area, usually along well-defined routes (Allaby 1998). Such movements often take much longer than the normal daily activities (Dingle & Drake 2007) (see Dingle 1996 for more detailed definitions). It is one of the most fascinating natural phenomena and occurs in several different forms. It could be the *annual* migration of the African ungulates crossing the African plain to follow the rains in search of fresh grass; it could be the *one-way* migration in monarch butterflies that fly across North America that forms a multiple-generation round trip; it could also be the diel *vertical* migration of jellyfish in different water depths, from deep ocean floor to the surface (Mills 1983). However, it is the *to-and-fro* migration in birds that involves the return to general breeding areas after a round trip of movements through a succession of non-breeding areas (Dingle & Drake 2007) that is perhaps most studied.

Birds are one of the most popular subjects studied in animal migration due to their visibility and often spectacular migration journeys. This behaviour has been described as a primary adaptation to exploit periodic and temporary resources, allowing the birds to stay in favourable habitat for as much of the year as possible (Alerstam *et al.* 2003; Dingle & Drake 2007; Harrington *et al.* 2002). Therefore, it is not surprising that migration is more common in higher latitudes, where food availability varies greatly through the year (Newton 2008). Among migratory birds, shorebirds stand out as they make the longest non-stop migratory flight record (>11,500 km in 8 days) ever documented in birds and show a wide range of migration strategies between and even within species (Battley *et al.* 2012; Buehler & Piersma 2008; Piersma 1987).

# 1.2 What are shorebirds?

Shorebirds, also known as waders in Europe, form part of the Order Charadriiformes, along with the gulls, terns, skuas and skimmers (suborder Lari) and the auks (suborder Alcae) (Campbell & Lack 1985; Cramp & Simmons 1983; Hayman *et al.* 1986). Functionally, however, the shorebirds are usually treated separately from those groups, and are generally distinguished by their relatively long legs, often long bills, and most importantly, their associations with wetlands and shorelines at some stage of their lifecycles or annual cycles (Ens *et al.* 2004; Warnock *et al.* 2002).

At least 215 shorebird species have been described (Colwell 2010) and their life history characteristics include long life-spans but low productivity, specialised feeding apparatus, and a gregarious and migratory nature (Piersma & Baker 2000). The annual survival rate of adult migratory shorebirds could be between 65–90% (Conklin & Battley 2011b; Milton et al. 2003) and some Bar-tailed Godwits Limosa lapponica, Great Knots Calidris tenuirostris and Greater Sandplovers Charadrius leschenaultii are known from banding data to be over 20 years old (Minton et al. 2008, 2012b; Minton et al. 2007). However, the maximum clutch sizes of migratory shorebirds are only four eggs and fledging rate is low, giving an overall low fecundity (Evans & Pienkowski 1984; Lack 1947). Many shorebird species have special bills for feeding on different prey on intertidal mudflats. The bills of the Oystercatcher Haematopus ostralegus, for example, grows continuously to resist wear so the birds can stab open hard-shelled prey (Ens et al. 2004). The bill of many shorebirds contains sensory organs to detect the vibrations of prey inside the substrate (Gerritsen & Meiboom 1986); some can even detect pressure in the substrate to locate static infaunal prey (Piersma et al. 1998). Shorebirds are often gregarious during the non-breeding season, which is perhaps a mechanism to reduce individual predation risk (Cresswell 1994) and increase the chance of locating profitable feeding patches (Piersma & Baker 2000). About 62% of shorebird species migrate (Warnock et al. 2002). Some are transoceanic and transcontinental long-distance migrants capable of flying 5–8 days non-stop, covering distances between 7,000–11,500 km (Battley et al. 2012; Driscoll & Mutsuyuki 2002; Minton et al. 2011a; Niles et al. 2010).

# 1.3 Annual cycle and adaptations for long-distance flight in migratory shorebirds

The annual life cycle of an adult arctic-breeding migratory shorebird contains many stages, illustrated here for the Bar-tailed Godwit *Limosa lapponica baueri* (Figure 1.1). Adults nest in the arctic tundra during the boreal summer and then move to the coast after breeding to prepare for a transoceanic southward migratory flight from their breeding grounds in Alaska to their non-breeding grounds in Australia or New Zealand. They spend 5–6 months on the non-breeding grounds during which they undergo primary wing moult and prepare for northward migration. In March, adult godwits undertake another transoceanic flight northward from their 'wintering' grounds to stopping areas in Asia, where they spend about 1.5 months refuelling before returning to their breeding grounds in Alaska (Battley et al. 2012; Conklin & Battley 2011a; Conklin & Battley 2012; Conklin et al. 2013; Conklin et al. 2010; Gill et al. 2009). The exact breeding, wintering and stopping grounds, flight distance and routes vary depending on the shorebird species, but the toand-fro, round-trip (same route) or loop (different routes) migration between breeding and non-breeding grounds is typical for many migratory shorebirds. It is also clear from the illustration that a significant amount of time during the annual cycle is spent fuelling or refuelling for the migratory flights.

One of the most remarkable adaptations to the long-distance flight in migratory shorebirds is the phenotypic flexibility, or the reversible changes, of the functional parts in the body of a shorebird. Unlike some migratory landbirds that stop regularly and make short migratory flights, many migratory shorebirds make transoceanic or transcontinental flights that take several days and large energy stores to complete. Comparisons between the body masses of Bar-tailed Godwits and Great Knots just before departing Australia and New Zealand to those shortly after arriving in China, indicated that some individuals lost more than 50% of their body mass (Battley & Piersma 2005b; Battley et al. 2000; Ma unpublished data). Migratory fuelling is reflected in the changes in the abdominal profile (Wiersma & Piersma 1995). In the extreme case of Bar-tailed Godwits, more than half of their body mass consisted of fat just before their transoceanic flight from Alaska to Oceania (Piersma & Gill 1998). In addition to the changes in appearance, there are significant changes inside the body of a migratory shorebird. A fully functional digestive apparatus allows birds to refuel efficiently and is important when preparing for a longdistance flight. However, the digestive apparatus becomes a burden during the longdistance flight. Indeed, it has been shown that some shorebirds are capable of building up and breaking down their digestive organs and flight muscles at appropriate times to

maximise their feeding efficiency or minimise the burden during long-distance flight (Battley & Piersma 1997; Battley *et al.* 2000; Piersma & Gill 1998; Piersma *et al.* 1999; Piersma & Lindstrom 1997). The *canutus* subspecies of Red Knot for example, decreased their stomach mass by half just before northward migratory departure from Mauritania (Piersma *et al.* 1993c). One of the most important prerequisites for the spectacular long-distance flight and those reversible changes in body parts is an ample food supply in places where shorebirds prepare for migration.



**Figure 1.1** The generalised annual life cycle of an adult arctic-breeding migratory shorebird, using Bar-tailed Godwits *Limosa lapponica baueri* as an example (adapted from Conklin *et al.* 2013). The average body masses are presented for males (first value) and females (second value) (Battley PF unpublished data; Ma ZJ unpublished data; Higgins & Davis 1996).

Another common feature for many long-distance migratory shorebirds is their reliance on wetland habitats at some stage in their annual life-histories. In the case of *baueri* godwits, despite the vast distances they cover every year, they spend most of their time on coastal intertidal mudflats except for the two months of nesting when they use the tundra habitat. However, productive coastal intertidal mudflat habitat is rather scarce which means large proportions or even entire populations of a migratory shorebird species occur together at a single site during boreal winter or stopover. A case in point would be the stopover of *canutus* subspecies of the Red Knot which stopover in the Wadden Sea (Davidson & Piersma 1992), *rufa* Red Knots which stopover in Delaware Bay (Piersma & Baker 2000), and the endangered Spoon-billed Sandpipers *Eurynorhynchus pygmeus* and Nordmann's Greenshank *Tringa guttifer* which stopover along the Jiangsu coast (Tong *et al.* 2014).

#### 1.4 Coastal intertidal mudflat

Coastal intertidal mudflat is a dynamic ecosystem strongly influenced by the tidal cycle. This is part of the critical transition zones between land, freshwater habitats, and the sea. It serves important ecosystem functions such as coastline protection, water quality improvement, nutrient cycling, fishery resources, and being the habitat for animals including migratory birds and fishes (Levin *et al.* 2001). The formation and extent of the intertidal mudflat is often associated with tidal range and depends mainly on sediment supply, which usually comes from adjacent rivers, offshore deposits and erosion of coastal sedimentary deposits and cliffs (Wang *et al.* 2002). Unlike the terrestrial or marine habitat, there are very few mammalian carnivores specialised to live on the coastal intertidal mudflats. Exceptions exist but none of them have the specialised bills and sensory organs of shorebirds, to locate and process the infaunal benthos resources buried in the substrate. This opened up a niche for migratory shorebirds to exploit, until humans moved into and started exploiting these sites several thousand years ago.

Water is the source of life and many ancient human civilizations began along rivers and coastal areas. It was estimated that more than 1/3 (39%) of the global human population lived within 100 km of the coast in 1995 (Burke *et al.* 2001), imposing enormous pressure on the fragile coastal intertidal mudflats, which are important habitats for migratory shorebirds. Due to the rich food resources on the intertidal flat, the habitat is extremely important to the livelihood of humans, who regularly harvest and cultivate seafood products such as fishes, crustaceans and molluscs (C.-Y. Choi pers. obs.; Reid *et al.* 2008). Apart from the human activities on the coastal intertidal mudflats, these areas have also been converted for farmland, fishponds, salt pans and infrastructure development. In fact, the analysis of satellite images of 14 river deltas worldwide indicated an irreversible loss of 52% of delta plain wetland in the last 10–20 years (Coleman *et al.* 2008). Similar analyses reported that the rate of coastal intertidal mudflat loss in some areas such as the Yellow Sea, where up to 65% of tidal flat was lost over the past 50 years, comparable to the losses that have occurred in tropical forests (MacKinnon *et al.* 2012; Murray *et al.* 

2014). Therefore, it is not surprising that three times as many populations of shorebirds are in decline as are increasing (International Wader Study Group 2003). Habitat loss or deterioration in the stopping sites for long-distance migratory shorebirds has been regarded as one of the main causes of such decline (Baker *et al.* 2004; Moores *et al.* 2008; Rogers *et al.* 2011).

## **1.5 Stopover ecology**

Stopover ecology is the scientific study of the behaviour of migrants, the interrelationships among migrants, and between migrants and their environment, at stopping sites (Allaby 1998; Newton 2008). This field generated increasing interest at the turn of the 21<sup>st</sup> century, partly due to the latest developments in tracking devices that allow researchers to track the entire migration route, thereby locating the stopping sites, and partly because of the realization that changes *en route* may lead to the decline of migratory birds (Moore 2000; Newton 2008). Stopping sites allow migratory birds to refuel, rest, moult (Warnock 2010) and even repair muscle damage (Guglielmo *et al.* 2001). Stopping sites were further differentiated into stopover and staging sites to recognise their ecological and conservation values. While all stopping sites that birds use during migration are stopover sites, only those with ample food resources that allow birds to acquire substantial fuel stores for next migratory flight, without which significant fitness costs would be incurred, should be regarded as staging sites (Warnock 2010).

The stopover period is an important annual life-history stage for migratory birds because they need to obtain more food than usual during stopover to accumulate enough fuel for their next migratory flight. Indeed, the highest fuelling rate for Red Knots (*C. c. rufa, C. c. canutus* and *C. c. islandica*) during their annual life-history stage was found in the final staging site during northward migration, just before flying to their breeding grounds (Piersma *et al.* 2005). Taking the time and energy during preparation into account, 90% of the time and 60% of the energy used on migration occurred at stopping sites (Lindström 2005). After leaving their main wintering ground, *baueri* and *menzbieri* Bar-tailed Godwits spent large proportions of time staging (47.5 and 69.5%, respectively, Battley *et al.* 2012). Migration schedules become tighter as birds get closer to the breeding grounds, which means that birds face greater time constraints and are under greater pressure to refuel quickly (Battley *et al.* 2004; Clark *et al.* 1993; Conklin *et al.* 2013). The importance of staging sites to migratory shorebirds is even more substantial because suitable and productive staging sites are scarce. Moreover, the staging sites may be used by large

numbers of waterbirds at the same time, leading to intense competition and potential food depletion. Therefore, the acquisition of adequate fuel during the limited time frame at staging sites could be an important constraint on the success and timing of migration (Newton 2008).

Fuel and nutrients gained during the final staging site before arriving on the breeding grounds are not only important for the migratory flight, but also for reproduction and survival after arriving on the breeding grounds (Newton 2008). It was shown that about three quarters of Great Knots, Red Knots and Red-necked Stints *C. ruficollis* captured at their final staging sites in Bohai Bay and Yalu Jiang coastal wetland during northward migration, carried more fuel than would be enough for a non-stop flight to their breeding grounds (Hua 2014). Such additional body stores carried from the final staging area played an important role in the survival of Red Knots *Calidris canutus islandica* after arrival on breeding grounds in Greenland (Morrison *et al.* 2007). Although the nutrients for egg formation in arctic-breeding shorebirds are derived mainly from local resources (Klaassen *et al.* 2001), some endogenous nutrients acquired from staging or wintering grounds are also used; the extent may vary depending on year, climatic conditions (Hobson & Jehl 2010; Morrison & Hobson 2004), and time of breeding and arrival at breeding grounds (Yohannes *et al.* 2010).

Studies at stopping sites indicated that individual Bar-tailed Godwits and Semipalmated Sandpipers *C. pusilla* that were able to refuel to higher levels were more likely to survive (Drent *et al.* 2003; Pfister *et al.* 1998). Meanwhile, it was shown that food shortage at a northward migration staging ground (Delaware Bay) led to an increasing proportion of Red Knots *C. c. rufa* that failed to reach the threshold departure mass, which lowered the annual survival of adults by 37% and the recruitment by 47% (Baker *et al.* 2004). Similarly, it was speculated that a drastic decrease in prey quality at staging sites might have led to a strong decline in Red Knots *C. c. canutus* that winter in west Africa (Piersma & Baker 2000). The worst impact thus far would be the near-extinction of Eskimo Curlew *Numenius borealis* due to hunting and destruction of habitats at their spring staging sites (Gill *et al.* 1998).

Despite the flexibility in controlling their body parts, migratory shorebirds seem to have limited ability to shift their migratory routes and move to alternative staging sites. It has been shown that some migratory shorebirds have very high site fidelity and returned to the same staging site year after year (Battley *et al.* 2012; Gudmundsson & Lindstrom 1992; Hassell *et al.* 2013). Therefore, it was not surprising that the loss of the most important northward migration staging ground in Saemangeum, South Korea, led to an 80% decline in the local Great Knot population as well as a possible 24% decline of the entire Great Knot population along the flyway (Moores 2012; Rogers *et al.* 2011).

In short, events at stopover may not only affect migration performance, but also subsequent reproduction or survival; these can become the limiting factor for the population sizes of migratory birds (Moore *et al.* 2005; Newton 2008), although more careful evaluation and detailed research are urgently needed (Harrington *et al.* 2002).

#### 1.6 Foraging studies on stopovers

The suitability of a stopping site depends mostly on food availability, level of competition, and predation or disturbance pressure (Moore 2000; Newton 2008). Therefore, foraging studies of shorebirds at stopping sites are particularly important. The shorebird ecology in the Dutch Wadden Sea is one of the most studied in the world and the location is an important stopover and wintering areas for shorebirds (Boere & Piersma 2012). Long-term studies on the macrozoobenthos in the Dutch Wadden Sea indicated that the seasonal and annual variation in macrozoobenthos accessible to shorebirds was much larger than the variation in numerical density, partly due to the change in burrowing depth and body condition between seasons (Zwarts & Wanink 1993). In other words, shorebirds need to adjust their dietary intake when prey availability changes.

Optimal foraging theory assumes that foragers should forage in a way that maximises their intake rate, which is generally used as a surrogate for fitness in foraging studies (Scheiner & Willig 2011). This explained why some shorebirds such as Oystercatchers Haematopus ostralegus and Red Knots C. c. canutus in the Dutch Wadden Sea avoided small-sized shellfish in studies that compared the size of shellfish taken to those available (Zwarts & Blomert 1992; Zwarts et al. 1996a). Exceptions have been documented in Red Knots C. c. piersmai and C. c. rogersi in Bohai Bay, China, where seemingly unprofitable small-sized shellfish were almost exclusively taken probably because of the small forces required to crush them, which allowed a high processing rate (Yang et al. 2013). Experimental studies indicated that shorebirds such as Oystercatchers and Red Knots were versatile and continued to make trade-off decisions regarding to which prey to take to maximise intake rate during feeding (van Gils et al. 2005b; Wanink & Zwarts 1985). However, the maximum intake rate may not be sustained for an entire tidal cycle as birds are forced to slow down their intake and to make more digestive pauses, when the intake rate exceeds the food-processing rate (Zwarts et al. 1996b). This was particularly applicable to Red Knots, which are bivalve-specialists that swallow bivalves whole and therefore, have a digestive processing rate that depends on the amount of shell mass per prey (van Gils *et al.* 2003). Through the studies on Red Knots, prey quality was found to be an important pre-requisite for the stopping sites selected by this species worldwide, it was further suggested that Red Knots may adjust their time of migration to coincide with the peaks of local prey quality at their stopping sites (van Gils *et al.* 2005a). There is growing evidence that digestion rate could affect the prey selection (van Gils *et al.* 2005b), patch choice (van Gils *et al.* 2005c) and flock size in shorebirds (van Gils & Piersma 2004).

#### **1.7 The East Asian-Australasian Flyway**

A flyway is a conceptual division that encompasses the entire range of many migratory bird species that overlap in the areas where they move on an annual basis, including breeding, non-breeding and stopover areas (Boere & Stroud 2006). One of the major functions of the flyway concept is to simplify the complexities of migration and to enhance international collaboration and cooperation between countries within the same flyway, to aid the conservation of migratory birds and the wetlands they rely on (Boere & Stroud 2006). Eight flyways for shorebirds have been recognised globally including the East Asian-Australasian Flyway (hereafter EAAF) (Boere & Stroud 2006), a sandglass-shaped flyway that includes Australia and New Zealand, extends northwards through South-east and East Asia, and stretches beyond the Arctic Circle in Russia and Alaska (USA) in the north. It passes through 23 countries as a whole and includes some of the largest and most influential economies in the world (Figure 1.2a) (Bamford *et al.* 2008).

Compared to other flyways, the EAAF holds the largest number of shorebird populations (79 populations) but also the highest proportion (85%) for which information on numbers and trends of populations are lacking (International Wader Study Group 2003; Stroud *et al.* 2006). This flyway is the home to not only at least 8 million shorebirds of 54 migratory species (Bamford *et al.* 2008), but also 45% of the world's human population (Barter 2002). Thus, the wetlands along this flyway are vulnerable to rapidly expanding social and economic development pressures. The sandglass-shape of the EAAF reflects how the suitable habitats for shorebirds are distributed; these habitats are widely distributed across the wintering and breeding ranges, but all converge around the Yellow Sea during the migration (Figure 1.2b). Despite the large human population along the EAAF, the stopover ecology of shorebirds in this flyway has been poorly studied (Melville & Battley 2006; Wilson & Barter 1998).



**Figure 1.2** Maps showing the locations mentioned in this thesis. a: The East Asian-Australasian Flyway; b: The Yellow Sea, including A - Yangtze River estuary (Chongming Dongtan), B - Laizhou Bay, C - Yellow River delta, D - Bohai Bay, E - Yalu Jiang coastal wetland, F - Ganghwa, G - Kyeonggi Bay (Namyang Bay), H - Saemangeum and I - Isahaya Bay; c: The Dandong Yalu Jiang Estuary Wetland National Nature Reserve in 2012; d: The 36 benthos sampling stations in the middle site (in the middle of each grid square), large circles and triangles denote experimental plots used in 2011 and 2012, respectively; black lines on the tidal flat denote fishnets, light polygons denote channel.

#### 1.8 Yellow Sea

The Yellow Sea, which is a semi-enclosed sea bounded by the Korean Peninsula in the east and China to the west, is strategically positioned at the heart of the EAAF. Shorebird surveys in the last twenty years show that the Yellow Sea region supports at least two million shorebirds during the northward migration, which is about 40% of all the migratory shorebirds along the EAAF (Barter 2002). Despite the importance of this region for shorebirds, very little is known about the stopover ecology of shorebirds and how those stopover sites are used by shorebirds, other than shorebird counts (Melville & Battley 2006; Wilson & Barter 1998). Moreover, the stopover sites within the Yellow Sea region are under serious threat; some of the sites are being lost before their importance to shorebirds is fully understood (Murray et al. 2014). Growing amount of evidence based on count data suggested that migratory shorebirds along the EAAF, especially those rely on the Yellow Sea for stopover or staging, are declining probably due to habitat deterioration in the Yellow Sea (Amano et al. 2010; Moores et al. 2008; Rogers et al. 2011; Wilson et al. 2011). The Saemangeum wetland in the Republic of Korea was once regarded as the most important shorebird site in the country and in the Yellow Sea during migration season (Moores et al. 2008), but it was reclaimed in 2006, before researchers could understand fully how the area was used by shorebirds. If no immediate conservation action is taken, a similar fate will happen to the Bohai Bay region in China, where at least 45% of the Red Knot population in the EAAF stage (Rogers *et al.* 2010).

## 1.9 Study aims

With the aid of light-weight tracking devices and colour-banding or flagging activities, the migration routes and important stopping sites used by different shorebird species along the EAAF has been revealed (Battley *et al.* 2012; Driscoll & Mutsuyuki 2002; Minton *et al.* 2011a; Minton *et al.* 2011b). In contrast to the rapid increase in knowledge on the migration routes and stopping sites, very few on-ground studies have been done to understand the three main factors that define the quality of a stopping site, namely the amount of food supplies, levels of competition and predation or disturbance pressure (Moore 2000; Newton 2008). In fact, even the most basic knowledge on species, habitats and ecosystems remains inadequate in Asia, which prohibits any further assessment to be made based on a strong scientific foundation (McNeely *et al.* 2009; UNDP/GEF 2007a).

Along the EAAF, descriptive dietary information of shorebirds at stopping sites are not uncommon (Kawaji & Shiraishi 1979; Tang & Yu 1996; Zhang *et al.* 2011), but the importance of different prey types for shorebirds cannot be determined unless the relative biomass contributions by different prey types are considered (Dekinga & Piersma 1993). The only quantitative work at a stopping site in the EAAF focused on the Red Knots staging at Bohai Bay, China, during northward migration (Yang *et al.* 2013), and Red-necked Stints staging in Japan (Kuwae *et al.* 2012).

In this study, I studied the stopover ecology of two shorebird species (Bar-tailed Godwit and Great Knot) at an important staging site on northward migration through the northern Yellow Sea. In a range of studies, I estimate the size of the migration population of the species through Yalu Jiang coastal wetland, provide detailed descriptions of the type, amount and characteristics of the benthos resources, and investigate shorebird diet, foraging patterns and predation impact. The overall aim was to better understand how such large numbers of shorebirds coexist at what is unarguably one of the major staging sites in East Asia. Understanding how and why shorebirds favour certain sites, and disentangling the relationship between shorebirds and their food supplies are not only scientifically appealing, but also have significant conservation implications in conserving the staging sites and the shorebirds (Battley 2002; Safran *et al.* 1997), which are both under serious threats along the EAAF (Moores *et al.* 2008; Murray *et al.* 2014; Rogers *et al.* 2011; Wilson *et al.* 2011; Yang *et al.* 2011).

### 1.10 Study site

Fieldwork was conducted in the Dandong Yalu Jiang Estuary Wetland National Nature Reserve (39°40′–39°58′N, 123°34′–124°07′E) and its surrounding area. The reserve is located west of the Yalu Jiang estuary in the northern part of the Yellow Sea, on the Chinese side of the China-North Korea border (Figure 1.2b). It encompasses 814 km<sup>2</sup>, with 20% (160 km<sup>2</sup>) being assigned as the core area; about 360 km<sup>2</sup> is intertidal flat habitat (Ministry of Environmental Protection The People's Republic of China 2013). The reserve was founded in 1987 and listed as a National Nature Reserve in 1997 to conserve the coastal wetland ecosystem and wildlife (Yan 2008). This wetland is regarded as an 'Important Bird Area' (BirdLife International 2009), supporting probably more than 250,000 migratory shorebirds such as Far-eastern Curlews *N. madagascariensis* (IUCN category Vulnerable), Great Knots (IUCN category Vulnerable) and Bar-tailed Godwits during northward migration (Chapter 2; IUCN 2012; Riegen *et al.* 2014). After the loss of

Saemangeum in South Korea, Yalu Jiang coastal wetland became the site that supports the highest density of shorebirds in the Yellow Sea (1,000 birds km<sup>-2</sup> of intertidal area), which is much higher than some of the most important shorebird sites in Europe (Barter & Riegen 2004).

The reserve comprises mainly bare intertidal mudflat with small scattered patches of Phragmites-dominated saltmarsh on the seaward side of the seawall, and with aquaculture ponds and paddy fields on the landward side; this is a typical Chinese coastal landscape (Barter 2002; Choi *et al.* 2014; Li *et al.* 2013; Ma *et al.* 2009; Yang *et al.* 2011). This reserve has many anthropogenic activities that are common to other areas within the Yellow Sea, but it has relatively less development pressure (MacKinnon *et al.* 2012), making it suitable for long-term monitoring. It remains unclear what impacts the extensive anthropogenic activities have on the intertidal ecosystem in the reserve. The aquaculture ponds were used for cultivating sea cucumber, jellyfish, shellfish, prawns, crabs and fish while the bare intertidal mudflat immediately on the seaward side of the seawall was used for farming shellfish. Extensive fishnets up to 2 m high run parallel to the coastline on the intertidal mudflat at the low neap tide water line (c. 3 km offshore), catching mostly fish, crabs and prawns. Shallow water in the subtidal zone is also used for farming shellfish (C.-Y. Choi, pers. obs.).

Tides in the reserve are semidiurnal, with two high and two low tides per day, and macrotidal in amplitude (mean 4.5 m, maximum 6.9 m) (Davies 1980; Wang *et al.* 1986). Tidal flats extend to c. 4 km from the seawall in the west and middle parts of the reserve, but up to 5 km in the east (Figure 1.2c). The supratidal zone in the study area has all been converted to aquaculture ponds and high spring tides completely inundate the mudflat. On neap tides, high-elevation upper tidal flats at some areas in the east and west are not covered at high tide. Drift ice could be found on the tidal flats during boreal winter until thawing in mid- to late March (C.-Y. Choi, pers. obs.). During our study, the boreal winter and spring mean temperatures in Dandong, 30 km northeast of our study area (the nearest city where data are available), were coldest in 2010 (-4.4°C and 7.6°C, respectively), followed by 2011 (-4.0°C and 8.5°C) and 2012 (-3.7°C and 8.9°C). The number of days with snow or ice pellets during the winter prior to sampling followed similar patterns as the temperature, occurring most often in 2010, followed by 2011 and 2012 (13, 11 and 9 respectively) (Tutiempo Network 2013).
# 1.11 Study species

This study focussed on two long distance migratory shorebird species, the Bar-tailed Godwit and Great Knot, both of which have been declining in their wintering ranges along the EAAF (Melville & Battley 2006; Rogers *et al.* 2011; Wilson *et al.* 2011).

The Bar-tailed Godwit is a fairly large, long-legged and long-billed shorebird. Males are usually substantially smaller than the females and develop more extensive reddish breeding plumage than females do before the breeding season (Figure 1.3) (Hayman et al. 1986; Piersma et al. 1996). Five Bar-tailed Godwit subspecies with spatially segregated breeding grounds, different morphometric measurements and plumage characters were proposed (Engelmoer & Roselaar 1998; Tomkovich 2010). The subspecies *baueri* is a large-sized and darkly coloured subspecies that breeds in Alaska and Bering Sea coast of Chukotka, and winters in East Australia and New Zealand (Engelmoer & Roselaar 1998; Higgins & Davis 1996; McCaffery & Gill 2001; Wilson et al. 2007). L. l. anadyrensis are generally smaller than L. l. baueri, and show more contrast in lines on underwing coverts and a lack of contrast in the upper greater secondary-coverts in the males' folded wing (Engelmoer & Roselaar 1998; Tomkovich 2010). L. l. anadyrensis breeds in the Anadyr River basin and along the south part of the Chukotka Peninsula, and part of this poorly-known subspecies potentially winters in New Zealand (Engelmoer & Roselaar 1998; Tomkovich 2010). L. l. menzbieri is an intermediate-sized subspecies that breeds between the Lena Delta and Chaunsk Bay (170°E) in Russia, and winters mainly in western Australia (Engelmoer & Roselaar 1998; Higgins & Davis 1996). This subspecies has a longer bill but shorter wings, as well as a more whitish appearance on the lower back and upper tail coverts than L. l. baueri (Engelmoer & Roselaar 1998; Higgins & Davis 1996; Wilson et al. 2007) (Figure 1.4). L. l. taymyrensis and L. l. lapponica are two European subspecies that do not occur in the EAAF (Engelmoer & Roselaar 1998; Wetlands International 2006).

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**Figure 1.3** The smaller and more reddish male Bar-tailed Godwit in the front, contrasting with the larger and less reddish female behind it (Photo by Phil Battley).



**Figure 1.4** Left – *L. l. menzbieri* from Northwest Australia. Right – *L. l. baueri* from New Zealand (Photos by the Australasian Wader Studies Group and Brent Stephenson)

The Bar-tailed Godwit has become one of the best-known shorebird species among birdwatchers and general public after extensive media coverage on a satellite telemetry study. The satellite tracking work revealed that the Bar-tailed Godwits could fly

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continuously for 7–8 days from Australia and New Zealand to the Yellow Sea on their way north (Battley *et al.* 2012). They refuelled in the Yellow Sea for about a month before continuing their northward migrations towards their breeding grounds in Siberia and Alaska. After breeding, *menzbieri* godwits returned south via the Yellow Sea, whereas Alaskan *baueri* embarked on the longest documented migratory bird flight known – a continuous transoceanic flight across the Pacific Ocean from Alaska to their non-breeding grounds (Battley *et al.* 2012; Gill *et al.* 2009). In light of *baueri*'s record migratory flights, the Bar-tailed Godwit has became a strong candidate for being the 'flagship species' to raise public awareness in wetlands conservation.

Previous studies on Bar-tailed Godwits along the EAAF have been mostly carried out in Australia and New Zealand. These improved our understanding on the subspecies differentiation of the Bar-tailed Godwits (Wilson *et al.* 2007), their foraging ecology (Dann 1979; Evans 1975), moult strategies (Battley 2007; Battley & Piersma 2005b), body composition before northward migration (Battley & Piersma 2005b), migration timing and migration route (Battley 2006; Conklin *et al.* 2010; Gill *et al.* 2009; Wilson *et al.* 2007). The population trends of Bar-tailed Godwit has been well documented in Australia (Kearney *et al.* 2008; Oliverira & Clemens 2009), New Zealand (Melville & Battley 2006; Sagar *et al.* 1999) and its most important staging site in the Yellow Sea – the Yalu Jiang Estuary National Nature Reserve in China, where more than a quarter (84,680 individuals) of the total Bar-tailed Godwit population in the EAAF staged during northward migration (Riegen *et al.* 2014). However, inconsistent population trends were found between wintering grounds and staging grounds, with the former having a declining trend in the last few years (Li *et al.* 2009b) and the latter a stable or increasing population trend (Riegen *et al.* 2014).

The Great Knot (Figure 1.5) is endemic to the EAAF; it breeds in north-east Siberia and spends the non-breeding season mainly in Australia and south-east Asia (Piersma *et al.* 1996). The distribution of Great Knots during the breeding and non-breeding seasons are similar to those of *L. l. menzbieri*, but Great Knots mainly use the eastern Yellow Sea for staging, with large numbers historically known at Saemangeum and Yalu Jiang coastal wetland (Moores *et al.* 2008; Riegen *et al.* 2014). Studies on Great Knots along the EAAF came mainly from their main wintering ground in Northwest Australia, where the moult, behaviour and diet were studied (Battley 2002; Tulp & de Goeij 1994). Their ecophysiology and migration strategies have also been studied in some detail (Battley *et al.* 2000; Choi *et al.* 2009; Hua 2014; Minton *et al.* 2011b).



Figure 1.5 Great Knot in flight (photo by Phil Battley).

The Bar-tailed Godwit tends to be a generalist feeder that take a variety of benthos such as bivalves, crustaceans and cumaceans, but predominantly polychaetes on non-breeding grounds (Duijns *et al.* 2013; McCaffery & Gill 2001; Piersma 1982; Piersma *et al.* 1993c; Ploegaert 2010; Scheiffarth 2001; Zharikov & Skilleter 2002). In contrast, the Great Knot is more specialised on bivalves, although other prey such as polychaetes, crustaceans and gastropods are also taken occasionally (Tulp & de Goeij 1994; Yang *et al.* 2013; Zhang *et al.* 2011).

# **1.12 Research chapters**

My research involved direct field observations and laboratory work. During fieldwork, I conducted field surveys near high tide to model the total number of Bar-tailed Godwits and Great Knots transiting. I also spent extensive amounts of time conducting behaviour scans and focal bird observations to document their foraging patterns and intake rates during low tide. Benthos and dropping samples were collected to understand the food availability and diet of shorebirds. Exclosure experiments were also set up to investigate the predation impact by shorebirds on benthic resources. In the laboratory, I identified, counted and measured the benthos and dropping samples collected from the field. Some of the benthos was incinerated for ash-free dry mass estimation. These data were then used to answer the following key questions in each of the six research chapters in this thesis.

1. How many Bar-tailed Godwits and Great Knots are using Yalu Jiang coastal wetland during northward migration?

2. What benthos resources are there on the intertidal flat at Yalu Jiang coastal wetland and how do they vary spatially and temporarily?

3. How do different species of shorebirds coexist at a single-prey-dominated staging site?

4. How do biotic and abiotic factors affect foraging patterns and intake rates?

5. Does a digestive bottleneck limit intake rates in bivalve-feeding shorebirds?

6. What impacts do shorebirds have on their prey numbers during their short but intense staging period?

Each research chapter was written for publication in a peer-reviewed journal and therefore there is a certain amount of repetition of background and methods across chapters. Additionally, Appendix 1 provides benthic biomass information that was used in the diet and foraging chapters when deriving prey availability and intake rate estimates.

# 1.13 Co-authors

I wrote all parts of this thesis, designed and conducted all the field and laboratory work, and also performed the data analyses. However, seven of my collaborators made significant contributions to my study and warrant co-authorship.

#### Phil F. Battley (Massey University, Ecology Group)

As my primary supervisor, Phil collaborated with me to design my study. He reviewed all the chapters in this thesis and helped proof the published manuscripts. He was involved in my first season of fieldwork and financed part of my field expenses and subsequent costs involved in laboratory work. He also provided some of the equipment that was essential for fieldwork.

#### Murray A. Potter (Massey University, Ecology Group)

As my secondary supervisor, Murray collaborated with me to design my study. He reviewed all the chapters in this thesis and helped proof the published manuscripts. He was involved in my second season of fieldwork. He also provided guidance in statistical analysis.

#### Zhijun Ma (Fudan University, China)

As my external supervisor, Dr Ma collaborated with me to design some parts of my study. He reviewed all the manuscripts written in this thesis and helped proof the publications. He was involved in all three seasons of my fieldwork. He covered the other part of my field expenses, assisted in logistic arrangement and provided some of the equipment essential for field and laboratory work.

#### David S. Melville

David assisted my fieldwork in the second and final field seasons. He helped to conduct bird surveys, focal bird observations, behaviour scans, dropping collection and benthos measurements. Therefore, he is a co–author in Chapters 4, 5 and 6.

#### Ken G. Rogers

Ken wrote the scripts and provided essential guidance for modelling shorebird populations. He also reviewed and helped proof Chapter 2, which he was co-author on.

#### Wenliang Liu (East China Normal University, China)

Wenliang is a taxonomist and provided important guidance in the identification of benthos specimens collected. He is therefore a co–author in Chapter 3.

#### Parinya Sukkaewmanee (Suratthani Rajabhat University, Thailand)

Parinya assisted with dropping analysis in the laboratory to quantify the diets of shorebirds. He is therefore a co–author in Chapter 4.

Chapter 1. Introduction

# Chapter 2. The Importance of Yalu Jiang Coastal Wetland in the North Yellow Sea to Bar-Tailed Godwits Limosa lapponica and Great Knots Calidris tenuirostris During Northward Migration

Choi C-Y, Battley PF, Potter MA, Rogers KG, & Ma ZJ. 2014. The importance of Yalu Jiang coastal wetland in the north Yellow Sea to Bar-tailed Godwits *Limosa lapponica* and Great Knots *Calidris tenuirostris* during northward migration. *Bird Conservation International*. doi: 10.1017/S0959270914000124

# 2.1 Abstract

Bar-tailed Godwits Limosa lapponica and Great Knots Calidris tenuirostris are long distance migratory shorebirds with declining numbers in the East Asian-Australasian Flyway. One of the most important staging sites for these two species during northward migration is Yalu Jiang coastal wetland in the north Yellow Sea. Historical counts have been limited to once a year and conducted at different periods; these yield inadequate data for population monitoring. We estimated the numbers of Bar-tailed Godwits and Great Knots and described their migration phenology during northward migration from 2010–2012 at the Yalu Jiang coastal wetland, using a combination of periodic area-wide counts over the migration period and a modelling approach that estimates passage times and total numbers of birds transiting. The mean arrival date for L. l. baueri godwits was 29 March and mean departure date was 8 May. Corresponding dates were 11 April and 15 May for L. l. menzbieri godwits and 7 April and 14 May for Great Knots. We estimated an annual average of over 68,000 Bar-tailed Godwits and 44,000 Great Knots used the area on northward migration from 2010–2012. Our results indicate that the Yalu Jiang coastal wetland supports on average at least 42% of the flyway's northward-migrating L. l. baueri godwits, 19% of L. l. menzbieri godwits, and 22% of the Great Knots. Comparisons with historical counts conducted during peak migration periods indicate a 13% decline in Bartailed Godwits since 2004 and an 18% decline in Great Knots since 1999. Our results confirm that the study area remains the most important northward migration staging site for Bar-tailed Godwits and indicate that it has become the most important northward migration staging site for Great Knots along the Flyway.

# 2.2 Introduction

Shorebird populations along the East Asian-Australasian Flyway (hereafter EAAF) are among the most poorly known of the different flyways (Stroud *et al.* 2006). Many are declining, mainly due to wetland habitat loss through reclamation (Amano *et al.* 2010; Moores *et al.* 2008; Rogers *et al.* 2011) and *Spartina* invasion (Gan *et al.* 2009). Coastal wetlands in East Asia are particularly vulnerable due to dense human populations and rapid economic development in this region (Barter 2002). More than half of all Chinese coastal wetlands were lost between 1950 and 2000 (An *et al.* 2007) while 75% of the historical tidal flat area in the Republic of Korea was lost by 2010 (Moores 2012); rates of intertidal flat loss show no sign of slowing (MacKinnon *et al.* 2012; Murray *et al.* 2012). These coastal wetlands are important staging areas where shorebirds must stop and replenish their energy reserves so that they can complete their migrations (Battley *et al.* 2012; Choi *et al.* 2009; Hua *et al.* 2013; Ma *et al.* 2013b; Warnock 2010). The loss of Saemangeum, in South Korea, led to significant local population declines in the Spoonbilled Sandpiper *Eurynorhynchus pygmeus* (IUCN category Critically Endangered) and the Great Knot *Calidris tenuirostris* (IUCN category Vulnerable) (IUCN 2012; Moores *et al.* 2008; Rogers *et al.* 2011). On a longer time-scale, little is known about trends in shorebird numbers at staging sites on the Chinese side of the Yellow Sea (but see Ma *et al.* 2009; Rogers *et al.* 2010; Yang *et al.* 2011).

The Chinese side of the Yalu Jiang coastal wetland (hereafter YLJ), located in the north Yellow Sea (Figure 2.1), is known to play an important role during northward migration for Bar-tailed Godwits *Limosa lapponica* and Great Knots, historically supporting more than 100,000 godwits and 55,000 knots (Barter *et al.* 2000; Riegen *et al.* 2014). Surveys on wintering grounds have shown declining trends for Bar-tailed Godwits in north-west Australia and in eastern Australia (Moreton Bay, Queensland) (Rogers *et al.* 2011; Wilson *et al.* 2011). Similar trends were recorded for wintering Great Knots in these two locations, as well as in Corner Inlet, Victoria (Minton *et al.* 2012a; Rogers *et al.* 2011; Wilson *et al.* 2011). Meanwhile, numbers of Bar-tailed Godwits and Great Knots on migration at Saemangeum and adjacent estuaries declined by 11% and 80%, respectively, from 2006–2008 (Moores 2012). There is an urgent need to quantify the current importance of YLJ to these two apparently declining species. Counts conducted at YLJ to date have been limited to once a year, often at different times of the migration period. These data are inadequate indicators of the true numbers of birds transiting the site and need reappraisal.

Bar-tailed Godwits are long-distance migrants, with two subspecies in the EAAF that are distinguishable morphologically in the field: *L. l. baueri*, which breeds in Alaska and spends the non-breeding season mostly in eastern Australia and New Zealand, and *L. l. menzbieri*, which breeds in north-east Siberia and spends the non-breeding season mainly in northern Australia (Battley *et al.* 2012; Engelmoer & Roselaar 1998; Wilson *et al.* 2007). A third, uncommon, Russian-breeding population has been suggested warrants separate status (*L. l. anadyrensis*) but is not considered further here as it is probably both rare and unable to be identified in the field (Engelmoer & Roselaar 1998; Tomkovich 2010). *L. l. menzbieri* and *L. l. baueri* are spatially segregated on their breeding areas and they seldom mix in their wintering ranges (Engelmoer & Roselaar 1998; Wilson *et al.* 2007). However, they do overlap spatially and temporally during northward migration in the Yellow Sea region, although *L. l. menzbieri* seems to predominantly use the western Yellow Sea and *L. l. baueri* mainly the eastern Yellow Sea (Battley *et al.* 2012). YLJ seems to be at the junction

of the ranges of these two subspecies on northward migration. It is estimated that 133,000 *L. l. baueri* and 146,000 *L. l. menzbieri* occur in the EAAF (Wetlands International 2013). The Great Knot is endemic to the EAAF; it breeds in north-east Siberia and spends the non-breeding season mainly in Australia and south-east Asia (Piersma *et al.* 1996). The distributions of Great Knots during the breeding and non-breeding seasons are similar to those of *L. l. menzbieri*, but Great Knots mainly use the eastern Yellow Sea for staging, with large numbers historically known at Saemangeum (Moores 2012) and YLJ (Riegen *et al.* 2014).



**Figure 2.1** Map of Yalu Jiang coastal wetland, showing the 16 pre-roosts counted during censuses. The inset shows the location of Yalu Jiang coastal wetland within the Yellow Sea region. Note that the eastern and western boundaries of the Dandong Yalu Jiang Estuarine Wetland National Nature Reserve were recently adjusted to exclude pre-roosts 1 and 15. The channel east of the ashpond is the western branch of Yalu Jiang, which marks the boundary between China and North Korea.

Shorebird populations in China are usually monitored through monthly synchronised censuses (China Coastal Waterbird Census Group 2009, 2011), with peak counts from these censuses during migration periods often being treated as the total number of birds transiting the area. Such an approach is applicable at non-breeding sites, but not at staging or stopover sites, where some individuals of a species may depart before all have arrived. In this circumstance, the maximum count underestimates the total number of birds passing through the site (Ma *et al.* 2013b; Thompson 1993). Recent attempts to overcome this problem took detection probability, sampled proportion of study area, length of stay or residence probability into account when estimating the number of birds transiting (Cohen *et al.* 2009; Farmer & Durbian 2006). However, a reliable estimate of the length of stay or residence probability often requires radio tracking, unbiased capture-recapture, or resightings of individual birds (Cohen *et al.* 2009; Farmer & Durbian 2006; Frederiksen *et al.* 2001; Matechou *et al.* 2013), and these are not easy to achieve or to apply on large scales for conservation purposes. Some of these modelling estimates tend to be less reliable with small sample sizes (Frederiksen *et al.* 2001) and the ways to estimate stopover duration remain debatable (Efford 2005; Pradel *et al.* 2005).

Here we describe the migration phenology and estimate the numbers of Bartailed Godwits and Great Knots on northward migration at YLJ, using count data collected across three consecutive years (2010–2012). To overcome the analytical issues mentioned above, we modelled numbers of birds and passage times using repeated within-season counts, following the approach of Thompson (1993) (developed in Rogers *et al.* 2010). We also discriminated between the two godwit subspecies by estimating subspecies proportions from photographs of flying flocks across the migration period. We evaluate the effectiveness of different counting approaches (periodic synchronised censuses and regular partial counts) as well as the accuracy of the models, by comparing the passage times obtained from model estimates to those from remote-tracking studies. Sightings of colour-banded individuals were used to provide an independent estimate of the proportion of the flyway population of these two species staging at YLJ.

# 2.3 Methods

# 2.3.1 Study area

This study was carried out in the Dandong Yalu Jiang Estuarine Wetland National Nature Reserve (39°40′–39°58′N, 123°28′–124°09′E, Figure 2.1) and its surrounding area. The study area has been historically referred as Yalu Jiang National Nature Reserve (Bamford *et al.* 2008; Barter 2002), Yalujiang River Estuary Wetland Nature Reserve (UNDP/GEF 2007a), Yalu Jiang Estuary (BirdLife International 2009), Yalu River Estuary Nature

Reserve (Li et al. 2009b), and Yalu Estuarine Wetland Nature Reserve (Ma et al. 2013b). However, there is another reserve, the Yalu Jiang Shangyou National Nature Reserve, located at the upper reaches of the river. For simplicity and clarity, we have used Yalu Jiang coastal wetland to describe the study area. The reserve within the study area was founded in 1987 and listed as a National Nature Reserve in 1997 (Yan 2008). It is located west of the Yalu Jiang estuary in the northern part of the Yellow Sea, near the border of China and North Korea (Figure 2.1). The reserve extends for about 80 km along the coast, with a total area of 101,000 ha, within which 14,082 ha is assigned as the core area (Yan 2008). The coastal area of the reserve is composed mainly of bare intertidal mudflat and sometimes Phragmites-dominated saltmarsh on the seaward side of the seawall, with aquaculture ponds and paddy fields on the landward side, a typical coastal landscape of the Chinese coast (Choi et al. 2014). Aquaculture ponds are used to cultivate sea cucumber, jellyfish, shellfish, prawn and fish while the bare intertidal mudflat is also used for shellfish farming. More than 250 species of birds have been recorded, with at least 29 species listed as 'Threatened' on the IUCN Red List (IUCN 2012; Yan 2008). The reserve was believed to support more than 200,000 shorebirds during the northward migration (Barter et al. 2000). The reserve is regarded as an 'Important Bird Area' but lacks Ramsar recognition (BirdLife International 2009; Ramsar 2012).

# 2.3.2 Bird counts

Tides at YLJ are semi-diurnal, with spring high tides inundating most, if not all, of the intertidal flats. As the tide approaches the seawall, birds are forced to concentrate at pre-roosts – upper intertidal flats that are last covered by tide – before flying towards aquaculture or abandoned ponds on the landward side of the seawall to roost (Barter & Riegen 2004). We adopted Barter and Riegen's (2004) approach and conducted counts among 15 identified fixed pre-roosts because the birds were often concentrated at these roosts. Counts from an additional roost (Ashpond, Figure 2.1) 7 km further east of the reserve's eastern boundary were also included as significant numbers of birds were recorded there (Riegen *et al.* 2014).

High tide counts of all shorebird species were conducted between March and May in 2010–2012, with priority given to Bar-tailed Godwit and Great Knot counts. Regular partial counts were conducted only on the eastern half of the reserve where more than 70% of our target species were recorded (Riegen *et al.* 2014). Pre-roosts 2, 5 and 6 were chosen as the main counting locations because the 'catchments' for these locations were less likely to overlap with nearby pre-roosts. Counts were conducted daily in at least one of these pre-roosts in 2011, yielding the most comprehensive counting effort; the next most frequent counts were in 2010. YLJ-wide periodic synchronised censuses were conducted four to five times each year at high tide during spring tide, covering up to 12 pre-roosts (average=7) and were completed within an average of 3 days. Most of the counts were conducted on incoming tides (243 cases) while a few were conducted during falling tides (17 cases). The latter may under-count the total number of birds because some individuals may not return until the tide dropped too far from the seawall for accurate counting. Therefore, we counted birds during falling tides only at locations with lower numbers of birds to minimise biases. Sightings of colour-banded individual Bartailed Godwits and Great Knots during fieldwork were also recorded to provide an independent measure of the proportion of the flyway migrant population of these two species staging at YLJ.

# 2.4 Data analysis

# 2.4.1 Subspecies analysis

In 2010 and 2011, photos of Bar-tailed Godwits in flight were taken in the field and used to estimate the proportions of L. l. baueri and L. l. menzbieri over the migration period. The two subspecies are differentiated by the whitish rump and lower back in L. l. menzbieri and darker rump and lower back in L. l. baueri (Engelmoer & Roselaar 1998; Tomkovich 2010; Wilson *et al.* 2007). For dates when more than one clear photo was available, numbers of each subspecies were summed, using photos considered most likely to be independent. Double-counting was possible, but given the small proportion of birds counted in photos compared to those counted in the field each day (mode 0.4% and median of 2.2%), the likelihood of double-counting was negligible. The overall patterns of subspecies proportions were similar in 2010 and 2011. Therefore, data were combined for analysis using weighted averages if photos were available for the same date in both years (Appendix 2.1). Daily subspecies proportions of L. l. baueri were smoothed (Systat Software Inc 2007: NONLIN Smooth and Plot Feature with polynomial smoothing, Gaussian kernel, nearest neighbour proportion = 0.25) with two outliers excluded (the largest positive and negative residuals that affect the overall shape of the curve). The resulting smoothed subspecies proportions were used in analyses. Our assumption that the passage times between 2010 and 2012 are the same should be reasonable as L. l. *baueri* has been found to have consistent migration timing between years (Battley 2006; Conklin & Battley 2011a; Conklin et al. 2013). The numbers of L. l. baueri and L. l. menzbieri at each pre-roost were calculated as the product of the number of Bar-tailed

Godwits counted in the field and the proportion of each subspecies estimated by the smoothing method described above. No adjustment was required for Great Knots which are monotypic.

#### 2.4.2 Parameter estimation

Thompson (1993) described a model of migrants transiting a staging site which estimates the number of birds present on any day based on the size of the transiting population and the difference between the proportion of transiting population which has arrived by that day and the proportion which has departed. Given enough daily counts over the staging period and assuming normally distributed arrival and departure times, the size of the transiting population and the parameters of the arrival and departure time distributions can be estimated. Our situation is more complex than that described by Thompson (1993) in that we have three years of data. Preliminary modelling (and experience elsewhere such as Riegen *et al.* 2014) indicated that whilst the numbers of birds transiting varied from year to year, arrivals and departures followed the same timing pattern in each year. Assuming the same species-specific passage times in each year for both species, we calibrated the following model:

$$Count_{j,day} = \sum_{j=1}^{3} (a_j n_j) * (ZCF(day, m1, s1) - ZCF(day, m2, s2))$$

Where *j* is the year index: *1* for 2010, *2* for 2011, *3* for 2012,

*Count*<sub>j, day</sub> is the observed number of birds present on the indicated day in year j,

*a<sub>j</sub>* is a dummy variable set to 1 for observations in year *j*, and 0 otherwise,

 $n_j$  is the estimated size of the transiting population in year j,

*m*1, *s*1 are the estimated mean and standard deviation of arrival dates,

m2, s2 are the estimated mean and standard deviation of departure dates,

*ZCF(day,m,s)* is the cumulative normal distribution for a mean of *m* and *a* standard deviation of *s*.

Stopover duration was calculated as the difference between the estimated arrival and departure dates. The variance of stopover duration was calculated using Systat outputs as Variance(arrival) + Variance(departure) + 2 x Covariance (arrival, departure). Calibration of this model followed Rogers *et al.* (2010) using the non-linear modelling procedure in SYSTAT 12 (Systat Software Inc 2007) with a least-squares loss function. Starting values of the parameters to be estimated are needed for the calibrations. We estimated starting values based on the number of birds counted during peak counts and tracking results from previous studies. Estimates from non-linear models may be sensitive to small differences in the initial estimates and different starting values may yield different parameter estimates. We used a range of starting values to check that our estimates were robust.

Estimates of passage times and total number of birds through modelling were made based on two different, but non-exclusive datasets to evaluate the effectiveness of different counting approaches. The first dataset "Periodic synchronised censuses" included data from broadscale censuses of the entire study area. These censuses were conducted 4–5 times per season but covered a larger area than the other dataset over the 3 years. Counts from different pre-roosts were summed for each survey except records where double counting was suspected. Two counts that only involved pre-roosts 2 and 6 before the arrival of birds in the early season were added to the dataset for 2011 and 2012 to improve the estimate of arrival time.

The second dataset "Regular partial counts" included data from selected preroosts (2, 5 and 6), which were counted frequently over the 3 years. The size of the area to be counted precluded a complete count of these three pre-roosts within one day. Accordingly, counts were made at different pre-roosts and summed for analysis in a 4-day block. For pre-roosts where more than one count was carried out within a 4-day block, the average was used. The core roosting site, pre-roost 2, typically held a disproportionate number of birds (42% of Bar-tailed Godwits and 25% of Great Knots, A. Riegen unpubl. data), and therefore we ensured in the analysis that the 4-day block always included one count from pre-roost 2. These yielded thirty-seven 4-day blocks and thirty-five 4-day blocks for Bar-tailed Godwits and Great Knots, respectively, over 3 years of study. More than half of these blocks consisted of counts from all three pre-roosts while most of the remaining consisted of two pre-roosts.

Both datasets provided estimates of passage times but only the periodic synchronised censuses (which covered the whole reserve) could yield an estimate of total number of birds at YLJ. Therefore, total numbers at YLJ were modelled from the synchronised censuses using (1) passage times and standard deviations generated directly from that dataset, and (2) passage times and standard deviations generated from the partial counts data set. The accuracy of estimates using these two approaches was evaluated by comparing their estimated passage times with available data from satellite tracking, radio tracking and geolocator studies on the same populations. This was achieved by obtaining the z-value (Zar 1999) and using a significance level ( $\alpha$ ) of 0.05 (arrival dates in Great Knots were not compared due to uncertainty in the accuracy of arrival dates based on radio tracking).

# 2.4.3 Importance of Yalu Jiang coastal wetland

The true number of migrants presumably varies between years according to differences in breeding success and mortality in previous years. To accommodate this concern in our estimates of the proportion of the flyway populations that occurred at YLJ, we used the non-breeding data (Bamford et al. 2008; Li et al. 2009b) to give estimates of the proportions of the total non-breeding populations of the two godwit subspecies and Great Knots that occur in north-west Australia (Eighty Mile Beach and Roebuck Bay) and New Zealand. We then used recent survey data from north-west Australia (C. Hassell, D. Rogers and the Australasian Wader Studies Group unpubl. data) and New Zealand (A. Riegen and the Ornithological Society of New Zealand unpubl. data) to estimate the size of the latest populations in these non-breeding grounds from 2010-2012. These latest population estimates in the survey regions were then divided by the proportions calculated above to give estimates of the the total Flyway populations in the years of our study. As most immature birds of both study species do not migrate north, we used survey data from the non-breeding and breeding periods to estimate the proportions of nonmigrating and migrating birds over the study period, and applied these to the adjusted Flyway estimates (Table 2.1). These processes yielded only a rough estimate of the size of the total flyway population due to limited study sites and old datasets, thus the results should not be treated as a reappraisal of flyway estimates. Nonetheless, this is the best possible approach we have in order to estimate the proportion of flyway populations that occurred at YLJ.

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Table 2.1 Estimated numbers of northward-migrating Bar-tailed Godwits and Great Knots from 2010–2012 along the East Asian-Australasian Flyway (EAAF), based on published literature and recent non-breeding count data in north-west Australia (Eighty Mile Beach, Roebuck Bay) (C. J. Hassell, D. I. Rogers, and the Australasian Wader Studies Group unpubl. data) and New Zealand (A. C. Riegen and the Ornithological Society of New Zealand unpubl. data).

Species	Location	Period	Proportion of EAAF population	Non-breeding population	Projected EAAF population	Migrant proportion in March	Number of migrants
Godwit	New Zealand	2009-10	0.67 <sup>A</sup>	87,590	130,457	0.86	111,748
L. l. baueri		2010-11		101,459	151,114	0.91	137,485
		2011-12		88,949	132,482	0.84	111,511
Godwit	NW Australia	2009-10	0.70 <sup>B</sup>	70,056	100,233	0.88	87,997
L. l. menzbieri		2010-11		81,229	116,219	0.89	103,781
		2011-12		86,498	123,758	0.84	104,405
Great Knot	NW Australia	2009-10	0.48 <sup>c</sup>	92,801	195,174	0.87	169,998
		2010-11		121,860	256,289	0.96	245,933
		2011-12		122,065	256,720	0.84	214,572
A Proportion of	f New Zealand Bar-tai	led Godwits to the F	AAF population based o	on Bamford <i>et al.</i> (200	)8)(104,068)/155,000.		
<sup>B</sup> Proportion of	f north-west Australia	ו Bar-tailed Godwits	to the EAAF population	l based on (Li <i>et al.</i> 200	09b)(25,000+93,818)/1	70,000.	

<sup>c</sup> Proportion of north-west Australia Great Knots to the EAAF population based on Bamford et al. (2008) (158,082+22,600)/380,000.

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The frequency of resighting colour-banded birds also provides evidence for the importance of YLJ. Not all colour-marked birds present could be seen due to the large area of the study sites and large numbers of birds present. The number of colour-banded birds overlooked was estimated by assuming a quadratic relationship between the number of colour-banded birds and the frequency with which such birds were recorded. This approach provided a better fit of the model to the data than other possible relationships (e.g. exponential relationship in Rogers *et al.* 2010) and yielded an estimate of the total number of colour-banded birds in the study area. In combination with the numbers banded in north-west Australia and New Zealand, and assuming a survival rate of 90% for *L. l. baueri* (P. F. Battley unpubl. data), 81% for *L. l. menzbieri* and for 82% for Great Knots (Milton *et al.* 2003), we calculated the proportions of birds from these non-breeding grounds estimated to have used YLJ during northward migration during the study period.

# **2.5 Results**

Regular counts at pre-roosts 2, 5 and 6 recorded the earliest first Bar-tailed Godwit on 11 March 2011, and around 150 were still present at the end of May 2011. The first Great Knot was recorded on 18 March in both 2010 and 2011 with about 200 remaining at the end of May 2010. Photographic assessment of godwit subspecies from 99 of 162 field days in 2010 and 2011 indicated that *L. l. baueri* dominated at YLJ from the beginning of the migratory season in the middle of March until early May (Figure 2.2, Appendix 2.1). The relative proportion between the two subspecies stabilised at 0.7 *L. l. baueri* between mid-April and early May before steadily reducing. Similar patterns in the relative proportion of *L. l. baueri* were found in both 2010 and 2011, therefore smoothed results from combining these two years' data were used for further analysis.

Chi-Yeung Choi-July 2014



**Figure 2.2** The change in proportion of *L. l. baueri* and *L. l. menzbieri* godwits over time at the Chinese side of Yalu Jiang coastal wetland during northward migration in 2010 and 2011. Open circles and open triangles denote the proportion of *L. l. baueri* obtained from photos taken in the field in 2010 and 2011, respectively. The solid line and dashed line denote the smoothed proportion of *L. l. baueri* in 2010 and 2011, respectively.

The estimates of passage times from modelling of the two datasets yielded different results (Table 2.2). There were no significant differences in the arrival dates, departure dates or stopover durations between the periodic synchronised census datasets and tracking studies (p>0.05) for all three populations. In contrast, the regular partial count dataset yielded substantially earlier departure (26 days earlier, p=0.11) and shorter stopover duration (16 days shorter, p=0.12) than the tracking data for *L. l. menzbieri* (Table 2.2). The estimated mean departure date from regular partial count dataset was even earlier than the earliest departure date recorded from tracking studies. Therefore, the periodic synchronised census dataset yielded more reasonable passage time estimates than the regular partial counts dataset did. Nevertheless, we present population estimates derived from the use of both sets of passage time estimates for comparison. Adjusting the starting values resulted in only very minor changes to parameter estimates, indicating that our estimates were reasonably robust (Appendix 2.2).

**Table 2.2** Estimated arrival dates, departure dates and stopover durations of Bar-tailed Godwits and Great Knots at Yalu Jiang coastal wetland (China) during northward migration, derived from counts (periodic synchronised censuses and regular partial counts) and from remote tracking data (satellite tracking, radio tracking and geolocator studies).

Species/Subspecies	Dataset	Mean arrival date	SD	Mean departure date	SD	Stopover duration	SD
	Synchronised censuses	29-Mar	10.5	8-May	6.2	39.7	2.9
L. l. baueri	Partial counts	26-Mar	6.2	27-Apr	11.1	31.8	2.0
godwit	Tracking records (n=20, 19 <sup>A</sup> )	30-Mar	6.2	6-May	5.6	37.0	5.9
	Synchronised censuses	11-Apr	5.4	15-May	0.1	34.1	2.5
L. l. menzbieri godwit	Partial counts	8-Apr	6.7	25-Apr	15.1	16.3	8.0
	Tracking records (n=3 <sup>A</sup> )	18-Apr	5.1	20-May	3.2	32.0	6.2
	Synchronised censuses	7-Apr	3.2	14-May	0.6	37.5	0.8
Great Knot	Partial counts	6-Apr	2.9	17-May	2.8	41.1	2.8
	Tracking records (n=24, 6 <sup>B</sup> )	NA		13-May	11.1	40.8 <sup>c</sup>	12.0

<sup>A</sup> Data obtained from satellite tracking (P. F. Battley unpubl. data) and geolocator studies (J. R. Conklin unpubl. data), n=20 for arrival date, n=19 for departure and stopover duration.

 $^{\rm B}$  Data obtained from radio tracking (Z. J. Ma unpubl. data); n=24 for departure, n=6 for stopover duration.

<sup>c</sup> Based on individuals that arrived before 10<sup>th</sup> April and departed after April, but likely to be an underestimate as it involved four birds radio-tagged locally when the arrival dates were not known.

Modelling results based on the periodic synchronised census dataset (counts plus derived passage times) indicated that *L. l. baueri* arrived and departed earlier than *L. l. menzbieri* and Great Knots, although the differences were not statistically significant between species (p>0.05) (Figure 2.3, Table 2.2). Small numbers of *L. l. baueri* evidently departed YLJ before all *L. l. baueri* had arrived, while there was no overlap in arrival and departure days in *L. l. menzbieri* and Great Knots (Figure 2.3). *L. l. baueri* staged at YLJ for 40 days while *L. l. menzbieri* and Great Knots staged for 34 days and 38 days respectively (Table 2.2). Total population estimates (based on the periodic synchronised census dataset) showed a significantly higher estimate in 2010 than the other two years for both

*L. l. baueri* and Great Knots (p<0.05, except *L. l. baueri* between 2010 and 2011 where p=0.07) (Table 2.3). On average, YLJ supported more than 68,000 Bar-tailed Godwits and 44,000 Great Knots during northward migration from 2010–2012 (Table 2.4).



**Figure 2.3** Total numbers of Bar-tailed Godwits and Great Knots staging at the Chinese side of Yalu Jiang coastal wetland during northward migration from 2010–2012. Bars represent observed count data from periodic synchronised censuses, solid lines the modelled estimate based on count data from periodic synchronised censuses (both were plotted against the left y-axis). Dotted lines represent the number of birds estimated to arrive and dashed lines the number of birds estimated to depart (both plotted against the right y-axis), thus areas under the dotted and dashed lines are equal and both represent the total number of birds.

#### Chapter 2. Importance of Yalu Jiang to shorebirds

**Table 2.3** Estimated total numbers of Bar-tailed Godwits and Great Knots at the Chinese side of Yalu Jiang coastal wetland during northward migration from 2010–2012. Numbers are modelling from periodic synchronised censuses, using passage time parameters from either synchronised census or regular partial count data. Values are presented as estimates±asymptotic standard error.

Year	Data type	L. l. baueri godwit	L. l. menzbieri godwit	Great Knot
2010	Estimate: synchronised	60,818±6,539	22,722±4,732	53,409±3,832
	Estimate: partial	82,425±13,452	38,394±8,727	39,574±5,491
	Actual: peak count	60,319	21,828	53,409
2011	Estimate: synchronised	44,090±6,550	14,775±2,197	41,198±2,709
	Estimate: partial	50,246±8,094	32,736±7,749	39,655±4,644
	Actual: peak count	43,011	18,087	42,357
2012	Estimate: synchronised	42,814±5,895	18,816±2,079	38,320±2,709
	Estimate: partial	45,070±8,367	32,533±7,640	37,187±4,139
	Actual: peak count	45,839	20,577	41,635
	R <sup>2</sup> : synchronised	0.97	0.96	0.99
	R <sup>2</sup> : partial	0.89	0.81	0.94

Based on the modelled estimates at YLJ and the estimate of flyway populations using counts from non-breeding grounds, YLJ supported an average of at least 42% of northward-migrating *L. l. baueri*, 19% of *L. l. menzbieri*, and 22% of Great Knot along the EAAF (Table 2.4). Resigning data suggested that an average of 52% of New Zealand colour-banded *L. l. baueri*, 10% of north-west Australia colour-banded *L. l. menzbieri* and 29% of north-west Australia colour-banded Great Knots staged at YLJ during northward migration between 2010 and 2012 (Table 2.4).

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Table 2.4 Estimates of the proportion of the flyway populations that occurred at the Chinese side of Yalu Jiang coastal wetland (YLJ) between 2010 and 2012 based on resighting data and modelled count estimates. The number of colour-banded birds overlooked was estimated by assuming a quadratic relationship between the number of colour-banded birds and the frequency with which such birds were recorded. The number of marked individuals estimated to be present was the sum of the number resighted and the number estimated to be overlooked. Number of marked L. l. baueri alive was estimated based on the number of Bar-tailed Godwits marked in New Zealand and a survival rate of 90% (P. F. Battley, unpubl. data); L. I. menzbieri and Great Knots were estimated based on the number marked in north-west Australia, with survival rates of 81% and 82% respectively (Milton et al. 2003). In the modelled counts estimates, the numbers at YLJ were adopted from the synchronised estimates in Table 2.3 and the flyway estimates from Table 2.1.

			<b>Marked</b> ind	ividuals				<b>Modelled counts</b>	
				Estimated	Estimated	Assumed	<b>Proportion of</b>	Estimated	<b>Proportion of EAAF</b>
Species	Location	Period	Resighted	overlooked	present	alive	individuals at YLJ	numbers at YLJ	population at YLJ
		2009-10	260	256	516	728	0.71	60,818	0.54
Godwit	New	2010-11	145	139	284	683	0.42	44,090	0.32
L. l. baueri	Zealand	2011-12	166	111	277	615	0.45	42,814	0.38
		Average					0.52	49,241	0.42
		2009-10	16	26	42	409	0.12	22,722	0.26
r v Louwit	NW	2010-11	17	13	30	429	0.09	14,775	0.14
L. l. monshioui	Australia	2011-12	13	21	34	470	0.10	18,816	0.18
naidzinam		Average					0.10	18,771	0.19
Godwit		3-year							
total		mean						08,012	
		2009-10	35	77	112	469	0.27	53,409	0.31
Current Vurren	NW	2010-11	29	73	102	591	0.20	41,198	0.17
ULEAL NIIUL	Australia	2011-12	101	124	225	690	0.39	38,320	0.18
		Average					0.29	44,309	0.22

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# **2.6 Discussion**

# 2.6.1 Estimation of migrant population sizes and migration phenology

Our modelling results confirm that YLJ is an important staging site for Bar-tailed Godwits and Great Knots, with an annual average of 68,000 Bar-tailed Godwits and 44,000 Great Knots using the area during northward migration over the period 2010 to 2012. The Bar-tailed Godwit population at YLJ is dominated by *L. l. baueri*, which comprises around 70% of the total godwit population. An average of at least 49,000 *L. l. baueri* and 18,000 *L. l. menzbieri* staged at YLJ during the study period. This is consistent with satellite tracking data and resightings of individually-marked birds that showed a more easterly distribution for *L. l. baueri* than *L. l. menzbieri* within the Yellow Sea (Barter & Riegen 2004; Battley *et al.* 2012; Wilson *et al.* 2007).

The estimated passage times at YLI for the two Bar-tailed Godwit subspecies were not statistically different, but L. l. baueri arrived on average on 29 March, 13 days ahead of *L. l. menzbieri* (11 April), which arrived at a similar time to Great Knots (7 April). The differences in arrival date between the two godwit subspecies were within the differences in departure date in Australia (10 to 14 days) (Wilson et al. 2007) and the first records of L. l. baueri at YLJ (11 March 2011, 12 March 2012) matched the earliest departure known from New Zealand (4 March 2012, J. R. Conklin and P. F. Battley unpubl. data; the flight time to China is approximately 7 days, Battley et al. 2012). L. l. baueri also departed YLJ earlier than L. l. menzbieri and Great Knots (early May versus mid-May). Late-arriving L. l. menzbieri and Great Knots have less time to refuel given their narrow departure windows. This similarity in phenology between Great Knots and menzbieri godwits is unsurprising, given that both have similar non-breeding and breeding ranges. Their narrower departure windows than L. l. baueri probably relate to their smaller latitudinal breeding range, and hence less geographical variation in thaw dates than in Alaska (Bamford et al. 2008; Conklin et al. 2010; Green et al. 2002; Wilson et al. 2007). The same reasoning could be applied to the relatively large numbers of *L. l. baueri* remaining at YLJ until the middle of May. These probably breed further north in Alaska than earlierdeparting L. l. baueri (Conklin et al. 2010).

# 2.6.2 Assessment of counting and modelling approaches

The modelling results based on periodic synchronised census data more realistically described the migration phenology of the study species than those based on regular partial counts, at least for godwits. In fact, the estimated departure dates for Bar-tailed Godwits based on regular partial counts were too early (late April) and in the wrong order (L. l. menzbieri ahead of L. l. baueri) compared to published results (Battley et al. 2012). These suggest that regular partial counts did not provide reliable estimates. Such a result is surprising because the three main pre-roosts were counted on a 4-day rotation during regular partial counts while periodic synchronised censuses were conducted only every two weeks. Nonetheless, regular partial counts may yield high variances because the countable number of birds could be affected by different tidal levels that affect local roosting patterns, or within-season changes in feeding and roost site choice as local food resources deplete (Rogers 2005). In contrast, the phenology and numbers of Great Knots estimated by the partial counts data set were similar to those estimated with the synchronised census dataset. This reflects the fact that Great Knots were concentrated more in areas covered during the partial counts – on average 75% of the Great Knots counted during the synchronised censuses were present at partial count sites, whereas only 43% of the godwits were. Overall, less frequent, but thorough periodic synchronised censuses at high tide during spring tides seem to be a more effective way to collect data for modelling shorebird populations at staging sites when survey resources are limited. The stable peak found in L. l. menzbieri (from late April to early May) and Great Knots (from mid April to early May) indicated that their transiting numbers can be reliably counted over the peak period (Appendix 2.3). Periodic synchronised censuses should be completed within the shortest period of time if they cannot be done on the same day, to minimise double-counting as birds move between surveyed sites during the census period. This might have yielded the significantly higher estimates for L. l. baueri and Great Knots in 2010 (one of the censuses spanned over 10 days) compared to other years, when the spans did not exceed 4 days.

The similar estimated passage times based on periodic synchronised census data to tracking records suggested that both periodic synchronised census and tracking methods with limited sample sizes provide reasonably good estimates for passage times. The estimated numbers of birds staging were similar to the peak counts in most cases, indicating that a single thorough survey during the peak season could still be used to represent the total number of *L. l. menzbieri* and Great Knots staging at YLJ if resources are limited. However, there were two occasions when the 95% range of estimated number of

birds was lower than the peak counts (*L. l. menzbieri* 2011, Great Knot 2012). Such inconsistency may arise due to statistical error in the count totals.

The accuracy of Thompson's modelling approach relies on the assumption that arrival and departure times are normally distributed, which may vary depending on species, site and time. This assumption may be violated in situations where there is substantial variation between the passage times of individuals. This is more likely to occur during southward migration when populations may comprise different age-groups or use the same site differently (e.g. staging or moulting) (Choi *et al.* 2009; Newton 2008). However, this modelling approach generated accurate passage time estimates in this study, which we could independently confirm from data from tracking studies (Battley *et al.* 2012; Ma *et al.* 2013b). We believe that its application for estimating total numbers would be more useful at stopover (rather than staging) sites, where there is a larger overlap between arriving and departing birds (e.g. *L. l. baueri* in this study) and the peak counts are likely to underestimate the total number of birds transiting (e.g. Chongming Dongtan, Ma *et al.* 2013b).

The use of photographs to estimate subspecies proportions in Bar-tailed Godwits could usefully be applied in similar studies where different subspecies, sexes or ages of birds, are identifiable by plumage and occur at the same study site. It is important to check whether different groups of birds in the study area have different distributions. Given that more than 70% of the Bar-tailed Godwits occur in the eastern half of the reserve (Riegen *et al.* 2014) and large numbers of photographs were used in our study, the potential impacts of uneven distribution between godwit subspecies are minimised.

# 2.6.3 Importance of Yalu Jiang coastal wetland

Our results reinforce the claim that YLJ is the most important northward migration staging site for Bar-tailed Godwits and indicate that the study area has become the most important known northward migration staging site for Great Knots along the EAAF (Bamford *et al.* 2008; Barter 2002; Moores 2012). According to the results of modelling count data, YLJ supports an average of at least 42% of northward-migrating *L. l. baueri*, 19% of *L. l. menzbieri*, and 22% of Great Knots along the EAAF. An independent check on the importance of YLJ based on colour-band data indicated that an average of 52% of New Zealand colour-banded *L. l. baueri*, 10% of north-west Australia colour-banded *L. l. menzbieri* and 29% of north-west Australia colour-banded Great Knots staged at YLJ. The differences between these estimates and the ones based on modelling count data could arise because of different scanning effort and different populations may have different tendencies to move in and out of the our main scanning area in different years, subject to

food availability. The low proportion of colour-banded *L. l. menzbieri* resighted could arise if the population at YLJ mainly comes from wintering areas further east of north-west Australia where the banding work has been conducted. Nonetheless, the resighting data are consistent with the modelling data in suggesting that YLJ supports a large proportion of *L. l. baueri* and Great Knot migrant populations along the EAAF.

Using the passage dates estimated and the peak count data from this study, a comparison with historical peak count data indicated an 18% decline in Great Knots (compared to 1999) and a 13% decrease in Bar-tailed Godwit (compared to 2004) (Barter & Riegen 2004) (Table 2.5). More recently, the number of Bar-tailed Godwits counted at YLJ during northward migration declined rapidly from 99,611 in 2009 to 63,479 in 2012 (36.3% decline). This decline coincided with a port development project at the eastern end of the reserve boundary (Figure 2.1, east of site 1), which started in June 2008, was half-completed in January 2011, and almost completed in February 2013, dividing the main foraging tidal flats of Bar-tailed Godwits at YLJ (as indicated by satellite-tracking, P. F. Battley unpubl. data) into two. It is difficult to determine whether the decline implies a drop in the total population or merely a redistribution of roosting birds. Despite the decline in numbers compared to historical counts, YLJ has become the most important known staging site for Great Knots during northward migration due to the destruction of the two most important staging sites, namely the Dongjin and Mangyeung Estuaries in South Korea (Bamford *et al.* 2008; Birds Korea 2010; Moores 2012).

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Table 2.5 The numbers of Bar-tailed Godwit and Great Knot recorded during periodic synchronised censuses at the Chinese side of Yalu Jiang coastal wetland between 1999 and 2012 (Barter & Riegen 2004; Barter et al. 2000; Chu et al. 2004; Riegen et al. 2014, Q. Bai pers. comm. and this study). The ashpond has only been counted since 2007 and numbers are presented separately from those within the reserve so direct comparison could be made between years.

		I	1				I							
Species /	Survey p	eriod												
locations	2-6 May	16-21	22-30	20-25	8-12	14-23	14-22	6-11	8-16	15-24	19-21	5 May	20-26	9-12
	1999	May 2000	April 2002	April 2004	May 2005	April 2006	April 2007	May 2008	April 2009	April 2010	April 2011	2011	April 2012	May 2012
Bar-														
tailed Godwit:	51,918	26,169	80,000 <sup>A</sup>	66,134	49,100	45,691	38,283	35,321	74,611	82,082	35,568		55,439	
reserve														
ashpond							45,000	20,000	25,000	65	25,530		8,040	
Great Knot:	55,178	26,093	3,000	32,880	20,270	16,268	19,906	26,972	20,393	53,467		41,357		41,635
reserve														
ashpond									5,000			1,000		
A Incidental	ectimate of	umbnomini <sup>1</sup>	the warning	rrefore not n	iced for any	tomparison	n for the no	nulation tre	րդ					

incluental estimate of unknown accuracy, therefore not used for any comparison for the population trend.

# 2.6.4 Conservation implications

It is clear that YLI plays an important role for Bar-tailed Godwits and Great Knots during northward migration. Thirteen other species are reported to occur in internationally important numbers during northward migration at the study area (Bamford et al. 2008). Additional evidence for the importance of this site will become available when latest count data from both northward and southward migration for species such as Nordmann's Greenshanks Tringa guttifer (IUCN category Endangered), Kentish Plovers Charadrius alexandrinus and Spotted Redshanks Tringa erythropus are analysed (IUCN 2012). It is strongly encouraged that the reserve seeks Ramsar recognition to further protect the area from reclamation such as the recent loss of 34 km<sup>2</sup> of tidal flat through port development at the east of the reserve boundary. The long-term impact of such development should not be overlooked. Previous reports of sediments at Yalu Jiang estuary being transported westwards under the influence of tides and waves (Wang & Aubrey 1987) imply that the new 10-km seawall extending towards the sea might not merely mean an immediate loss of intertidal flat but a further loss of intertidal flat in the study area due to the loss of sediment supply from the river (Figure 2.1). On the other hand, our results indicate that the ashpond, a high tide roost located further east of the reserve boundary, holds an average of 20% of the Bar-tailed Godwits counted during our periodic synchronised censuses. The existence of important roosting habitat outside the reserve boundary, and activities outside the reserve that may have damaging effects on the reserve, indicate that the status of surrounding areas should be taken into consideration when making management decisions.

Finally, with the advantage of a good understanding of the study area and independent tracking dataset to examine the modelling results, we have shown that a combination of periodic synchronised censuses and Thompson's modelling approach can provide reliable estimates of passage times and numbers of transiting birds at staging sites. Such an approach should be applied elsewhere to test for its validity. This is particularly relevant to the growing amount of data available along the east China coast, where shorebirds from 13 areas have been surveyed monthly since 2005 (China Coastal Waterbird Census Group 2009, 2011).

**Appendix 2.1** Summary of the data used in Bar-tailed Godwits subspecies analysis based on flight photos taken in the field at the Chinese side of the Yalu Jiang coastal wetland between 2010 and 2011. Data from some of the dates was summed from more than one photo, as long as they were most likely to be independent.

Date	Location	Number of photos used	Number of <i>baueri</i>	Number of menzbieri	Total number of birds with subspecies identified
16-Mar-2011	Site 6	1	123	0	123
17-Mar-2010	Site 2	2	119	0	119
18-Mar-2010	Site 2	1	18	1	19
18-Mar-2011	Site 6	1	102	0	102
20-Mar-2011	Site 2	1	133	1	134
21-Mar-2010	Site 2	1	50	0	50
23-Mar-2010	Site 2	3	139	0	139
23-Mar-2010	Sites 2 & 5	2	221	4	225
26-Mar-2011	Site 2	1	140	9	149
27-Mar-2011	Site 2	6	205	1	296
27-Mar-2010	Site 2	1	67	1	68
27-Mar-2011 28 Mar 2011	Site 6	1	25	1	26
20-Mar-2011	Site 2	1	55	1	50
29-Mai-2010	Sites 2.9 F	2	54 260	0	54 260
29-Mai-2011	Sites 2 & 5	۲ 1	200	1	209
30-Mar-2011	Site 6	1	21 105	1	
31-Mar-2010	Site 2	2	105	9	114
1-Apr-2010	Site 2	3	38	3	41
1-Apr-2011	Site 2	1	292	8	300
2-Apr-2011	Site 2	2	618	11	629
3-Apr-2010	Site 2	1	92	8	100
3-Apr-2011	Site 6	1	126	15	141
4-Apr-2011	Site 12	2	47	6	53
5-Apr-2010	Site 2	1	288	4	292
5-Apr-2011	Site 2	1	133	2	135
6-Apr-2011	Site 6	1	232	13	245
7-Apr-2011	Site 2	4	504	19	523
9-Apr-2011	Sites 2 & 5	2	171	12	183
10-Apr-2010	Site 2	1	139	32	171
10-Apr-2011	Sites 2 & 6	3	109	34	143
11-Apr-2010	Site 2	1	9	3	12
11-Apr-2011	Site 6	1	129	37	166
12-Apr-2010	Site 2	2	170	55	225
12-Apr-2011	Site 5	1	55	19	74
13-Apr-2011	Site 6	1	24	22	46
14-Apr-2010	Site 2	2	112	51	163
14-Apr-2011	Site 6	1	17	3	20
15-Apr-2010	Site 2	2	62	16	78
15-Apr-2011	Site 2	2	200	25	225
16-Apr-2010	Site 2	2	96	36	132
16  Apr 2010 16- $\text{Apr} 2011$	Site 6	2	17	65	82
$17_{-}$ Apr-2011	Site 6	1	1/	86	222
10 Apr 2011	Sites 2 & 6	1	290	55	233
20  Apr 2010	Site 2 & 0	т 2	207	10	126
20-Apr-2010	Site 2	3 1	00	40	130
20-Apr-2011 21 Apr 2010	Site 2	1 2	07 159	65	20 222
21-Apr-2010	Sites 2.9 C	۲ ک	130	05	223 215
21-Apr-2011	Siles 2 & b	2	139	/0 211	215 0FF
23-Apr-2010	SITE Z	<u>ک</u>	/44	211	755 104
23-Apr-2011	Asnpond	1	153	31 15	184
24-Apr-2010	Site 6	1	11	15	26
24-Apr-2011	Site 6	1	195	187	382

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26-Apr-2011	Site 5	1	10	2	12
27-Apr-2010	Site 6	1	3	2	5
27-Apr-2011	Site 5	3	35	49	84
28-Apr-2010	Site 6	3	257	75	332
28-Apr-2011	Site 5	2	88	118	206
29-Apr-2011	Site 5	1	305	38	343
30-Apr-2010	Site 2	2	125	46	171
30-Apr-2011	Site 2	2	210	11	221
1-May-2011	Sites 2 & 5	3	645	95	740
2-May-2010	Site 6	1	3	3	6
2-May-2011	Site 2	1	57	8	65
3-May-2010	Site 2	1	80	30	110
3-May-2011	Site 5	2	56	75	131
4-May-2010	Site 6	3	55	11	66
4-May-2011	Ashpond	1	46	17	63
5-May-2010	Site 2	2	54	18	72
5-May-2011	Sites 5 & 6	4	179	123	302
6-May-2010	Sites 2 & 6	3	111	32	143
7-May-2011	Site 2	2	244	54	298
9-May-2011	Site 2	1	291	92	383
10-May-2011	Sites 5 & 6	5	301	238	539
11-May-2010	Site 2	3	50	51	101
12-May-2010	Site 2	2	8	15	23
12-May-2011	Site 5	1	3	6	9
13-May-2010	Site6	1	41	55	96
13-May-2011	Site 5	2	50	18	68
14-May-2010	Site6	1	8	17	25
14-May-2011	Site 5	1	7	28	35
15-May-2010	Site6	2	34	76	110
15-May-2011	Site 2	2	63	88	151
16-May-2010	Ashpond	4	228	283	511
16-May-2011	Site 5	2	18	75	93
17-May-2010	Ashpond	1	24	42	66
17-May-2011	Ashpond	2	326	424	750
18-May-2011	Site 5	2	56	87	143
19-May-2010	Site2	1	15	56	71
19-May-2011	Site 2	2	54	46	100
20-May-2010	Site 6	5	35	97	132
20-May-2011	Site 12	1	49	90	139
21 May 2011	Ashpond & Site	2	62	207	270
21-May-2011	5	Z	03	207	270
22-May-2010	Site2	1	7	90	97
22-May-2011	Sites 5 & 6 & 10	4	48	176	224
23-May-2011	Ashpond	1	67	139	206
25-May-2010	Ashpond	1	1	21	22
26-May-2010	Site2	1	13	45	58
27-May-2010	Site2	1	5	7	12
29-May-2010	Ashpond	1	2	15	17
30-May-2010	Site2	1	5	45	50
30-May-2011	Site 2	2	3	10	13

Appendix 2.2 Results of modelling estimates on the total number of *L. I. baueri, L. I. menzbieri* and Great Knot at the Chinese side of Yalu Jiang coastal wetland and their passage times using different starting values. The upper and lower end of starting values presented were either the maximum or minimum limits that give the similar are the mean and standard deviation of arrival date, respectively. M2 and S2 are the mean and standard deviation of departure date, respectively. All dates were presented as the number of days since the end of February. The first row for each species represents the starting values that generated the estimates adopted in this study. Starting modelling estimates, or the reasonable limits that were considered. Year1, Year2 and Year3 are the total number of birds in 2010, 2011 and 2012, respectively. M1 and S1 values in bold below represents the parameter that has been changed from the one used to generate the estimates adopted in this study.

Species	Starting	values						Modelling	estimates					
	Year1	Year2	Year3	M1	<b>S1</b>	M2	S2	Year1	Year2	Year3	M1	<b>S1</b>	M2	S2
Godwit	60000	40000	40000	29	8.5	70	8.5	60817.95	44089.87	42814.45	29.34	10.53	69.04	6.21
L. l. baueri	10000	40000	40000	29	8.5	70	8.5	60817.94	44089.84	42814.40	29.34	10.53	69.04	6.21
	100000	40000	40000	29	8.5	70	8.5	60818.01	44089.94	42814.51	29.34	10.53	69.04	6.21
	60000	20000	40000	29	8.5	70	8.5	60817.94	44089.85	42814.40	29.34	10.53	69.04	6.21
	60000	100000	40000	29	8.5	70	8.5	60817.94	44089.85	42814.42	29.34	10.53	69.04	6.21
	60000	40000	10000	29	8.5	70	8.5	60817.92	44089.83	42814.38	29.34	10.53	69.04	6.21
	60000	40000	100000	29	8.5	70	8.5	60817.90	44089.79	42814.32	29.34	10.53	69.04	6.21
	60000	40000	40000	10	8.5	70	8.5	60818.00	44089.93	42814.53	29.34	10.53	69.04	6.21
	60000	40000	40000	38	8.5	70	8.5	60817.94	44089.84	42814.40	29.34	10.53	69.04	6.21
	60000	40000	40000	29	5.5	70	8.5	60817.89	44089.78	42814.32	29.34	10.53	69.04	6.21
	60000	40000	40000	29	20.5	70	8.5	60817.91	44089.82	42814.37	29.34	10.53	69.04	6.21
	60000	40000	40000	29	8.5	64	8.5	60817.95	44089.86	42814.42	29.34	10.53	69.04	6.21
	60000	40000	40000	29	8.5	80	8.5	60817.94	44089.85	42814.42	29.34	10.53	69.04	6.21
	60000	40000	40000	29	8.5	70	2.5	60817.97	44089.90	42814.48	29.34	10.53	69.04	6.21
	60000	40000	40000	29	8.5	70	20.5	60818.01	44089.95	42814.52	29.34	10.53	69.04	6.21
Godwit	30000	15000	20000	40	8.5	74	8.5	22721.63	14775.32	18816.45	41.73	5.39	75.80	0.13
L. l. menzbieri	5000	15000	20000	40	8.5	74	8.5	22721.63	14775.32	18816.44	41.73	5.39	75.42	0.63
	60000	15000	20000	40	8.5	74	8.5	22721.63	14775.32	18816.45	41.73	5.39	75.81	0.12
	30000	5000	20000	40	8.5	74	8.5	22721.63	14775.33	18816.45	41.73	5.39	75.75	0.19
	30000	60000	20000	40	8.5	74	8.5	22721.63	14775.33	18816.45	41.73	5.39	75.79	0.14
	30000	15000	5000	40	8.5	74	8.5	22721.61	14775.32	18816.44	41.73	5.39	75.67	0.30

00 1	5000	00009	40	8.5	74	8.5	22721.63	14775.32	18816.45	41.73	5.39	75.61	0.38
5000 200	200	00	28	8.5	74	8.5	22721.63	14775.32	18816.45	41.73	5.39	75.43	0.61
5000 2000	2000	0	52	8.5	74	8.5	22721.63	14775.32	18816.45	41.73	5.39	75.78	0.16
5000 20000	20000	_	40	1.5	74	8.5	22721.63	14775.32	18816.44	41.73	5.39	75.60	0.39
5000 20000	20000		40	12.5	74	8.5	22721.63	14775.32	18816.45	41.73	5.39	75.45	0.58
5000 20000	20000		40	8.5	63	8.5	22721.63	14775.32	18816.45	41.73	5.39	75.80	0.13
5000 20000	20000		40	8.5	83	8.5	22721.63	14775.32	18816.45	41.73	5.39	75.78	0.15
5000 20000	20000		40	8.5	74	2.5	22721.63	14775.32	18816.45	41.73	5.39	75.80	0.13
5000 20000	20000		40	8.5	74	12.5	22721.63	14775.33	18816.45	41.73	5.39	75.81	0.12
0000 40000	40000		40	8.5	75	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.31	0.64
0000 40000	40000		40	8.5	75	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.70	0.13
0000 40000	40000		40	8.5	75	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.32	0.63
<b>000</b> 40000	40000		40	8.5	75	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.70	0.13
00000 40000	40000		40	8.5	75	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.72	0.11
0000 5000	5000		40	8.5	75	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.28	0.68
0000 100000	100000		40	8.5	75	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.30	0.66
0000 40000	40000		28	8.5	75	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.70	0.13
0000 40000	40000		52	8.5	75	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.35	0.59
0000 40000	40000		40	2.5	75	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.30	0.65
0000 40000	40000		40	14.5	75	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.46	0.45
0000 40000	40000		40	8.5	61	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.33	0.62
0000 40000	40000		40	8.5	84	5.5	53409.42	41197.58	38230.17	37.86	3.21	75.29	0.68
0000 40000	40000		40	8.5	75	1.5	53409.42	41197.58	38230.17	37.86	3.21	75.31	0.65
0000 40000	40000		40	8.5	75	11.5	53409.42	41197.58	38230.17	37.86	3.21	75.29	0.67



**Appendix 2.3** The changes in percentage of staging Bar-tailed Godwit (solid line) and Great Knot (dashed line) through time at the Chinese side of the Yalu Jiang coastal wetland based on the non-linear model.

**DRC 16** 



#### MASSEY UNIVERSITY GRADUATE RESEARCH SCHOOL

#### STATEMENT OF CONTRIBUTION TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

#### Name of Candidate: Choi Chi Yeung

#### Name/Title of Principal Supervisor: Dr Phil Battley

#### Name of Published Research Output and full reference:

Journal article

Choi C-Y, Battley PF, Potter MA, Rogers KG, Ma ZJ (2014) The importance of Yalu Jiang coastal wetland in the north Yellow Sea to Bar-tailed Godwits Limosa lapponica and Great Knots Calidris tenuirostris during northward migration. Bird Conservation International. doi:10.1017/S0959270914000124

#### In which Chapter is the Published Work: 2

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate: 85% and / or
- · Describe the contribution that the candidate has made to the Published Work:

I designed the study, conducted the fieldwork, performed the analysis and wrote the article, with assistance from collaborators who are the co-authors of the article.

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	28-July-2014
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30-July-2014
Date

GRS Version 3-16 September 2011
Chapter 2. Importance of Yalu Jiang to shorebirds

### Chapter 3. Factors Affecting the Distribution Patterns of Benthic Invertebrates at a Major Shorebird Staging Site in the Yellow Sea, China

Choi C-Y, Battley PF, Potter MA, Ma ZJ, & Liu WL. 2014. Factors affecting the distribution patterns of benthic invertebrates at a major shorebird staging site in the Yellow Sea, China. *Wetlands*. doi: 10.1007/s13157-014-0568-4

#### 3.1 Abstract

The tidal flats of the Yellow Sea support benthic communities that are vitally important to migratory birds, but baseline information on benthic community structure and variability is largely lacking. We investigated spatial and temporal patterns of macrobenthic invertebrates in areas used by large numbers of shorebirds and how these patterns related to environmental factors at Yalu Jiang coastal wetland in the north Yellow Sea during boreal spring (March-May) from 2010–2012. At least 61 species were documented during the study. Monthly benthos sampling from 54 stations indicated that polychaetes and bivalves dominated the benthic communities, with capitellid or maldanid polychaetes dominating upper tidal flats and the bivalve Potamocorbula laevis dominating intermediate and lower tidal flats. The middle and eastern sites approximately 10 km apart showed substantial differences in benthic species abundance and distribution, with bivalves dominating in the middle but not the eastern site. The spatial distribution of benthos was correlated with both exposure time during the tidal cycle and sediment particle size. Benthic communities showed both annual and within season variation. Two of the frequent prey for migratory birds, namely ghost shrimps *Nihonotrypaea japonica* and young Potamocorbula laevis, were relatively common in 2010 and 2011, respectively, but not in 2012.

#### **3.2 Introduction**

Benthic communities are important components of intertidal wetland ecosystems with particulate substrates. These communities play important roles in nutrient cycling (Cloern 1982; Levin *et al.* 2001) and sediment movement (Reise 2002; Vaughn & Hakenkamp 2001), and may determine the distribution and abundance of secondary consumers such as shorebirds (Colwell & Landrum 1993; Rogers 2005; Yates *et al.* 1993). Macrobenthos are often exploited as food resources for people (Bennett & Reynolds 1993; Ronnback 1999; van de Kam *et al.* 2008) and the characteristics of benthic communities are indicators of environmental quality (Borja *et al.* 2000; Dauer 1993; UNDP/GEF 2007a). Studies of benthic communities at intertidal wetlands provide baseline information for scientific research and monitoring, but such information is very limited in Asia (McNeely *et al.* 2009; Yu 1994).

The Yellow Sea in northeast Asia is a productive semi-enclosed shallow marine ecosystem (Figure 3.1a) that is used by at least 40% of the migratory shorebirds of the East Asian-Australasian Flyway (>2,000,000 individuals) for refuelling during their annual

migrations (Barter 2002; Choi et al. 2009; Hua et al. 2013; Ma et al. 2013b). However, approximately 600 million people live in the adjacent region (10%) of the world's population) and rely heavily on the Yellow Sea for food and economic development, exerting enormous pressures on the local ecosystem (UNDP/GEF 2007b). In the Yellow Sea and adjacent Bohai Sea (west of the Yellow Sea), 35% of the intertidal flats of six key areas (more than 2,511 km<sup>2</sup>) was lost since the early 1980s, mostly through conversion into agricultural land, salt pans and aquaculture ponds for food production (MacKinnon et *al.* 2012). The remaining intertidal flats in the Chinese portion of the Yellow Sea are also under anthropogenic pressure, not only from land conversion, but also from extensive use for mudflat culture of shellfish, seabed seeding of shellfish and marine enhancement of depleted fish stocks (Chang & Chen 2008), as well as from pollution (Liu et al. 2008). These anthropogenic activities have created a heavily-disturbed intertidal ecosystem, where little quantitative information is known about the distribution and temporal dynamics of benthic taxa (UNDP/GEF 2007b), let alone the influences of anthropogenic activities on the benthic communities. Previous studies in Europe indicated that anthropogenic activities on intertidal flats can negatively affect local benthic macrofauna (Godet et al. 2009; van Gils et al. 2006a) and baseline information is needed urgently in the Yellow Sea if such impacts are to be monitored and managed effectively.

The Dandong Yalu Jiang Estuary Wetland National Nature Reserve (hereafter the 'reserve') is located in the north of Yellow Sea (Figure 3.1b). This reserve has many anthropogenic activities that are common to other areas within the Yellow Sea, but it has relatively less development pressure (MacKinnon et al. 2012), making it suitable for longterm monitoring. This area is notable for a near absence of saltmarsh, which is typically the major primary producer and which drives the primary production on tidal-flat ecosystems through nutrients and carbon fixation (Semeniuk 2005). This wetland is regarded as an 'Important Bird Area' (BirdLife International 2009), supporting probably more than 250,000 migratory shorebirds such as Far-eastern Curlews Numenius madagascariensis (IUCN category Vulnerable), Great Knots Calidris tenuirostris (IUCN category Vulnerable) and Bar-tailed Godwits *Limosa lapponica* during northward migration (Chapter 2; IUCN 2012; Riegen et al. 2014). Improved understanding of the benthic community structure and variability in the reserve will provide not only baseline information for long-term monitoring, but also insights into food availability for secondary consumers. In the context of a broader study of the stopover ecology of shorebirds, we investigate the temporal and spatial patterns of the macrobenthic taxa in the reserve during the boreal spring. We also explore how such patterns are associated with environmental factors such as sediment particulate composition, distance to the channels and duration of submergence, all of which have been found to influence the distribution and composition of benthic communities elsewhere (Compton *et al.* 2013; Newell 1970; Ryu *et al.* 2011a).



**Figure 3.1** Maps showing the locations mentioned in this paper. (*a*) The Yellow Sea, including (A) Yangtze River estuary, (B) Laizhou Bay, (C) Yellow River delta, (D) Bohai Bay, (E) Yalu Jiang coastal wetland, (F) Ganghwa, (G) Kyeonggi Bay (Namyang Bay), (H) Saemangeum and (I) Isahaya Bay. (*b*) The Dandong Yalu Jiang Estuary Wetland National Nature Reserve in 2012, with the boundary marked by the dashed line. (*c*) The two grids and 54 sampling stations at the middle and eastern sites.

#### 3.3 Materials and methods

#### 3.3.1 Study site

The Dandong Yalu Jiang Estuary Wetland National Nature Reserve (39°40′–39°58′N, 123°34′–124°07′E) is west of the Yalu Jiang estuary in the northern part of the Yellow Sea, on the Chinese side of the China-North Korea border (Figure 3.1a). It encompasses 814 km<sup>2</sup>, with 20% (160 km<sup>2</sup>) being assigned as the core area. It was founded in 1987 and

listed as a National Nature Reserve in 1997 to conserve the coastal wetland ecosystem and wildlife (Yan 2008). The reserve comprises mainly bare intertidal mudflat with small scattered patches of *Phragmites*-dominated saltmarsh on the seaward side of the seawall, with aquaculture ponds and paddy fields on the landward side; this is a typical Chinese coastal landscape (Barter 2002; Choi *et al.* 2014; Li *et al.* 2013; Ma *et al.* 2009; Yang *et al.* 2011). In this reserve, extensive anthropogenic activities were present but their impacts on the intertidal ecosystem were unclear. The aquaculture ponds were used for cultivating sea cucumber, jellyfish, shellfish, prawn, crab and fish while the bare intertidal mudflat immediately on the seaward side of the seawall was used for farming shellfish. Extensive fishnets up to 2 m high ran parallel to the coastline on the intertidal mudflat at the low neap tide water line (c. 3 km offshore), catching mostly fish, crabs and prawns. Shallow water in the subtidal zone was also used for farming shellfish (C.-Y. Choi, pers. obs.).

Tides are semidiurnal, with two high and two low tides per day, and macrotidal in amplitude (mean 4.5 m, maximum 6.9 m) (Davies 1980; Wang *et al.* 1986). Tidal flats extend to c. 4 km from the seawall in the west and middle parts of the reserve, but up to 5 km in the east (Figure 3.1b). The supratidal zone in the study area has all been converted to aquaculture ponds and high spring tides completely inundate the mudflat. On neap tides, high-elevation upper tidal flats at some areas in the east and west (Figure 3.1b) are not covered at high tide. Drift ice could be found on the tidal flats during boreal winter until thawing in mid- to late March (C.-Y. Choi, pers. obs.). During our study, the boreal winter and spring mean temperatures in Dandong, 30 km northeast of our study area (the nearest city where data are available), were coldest in 2010 (-4.4°C and 7.6°C, respectively), followed by 2011 (-4.0°C and 8.5°C) and 2012 (-3.7°C and 8.9°C). The number of days with snow or ice pellets during the winter prior to sampling followed similar patterns as the temperature, occurring most often in 2010, followed by 2011 and 2012 (13, 11 and 9 respectively) (Tutiempo Network 2013).

#### 3.3.2 Sampling methods

Benthos was sampled in March–May 2010–2012. Given the aim to investigate the temporal and spatial patterns of the macrobenthic taxa in the context of a broader study of shorebirds, we set up grids at the east and the middle of the reserve. These correspond to shorebird count sites 2 and 5 respectively in earlier studies and these sites hold large numbers of shorebirds during northward migration (Chapter 2; Riegen *et al.* 2014). Sample stations within grids had 500 m inter-sample distances (Figure 3.1c). Benthos samples (see below for details) were taken from the eastern site in 2010 (18 stations), the middle site in 2011 (36 stations) and both sites in 2012 (54 stations). Grid sampling is

regarded as the best way to describe temporal and spatial differences in abundance in systems such as this one (Bijleveld *et al.* 2012). As the sample stations were aligned along the direction of tidal ebb, stations with different distances to the seawall represented different elevation levels and had different exposure times.

Benthos sampling was conducted once a month from March–May. The first sampling was done soon after the thaw and before the peak arrival of migratory shorebirds (12–24 March) while the last sampling was carried out at the end of the migratory period. This allowed investigation of the potential changes of food availability to shorebirds during their migratory period. One core sample (diameter 15.5 cm, area 0.019 m<sup>2</sup>, 30 cm deep) was taken per station and the core sample was then washed through a 0.5-mm sieve. All soft-bodied organisms were either stored in 70% ethanol or soaked in 5% formalin for at least 72 hours before being placed into 70% ethanol. Hard-bodied organisms were kept frozen until further analysis. Opportunistic collections were also taken but those results were only used in the benthic species list of the reserve (Appendix 3.1). In addition to benthos core sample, a 3.5 m x 3.5 m square was set towards the east of the sampling station and the total number of ghost shrimps *Nihonotrypaea japonica* on the surface within the square was counted. All benthos density results were based on benthos core samples unless stated otherwise.

All organisms were identified to the finest practicable taxonomic level using a dissecting microscope (Appendix 3.1). In general, polychaetes were identified to family, molluscs and crustaceans to species or genus. Some soft-bodied organisms were broken during collection, which is not uncommon in benthos study (Esselink & Zwarts 1989). Measurements of these were still taken and recorded, and they were noted as the head, tail or body segment. Only the larger number of either head or tail parts was counted as the number of individuals of that taxon for the particular sample. Two abundant bivalve species (*Potamocorbula laevis, Mactra veneriformis*) were separated into two groups according to shell length (less than and greater or equal to 10 mm for both species) due to their strong bimodal size distribution that represented different age-classes (young and adult) (Hashizume *et al.* 2012; Wei & Guan 1985b).

Sediment particle size was determined by collecting sediment samples from all sample stations in May 2012, using a 2.6 cm diameter corer to 20 cm deep (n=54 cores). Cores were bagged and frozen until further treatment. Samples were oven-dried at 55°C for at least 72 h and then dried at room temperature for one week. The dried samples were then shaken through four stacked sieves (0.5, 0.25, 0.125, 0.063 mm) and the masses of sediment retained in each weighed to the nearest 0.01 g. Following the Wentworth scale, these sediments represent coarse sand (retained on a 0.5 mm sieve), medium sand

(>0.25 mm), fine sand (>0.125 mm), very fine sand (>0.063 mm) and silt (<0.063 mm) (Wentworth 1922). The distribution of sediment particle size was summarised as the proportion of the sediment dry weight at each of these size classes, representing five different environmental variables.

Two remaining environmental variables, distance to the nearest channel and distance to the seawall (which relates to the duration of submergence), were measured in ArcGIS 10.0 software (ESRI 2010), using the geographic features mapped with GPS in the field.

# 3.3.3 Statistical analysis – Spatial and temporal patterns of the benthic community

Spatial and temporal differences in benthic communities were investigated by using the procedures described in Legendre et al. (2010), which allow a test on the presence of space-time interaction in the community without replication of sampling. Taxa with zero abundance throughout the sampling period were excluded in analyses. We first tested for space-time interactions using y'=log(y + 1) transformation of the benthos abundance data (STI package; Legendre *et al.* 2012). The procedures described above were run three times, the first time using data collected from both sites during 2012, the second time using data collected from the middle site only but between 2011 and 2012, and the third time using 2010 and 2012 data from the eastern site only (period 2 in 2010 was excluded due to missing data from four stations).

Hellinger-transformed benthic abundance data from the entire study were then used in the K-means partitioning and simple structure index described below to visualise the space-time interaction ('cascadeKM' function of the vegan package; Oksanen *et al.* 2013). After that, we assessed the strength and statistical significance of the relationship between benthic taxa distribution and groups of stations partitioned above using indicator species analysis as described below (De Caceres & Jansen 2013).

# 3.3.4 Statistical analysis – Relationship between benthos distribution and environmental variables

Redundancy analysis was used to investigate the relationship between the distribution of benthic taxa in 2012 and seven environmental variables at the sampling stations, namely the proportion of the five different sediment particle size classes (arcsin-transformed to stabilise variances), distance to nearest channel and distance to seawall (both log<sub>10</sub>-transformed to make them close to normal distribution). Benthos abundance data (count

per sample) from all periods within the same year of each sampling station were summed in this particular analysis and taxa with total abundance equal to zero were excluded. Benthos abundance data were Hellinger-transformed before analysis using the 'rda' and 'permutest' function in R's *vegan* package (Oksanen *et al.* 2013). This transformation calculates the Euclidean distance while preserving the asymmetrical distance among stations, which allow the use of redundancy analysis with benthos abundance (Borcard *et al.* 2011). Partial redundancy analysis was carried out to investigate the effect of sediments separately from the nearest distance to channel and seawall. The 'envfit' function (ver 2.0-7, Oksanen et al. 2013) in R's *vegan* package was then used to test the significance of each environmental variable.

The relationship between all benthic taxa and environmental variables was investigated further as follows. First, K-means (a non-hierarchical clustering approach) was used to partition the stations (based solely on Hellinger-transformed benthic abundance data) into two to five groups, then group membership of stations was iteratively re-evaluated by a simple structure index to identify the best partition ('cascadeKM' function of the vegan package; Oksanen *et al.* 2013). Second, ANOVA or Kruskall-Wallis tests were then used to test whether the environmental variables differed significantly between the taxon groups generated from the K-means partitioning.

These redundancy analysis and partitioning procedures were conducted independently using data from the eastern and middle sites to test if associations between benthic taxa distribution and environmental variables were consistent between the two sites. The location of the channel at the eastern site was not recorded, so only six environmental variables were analysed for that site.

After identifying any common environmental variable affecting benthic taxa distributions at both sites, we used this variable to partition the sampling stations into different groups and the association between these groups of stations and benthic taxa was investigated using indicator species analysis. The indicator value index was calculated based only on within-taxa abundance comparisons, which identify the group with the highest association value. The statistical significance of the value of each taxa was assessed by a permutation procedure that compared the observed test statistic with a distribution obtained by permuting the data. The P-value of the permutation test of taxa preference is the proportion of permutations that yielded different association values than that observed within the data (De Caceres & Legendre 2009; Legendre & Legendre 1998). This analysis was done by using 'multipatt' function in *indicspecies* package (De Caceres & Jansen 2013). Holm correction for multiple testing was performed before identifying the significant indicators of the different groups of stations.

An additional redundancy analysis was carried out to analyse the relationship between sediment composition (arcsin-transformed) and distance to seawall ( $log_{10}$ -transformed).

All analyses were performed with R v3.0.1 (R Core Team 2013), using packages *vegan, indicspecies* and *STI*. A significance level of ( $\alpha$ ) 0.05 was used for all statistical tests, with means given±SD unless stated otherwise.

#### **3.4 Results**

#### 3.4.1 Diversity

At least 8,350 specimens of 61 benthic species from 26 different orders were recorded from both grid samples and opportunistic collection (Appendix 3.1). A minimum of twenty four species were new records or clarified the identity of taxa known previously in the study area (Melville 2010; Yan 2008). Among the benthic core samples collected over 3 years, *Potamocorbula laevis* and Flabelligerimorpha worms were the most common taxa sampled, with an average overall density of 605.2±1,516.9 m<sup>-2</sup> and 130.3±197.2 m<sup>-2</sup>, respectively. *P. laevis* was the most abundant species in the sampled area, constituting more than 40% of all specimens collected (Appendix 3.1).

#### 3.4.2 Benthos spatial and temporal patterns

Space-time interaction tests based on benthic samples collected from the eastern and middle sites in 2012 indicated significant spatial and temporal differences in the benthic community within season (p<0.01) (Table 3.1). Significant spatial differences in benthic community occurred within both sites consistently in all years (p<0.05) (Table 3.1). Meanwhile, there were significant temporal differences (p<0.05) in benthic communities at both sites between the periods with enough degrees of freedom for testing, except the temporal differences between April and May in 2012 at the eastern site, which were close to significant (p=0.052) (Table 3.1).

**Table 3.1** Results of space-time interaction analysis of the benthic abundance data collected in theDandong Yalu Jiang Estuary Wetland National Nature Reserve between 2010 and 2012 (all p-valuesafter 9999 permutations; NA - Not enough degrees of freedom to perform test).

		Interac	tion	Temp differ	oral ences	Spatial differe	nces
Site	Period	R <sup>2</sup>	p-value	R <sup>2</sup>	p-value	<b>R</b> <sup>2</sup>	p-value
Eastern and	2012 Mar–Apr	0.10	0.55	0.01	< 0.01	0.80	< 0.01
middle	2012 Apr–May	0.16	0.08	0.02	< 0.01	0.69	< 0.01
Middle	2011 Mar-Apr	0.16	< 0.01	NA	NA	0.64	< 0.01
	2011 Apr–May	0.13	0.29	0.03	< 0.01	0.73	< 0.01
	2011 May–2012 Mar	0.22	0.04	NA	NA	0.60	< 0.01
	2012 Mar–Apr	0.09	0.53	0.01	< 0.01	0.82	< 0.01
	2012 Apr–May	0.14	0.31	0.02	< 0.01	0.72	< 0.01
Eastern	2010 Mar-May	0.25	< 0.01	NA	NA	0.62	0.01
	2010 May–2012 Mar	0.20	0.62	0.05	0.03	0.56	0.04
	2012 Mar–Apr	0.18	0.40	0.05	0.02	0.61	< 0.01
	2012 Apr–May	0.25	0.12	0.06	0.05	0.53	0.02

Results from partitioning indicated that the three-year community data were best partitioned into five groups, and six out of 52 taxa were strong indicators for these groups (Appendix 3.2). The spatiotemporal map based on these results above showed that the middle site (stations A-F) had a mix of all the five different taxa-groups with *P. laevis*-dominated groups being the most common, particularly at stations 1,500 m offshore (Figure 3.2). Areas within 1,000 m of the seawall (stations 1 and 2) were mostly represented by Polychaete, *Ilyoplax* sp. or young *M. veneriformis*-dominated groups. The dominant groups at some individual stations did change over time. The young *P. laevis*-dominated group was widespread in 2011 but not in 2012, having been replaced by adult *P. laevis*, indicating a possible growth in size of the same cohort. Adult *P. laevis* also became less dominant between the start and end of the 2012 sampling period (Figure 3.2) due to its decrease in abundance. In contrast to these patterns at the middle site, the eastern site was characterised mostly by the Polychaete-dominated groups with just a few stations having the *P. laevis*-group as the dominant group.

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Figure 3.2 Spatiotemporal map showing the K-means partition of the sampling stations into five groups. Abscissa: station numbered 1 (nearest to seawall) to 6 (furthest to seawall). Ordinate: sampled period.

Middle site

Eastern site

The number of ghost shrimps counted on the mud surface based adjacent to sample stations also varied between sampling periods and years. It was present at densities of  $0.66\pm1.66$  m<sup>-2</sup> in March 2010 and  $0.05\pm0.14$  m<sup>-2</sup> in April 2010 but was not recorded on the mud surface again in 2011 or 2012.

## 3.4.3 Relationship between benthos distribution and different environmental variables

Sediments were mainly sandy, with fine sand (75.8 $\pm$ 13.2%) as the dominant class, followed by medium sand (14.0 $\pm$ 10.7%). Redundancy analysis of sediment data indicated that there were significant associations between the proportions of different sediment size classes and distances to channel and seawall at both the middle (Pr(>r)=0.0001) and eastern sites (Pr(>r)=0.007), with fine sand being positively associated with the nearest distance to seawall and very fine sand and silt being negatively associated with the nearest distance to seawall at both sites (Appendix 3.4).

The redundancy analysis for the middle site (2012 data) indicated that the environmental variables as a whole explained 41.7% of the variation in the benthos data. The first two canonical axes together explained 19.1% (adjusted R<sup>2</sup>) of the total variance. The permutation test showed that the seven environmental variables as a whole have significant impacts on the distribution of benthic taxa (Pr(>r)=0.0001). Six of the seven environmental variables (all except medium sand) significantly affected the distribution of benthic taxa, with coarse sand ( $R^2=0.73$ ) having the largest impact, followed by the nearest distance to seawall ( $R^2=0.57$ ). However, there was high collinearity among sediment size classes. Parsimony was used to improve the quality of the model, which remained significant (Pr(>r)=0.0001) with a moderate cost in explanatory power (Adjusted  $R^2$  before=0.27, after=0.25).

The triplot based on redundancy analysis (Figure 3.3a) showed that the nearest distance to seawall played an important role in the separation of stations along the first axis, while the proportion of coarse sand played an important role in the separations of stations along the second axis. Adult *P. laevis* were strongly and positively correlated with the nearest distance to seawall, to channel and proportion of fine sand. This was further supported by fine sand having the strongest correlation with adult *P. laevis* when different sediment size classes were fitted onto the ordination (overall Pr(>r)=0.006). Decapoda, *Hemigrapsus* sp., and *Macrophthalmus abbreviatus* were more related to a high proportion of coarse sand. Most other taxa were clumped away from these extremes. They showed

mostly shorter projections, indicating that they are either present over most stations or related to intermediate ecological conditions (Figure 3.3a).



**Figure 3.3** Triplot of the redundancy analysis of the Hellinger-transformed benthic abundance data with fitted station scores at the middle (*a*) and eastern site (*b*) as linear combinations of environmental variables (sediment proportion was arcsin-transformed; nearest distance to channel and seawall were log<sub>10</sub>-transformed), scaling 1. Names of different benthic taxa are represented by the combination of three initial letters from genus and species names, respectively. For benthic taxa that could not be identified to species level, the three initial letters of its finest taxonomic level are used. Full details can be found in Appendix 3.1. Bivalve species ending with '1' and '2' denote young and adult, respectively. "Dist\_cha" and "Dist\_wall" denote distance to channels and distance to seawall, respectively.

Similarly, at the eastern site, the six environmental variables (which did not include distance to channel) had a significant impact overall on the distribution of benthic taxa (Pr(>r)=0.0001). Five environmental variables had significant individual effects (all except coarse sand), with nearest distance to seawall having the largest impact ( $R^2=0.84$ ). The triplot based on redundancy analysis (Figure 3.3b) showed that the proportion of silt and very fine sand played an important role in the dispersion of the stations along the first axis, while the proportion of medium sand played an important role in the dispersion of the dispersion of the stations along the second axis. Young *P. laevis* were strongly correlated with a high proportion of silt and very fine sand. *Nephtys caeca* was positively associated with the proportion of fine sand. Adult *P. laevis*, young *Mactra veneriformis* and *Glycera chirori* were positively associated with the nearest distance to seawall and proportion of medium sand (Figure 3.3b).

Partitioning of different stations at the middle site based on benthic taxa data showed that the stations were best partitioned into three groups, represented by young *M. veneriformis* (p=0.002, Holm-corrected p=0.074), Capitellidae or Maldanidae (p=0.014, Holm-corrected p=0.434), and adult *P. laevis* (p=0.0001, Holm-corrected p=0.0033), respectively. Kruskall-Wallis test showed that the proportion of very fine sand, coarse sand, distance to channel and distance to seawall were significantly different between groups. In comparison to other groups, adult *P. laevis* tended to have a higher proportion of very fine sand (Figure 3.4).



**Figure 3.4** Boxplot of environmental variables in three groups partitioned using data from the middle site in 2012, in the Dandong Yalu Jiang Estuary Wetland National Nature Reserve. Abscissa: group 1 represented by young *Mactra veneriformis*, group 2 mainly by Capitellidae or Maldanidae, group 3 by adult *Potamocorbula laevis*.

Partitioning at the eastern site identified five groups, represented by young *M. veneriformis*, Capitellidae/Maldanidae (non-significant after Holm correction), adult *P. laevis*, young *P. laevis* and *Bullacta exarata*. ANOVA and Kruskall-Wallis tests showed that the proportions of silt and very fine sand and distance to seawall were significantly different between groups. The young *P. laevis*-dominated group was characterised by a high proportion of silt, very fine sand and short distance to seawall, while the adult *P. laevis*-dominated group had larger distances to the seawall (Figure 3.5).



**Figure 3.5** Boxplot of environmental variables in five different groups partitioned using data from the eastern site in 2012, in the Dandong Yalu Jiang Estuary Wetland National Nature Reserve. Abscissa: group 1 represented by young *Mactra veneriformis*, group 2 by Capitellidae or Maldanidae, group 3 by adult *Potamocorbula laevis*, group 4 by young *Potamocorbula laevis* and group 5 by *Bullacta exarata*.

In short, the relationship between taxa and different environmental variables were consistent between redundancy analysis and K-means partitioning approaches. Among taxa commonly found at both sites, adult *P. laevis* were strongly and positively associated with the nearest distance to seawall, while Capitellidae or Maldanidae associated strongly with very fine sand. Since the nearest distance to seawall was the environmental variable that associated strongly and consistently with benthic communities in both the eastern and middle sites, detailed indicator species analysis of the relationship between this environmental variable and benthos was carried out. This

indicated that two of 35 taxa were strong indicators for different groups (Appendix 3.3). *Glycera chirori* was a good indicator of tidal flats 1,000–3,000 m from the seawall (because it mostly occurred in stations across this range; A=0.97, Holm-corrected p=0.051). Adult *P. laevis* were associated with stations 2,000–3,000 m from seawall; it occurred mostly in stations at these distances, although not all stations in this group included the species (A=0.98, B=0.67, Holm-corrected p=0.035).

#### **3.5 Discussion**

This study indicated that bivalve molluscs and polychaete worms dominated the benthic community in the Dandong Yalu Jiang Estuary Wetland National Nature Reserve during the boreal spring, which is consistent with other intertidal flats of the Yellow Sea and Bohai Sea, such as the Yellow River delta in China (Wang *et al.* 2010), and Ganghwa and Saemangeum in South Korea (Choi & Koh 1994; Choi *et al.* 2010). The cultivated shellfish species (*Sinonovacula constricta, Ruditapes philippinarum*) were relatively scarce compared to the naturally-occurring species (Appendix 3.1), indicating that the cultivation was carried out in relatively small patches on the intertidal flat, which was in accordance to our field observations on the scale of shellfish farming (C.-Y. Choi, unpublished data).

#### 3.5.1 Spatial patterns

There were clear spatial zonation patterns of benthos and sediment particle size across the tidal flat in the study area. At the middle site, polychaetes dominated within 1,000 m of the seawall, while bivalves (*Potamocorbula laevis* and *Mactra veneriformis*) dominated from 1,500–3,000 m from the seawall. The eastern site, just 10 km away, was dominated by polychaetes. Sediment compositions between the two sites, however, were similar, being dominated by fine sand that is likely to be transported from the estuary (Wang *et al.* 1986). There was also a generally decreasing proportion of silt and very fine sand but increasing proportion of fine sand towards the sea, which is similar to that reported in the intertidal flat at the Korean side of Yellow Sea (Koh & Shin 1988). As in other studies that investigated the relationship between benthic distribution and different environmental factors (Honkoop *et al.* 2006; Ryu *et al.* 2011a; Sato 2006; VanDusen *et al.* 2012; Wade & Hickey 2008; Yates *et al.* 1993), our results indicated that the distribution of benthic taxa was associated with exposure time (measured as the nearest distance to seawall) and sediment size, both of which might affect the food availability to the benthos (Choi *et al.* 2010; Ysebaert *et al.* 2005).

#### 3.5.2 Temporal patterns

Benthic communities varied both annually and within season. Between-year differences in winter temperatures can have an important influence on mortality and recruitment success of benthic animals (Beukema 1979, 1982; Kimmel & Newell 2007), but whether the temperature differences across the winters were sufficient to cause the observed changes in benthos is unknown (as these values were monthly averages there is no information on how variable or extreme individual days were within those months). The changes in benthos at the middle site between 2011 and 2012 were likely to represent the growth of *P. laevis* of the same cohort, as well as a relatively low recruitment of young *P. laevis* between the years. Large annual variation in bivalve density was also reported in the Dutch Wadden Sea, due to infrequent occurrence of heavy spatfall (Zwarts et al. 1992). Within-season changes could also result from differences in the timing of reproduction between species or result from sustained predation pressure (Weber & Haig 1997). The latter explanation was particularly applicable to this study, where 250,000 migratory shorebirds feed intensively during their northward migration (Riegen et al. 2014). Temporal variations between years and within season in benthic communities indicate that careful assessments are needed when relating different benthic taxa densities to environmental degradation such as seawall construction (e.g. Potamocorbula sp. in Saemangeum; Sato 2006).

One taxon that deserves special attention is the bivalve *Potamocorbula laevis*, which is the main food source for hundreds of thousands of migratory shorebirds in the reserve (C.-Y. Choi et al., in preparation) and Bohai Bay (Yang *et al.* 2013). This mollusc accounted for more than 40% of all specimens collected in our grid samples, and dominated our study area both in terms of abundance and biomass (C.-Y. Choi et al., unpublished data). Interestingly, different *Potamocorbula* species are present in many of the important shorebird sites in the Yellow Sea (BirdLife International 2005) such as the Laizhou Bay (P. laevis; Luo et al. 2013), Yellow River delta (P. laevis; Wang et al. 2010) and Yangtze River estuary in China (P. ustulata; Chen et al. 2009), Ganghwa (P. laevis; Choi et al. 2010), Kyeonggi Bay (*P. amurensis*; Koh & Shin 1988) and Saemangeum in South Korea (*P. amurensis*; Choi & Koh 1994), and Isahaya Bay in Japan just 400 km east of the Yellow Sea in Japan (*Potamocorbula* sp.; Sato & Azuma 2002). Studies on the intertidal flats in Saemangeum and Isahaya Bay seemed to indicate that Potamocorbula sp. increased in density after seawall construction, and therefore this species might do particularly well in disturbed environments (Sato 2006; Sato & Azuma 2002). However, given the timing of their sampling in Saemangeum, those patterns could equally well represent natural instead of seasonal changes similar to those that occur in our study area. At Yalu Jiang

coastal wetland, extensive intertidal flats in the reserve 4 km east of the eastern site were converted to land since 2008. This could be or have become a barrier to the transportation of sediments from the estuary towards the study area (Wang *et al.* 1986). Taking into account extensive pollution created by the aquaculture ponds and paddy fields on the landward side of the seawall (Chang & Chen 2008), as well as anthropogenic activities on the intertidal flats described earlier, it might seem reasonable to link the dominance of *P. laevis* in our study area to environmental disturbances (as attributed in studies in South Korea and Japan; Sato 2006; Sato & Azuma 2002). However, we believe that this is unlikely to be the sole cause as *P. laevis* was reported to be common in the study area back in the early 2000s (Liu & She 2003). Decreasing predatory pressure due to over-exploitation of their predators (such as fishes and crabs), as well as decreasing demand as prawn feeds after a disease outbreak in 1993 (Chang & Chen 2008; Yu 1994) are two other potential causes for the current dominance of *P. laevis* in the study area.

*P. laevis* in the reserve were restricted to the intermediate and lower tidal flats (except the spat at the eastern site in the last sampling period in 2012) and its distribution might therefore be related to the duration of submergence, as with its counterpart *P. amurensis* in Kyeonggi Bay, east of the Yellow Sea in South Korea (Koh & Shin 1988). Reasons for the relatively low abundances of *P. laevis* at the eastern site remain unclear although shellfish farming might play a role because areas with few *P. laevis* in both eastern and middle sites were used for shellfish farming during the study (C.-Y. Choi, pers. obs., mainly *Sinonovacula constricta*). Future study should quantify the potential impact of anthropogenic activities such as shellfish farming and pollution on local benthic communities. The dramatic recruitment variation in *P. laevis* between years was also reported in the *Potamocorbula* sp. in Isahaya Bay (Sato & Azuma 2002). Given the importance of this species as a food source to migratory shorebirds (Yang *et al.* 2013; Choi et al. in preparation), many of which are in rapid decline (Rogers *et al.* 2011; Rogers *et al.* 2010; Wilson *et al.* 2011), there is an urgent need to investigate factors that affect the distribution, abundances and recruitment success of *P. laevis*.

#### 3.5.3 Conclusions

This study confirmed that the distribution of benthic taxa was linked to the duration of submergence, sediment composition and the nearest distance to channels. Significant spatial differences were found between sites that were only 10 km apart, with *P. laevis* dominant at the middle site but less so at the eastern site. Temporal differences also existed, with changes in the dominant groups occurring within a single season. Temporal differences between years were also found in taxa such as young *P. laevis* and surface

ghost shrimps, which were both common in 2010 but not afterwards. These findings are of regional importance as they provide important baseline information for long-term monitoring in a disturbed ecosystem with anthropogenic activities.

Appendix 3.1 Benthos species collected during three years of study in the Dandong Yalu Jiang Estuary Wetland National Nature Reserve. Count was the minimum number of individuals collected from core samples (eastern site in 2010 and 2012; middle site in 2011 and 2012), while the density was presented as mean±SD (individuals per m<sup>2</sup>). Taxon collected from incomplete transects or opportunistic collection was presented without count and density data. Species followed by asterisk are new record or refined record of the study area (Melville 2010; Yan 2008).

	S	Order	Family	Species	Cou	Overall mean	2010	2012	2011 Middle	2012 Middle
			3	4	nt	density	Eastern site	Eastern site	site	site
nozoa Actin	Actin	iaria			23	$3.80 \pm 15.49$	$1.06\pm7.48$	0	$6.37\pm 21.36$	$4.41\pm14.69$
					58	$9.59\pm 20.84$	$1.06\pm7.48$	$15.68\pm 24.39$	$8.32 \pm 20.67$	$11.76\pm 22.1$
ulvia Myo	Myo	ida	Corbulidae	Young	137	226.85±854.0	$1.06\pm7.48$	$167.55\pm 621.$	566.82±1337.	$21.07\pm102.5$
				Potamocorbul	2	6		11	16	4
				a laevis (<10						
				mm)						
				Adult	228	378.31±1221.	0	$5.88\pm 22.20$	336.57±804.3	781.4±1869.
				Potamocorbul	8	11			6	65
				a laevis (≥10						
				mm) *						
Pho	[ohd]	ladomyoida	Laternulidae	Laternula sp.	1	$0.17\pm2.96$	0	0	$0.49\pm5.09$	0
Ven	Ven	eroida	Mactridae	Adult Mactra	9	$0.99\pm 8.32$	0	3.92±17.36	$0.98 \pm 7.17$	0
				veneriformis						
				(≥10 mm)						
				Young Mactra	91	$15.05\pm55.51$	$2.12\pm 14.97$	$41.15\pm 85.17$	$2.94\pm 12.18$	$20.09\pm 68.90$
				veneriformis						
				(<10 mm)						
			Solenidae	Sinonovacula	4	$0.66\pm5.89$	$1.06\pm7.48$	2.94±12.23	0	0
				constricta						
			Tellinidae	Moerella	17	$2.82\pm15.15$	0	$10.80 \pm 31.53$	$0.98\pm7.18$	$1.96\pm10.04$
				iridescens *						
			Tellinidae	Moerella	8	$1.32 \pm 9.29$	0	$3.93\pm 14.01$	$1.96\pm 12.39$	0
				jedoensis *						
			Veneridae	Ruditapes	4	$0.66 \pm 7.23$	0	0	$1.96\pm 12.37$	0
				philippinarum						
				Meretrix	36	$5.95\pm55.73$	0	$0.98\pm7.20$	$16.66\pm95.05$	$0.49\pm5.09$

			meretrix						
Cep	halaspidea	Atyidae	Bullacta exarata	128	21.16±52.73	16.93±47.13	36.25±55.18	26.46±70.32	10.29±23.39
		Restusidae	Retusa cecillii *	2	0.33±5.92	2.12±14.97	0	0	0
		Triclidae	Eocylichna braunsi *	2	0.33±5.92	2.12±14.97	0	0	0
Me	sogastropoda	Stenothyridae	Stenothyra glabrata *	6	1.49±14.74	$1.06\pm7.48$	3.92±28.8	$0.98\pm10.18$	$0.98\pm10.18$
Nec	ogastropoda	Nassariidae	Nassarius variciferus	7	$1.16 \pm 11.41$	0	1.96±14.4	0	2.45±16.79
Euı	nicida	Lumbrineridae		6	$1.49\pm10.58$	0	0	$3.43\pm 16.61$	$0.98\pm7.17$
		Onuphidae	Diopatra bilobata *	33	$0.50\pm 6.61$	0	0	0	1.47±11.34
Fla ha	belligerimorp	Capitellidae or Maldanidae		788	130.29±197.1 6	182.01±258. 80	273.37±263	72.02±133.67	93.08±129.1 7
Neı	reidida	Nephtyidae	Nephtys caeca *	193	31.91±51.53	9.52±34.95	50.96±77.57	29.39±41.13	35.27±47.43
		Nereididae	Perinereis nuntia *		0.17±2.96	$1.06\pm7.48$	0	0	0
0p	heliida	Opheliidae		23	$3.8\pm 17.11$	0	0.98±7.2	$2.94\pm 12.18$	$7.84\pm 25.90$
Ph	yllodocida	Glyceridae	Glycera chirori *	118	19.51±33.32	17.99±31.37	15.68±26.46	17.64±29.83	24.01±39.87
		Goniadidae		53	8.76±27.82	7.4±23.93	$11.76 \pm 44.41$	$12.25\pm 26.68$	$4.41\pm17.9$
Sp	ionida	Spionidae		10	$1.65\pm 12.46$	$4.23\pm 20.95$	0	2.94±15.9	0
Un	identified			372	61.51±90.22	114.29±123. 91	74.47±78.63	52.91±97.59	39.19±51.85
Am	Iphipoda	Haustoriidae		<del>, ,</del>	$0.17\pm2.96$	0	0	0.49±5.09	0
		Odicerotidae	Perioculodes meridichinens is *	20	3.31±15.88	2.12±10.47	2.94±15.98	4.41±16.38	2.94±17.47
		Phoxocephalid ae		1	$0.17\pm2.96$	0	0	0.49±5.09	0
		Talitridae	Orchestia sp.	1	$0.17\pm2.96$	0	0	0	$0.49\pm5.09$

5.39±20.38	$1.47\pm 8.74$	0	$1.96\pm10.04$	0	0.98±10.18	0	0	0	$1.47\pm 8.74$	0	0.49±5.09	3.43±13.09					
4.9±18.5	22.54±61.04	$0.49\pm 5.09$	0	$0.98\pm7.17$	0.49±5.09	$0.49\pm5.09$	$0.98\pm7.17$	$0.49\pm5.09$	0	$0.49\pm5.09$	$1.47\pm 11.34$	5.39±17.63					
6.86±17.94	0	0	0	0	0	0	0	0	0	0	0	0					
$1.06 \pm 7.48$	19.05±69.9	0	0	0	0	14.81±42.81	0	0	0	$1.06\pm7.48$	0	6.35±17.37					
4.79±17.87	$11.08 \pm 46.18$	0.17±2.96	$0.66\pm 5.89$	0.33±4.18	0.50±6.61	2.48±17.85	$0.33 \pm 4.18$	0.17±2.96	0.50±5.11	$0.33 \pm 4.18$	0.66±7.23	3.97±14.57					
29	67	1	4	2	ŝ	15	2	H	ŝ	2	4	24					
Diastylis tricincta *	Nihonotrypae a japonica	llyoplax dentimerosa *	Philyra pisum	Tritodynamia horvathi *	Macrophthal mus abbreviatus *	Macrophthal mus japonicus	Ogyrides orientalis *	Metaplax longipes *	Hemigrapsus sp.			Lingula sp.	Cavernularia sp.	Cyclina sinensis	Umbonium thomasi	Lunatia gilva	Neverita didyma
Diastylidae	Callianassidae	Dotilidae	Leucosiidae	Macrophthalm ida			Ogyrididae	Varunidae				Lingulidae	Veretillidae	Veneridae	Trochidae	Naticidae	Naticidae
Cumacea	Decapoda											Lingulida	Pennatulacea	Veneroida	Archaeogastrop oda	Mesogastropoda	
											Holothuroid ea	Lingulata	Anthozoa	Bivalvia	Gastropoda		
										Chaetognath a	Echinoderm ata	Branchiopod a	Cnidaria	Mollusca			

<i>Thais</i> sp. or <i>Reishia</i> sp.	Salinator sp.	Diopatra chiliensis *	Neanthes japonica *		Sternaspis	scatata .	Heterocuma s	p.	Lophomastix	japonica *	<i>Crangon</i> sp.	Heikea	japonica or	Dorippe	japonica	Latreutes	planirostris *	Exopalaemon	carinicauda	Ligia exotica *	Asterias	amurensis *
Muricidae	Amphibolidae	Onuphidae	Nereididae	Polynoidae	Sternaspidae		Bodotriidae		Blepharipodid	ae	Crangonidae	Dorippidae				Hippolytidae		Palaemonidae		Ligiidae	Asteriidae	
Neogastropoda	Pulmonata	Eunicida	Nereidida	Phyllodocida	Sternaspida		Cumacea		Decapoda											Isopoda	Forcipulatida	
		Polychaeta					Malacostrac	а													Asteroidea	
		Annelida					Arthropoda														Echinoderm	ata

**Appendix 3.2** Indicator species analysis of benthic taxa for the five groups partitioned through Kmeans partition of sampling stations throughout the study. Column 'A' represents the probability that the surveyed station belongs to the target station group given the fact that the species has been found. Column 'B' represents the probability of finding the species in stations belonging to the station group.

Таха	Group	p-value (Holm-corrected)	Α	В
Young Mactra veneriformis	1	0.0517	0.56	0.24
Nephtys caeca	1	0.5535	0.3	0.54
Macrophthalmus japonicus	1	1		
Perioculodes meridichinensis	1	1		
Nihonotrypaea japonica	1	1		
Moerella iridescens	1	1		
Adult Mactra veneriformis	1	1		
Amphipoda	1	1		
Bullacta exarata	1	1		
<i>Orchestia</i> sp.	1	1		
Haustoriidae	1	1		
Macrophthalmus abbreviatus	1	1		
Young Potamocorbula laevis	2	0.0052	0.9	1
Phoxocephalus sp.	2	0.3312	0.47	0.19
Ogyrides orientalis	2	1	1	0.04
Ruditapes philippinarum	2	1		
Lumbrineridae	2	1		
Glycera chirori	2	1		
Laternula sp.	2	1		
Actiniaria	2	1		
<i>Lingula</i> sp.	2	1		
Chaetognatha	2	1		
Opheliidae	2	1		
Cumacea	2	1		
Goniadidae	2	1		
Nemertea	2	1		
Annelida Polychaeta	3	0.0052	0.52	1
<i>Ilyoplax</i> sp.	3	0.0336	1	0.07
Mollusca Bivalvia	3	1	0.88	0.05
Hemileucon hinumensis	3	1		
<i>Hemigrapsus</i> sp.	3	1		
Metaplax longipes	3	1		
Retusa cecillii	3	1		
Eocylichna braunsi	3	1		
<i>Heterocuma</i> sp.	3	1		
Decapoda	3	1		
Echinodermata Holothuroidea	3	1		
Philyra pisum	3	1		
Adult Potamocorbula laevis	4	0.0052	0.91	1
Meretrix meretrix	4	1	0.71	0.1
Nereididae	4	1		
Diopatra bilobata	4	1		
Tritodynamia horvathi	4	1		
Odicerotidae	4	1		
Nassarius variciferus	4	1		
Mollusca Gastropoda	4	1		

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Capitellidae or Maldanidae	5	0.0052	0.56 1
Spionidae	5	1	
Stenothyra glabrata	5	1	
Sinonovacula constricta	5	1	
Diastylis tricincta	5	1	
Veneridae	5	1	

**Appendix 3.3** Indicator species analysis of benthic taxa grouped by nearest distance to seawall, with group 1 being the closest to the seawall (500 m) while group 6 the farthest (3000 m). Column 'A' represents the probability that the surveyed station belongs to the target station group given the fact that the species has been found. Column 'B' represents the probability of finding the species in stations belonging to the station group (De Caceres & Jansen 2013).

Таха	Group	p-value (Holm-corrected)	Α	В
Cumacea	1	1		
Decapoda	1	1		
<i>Hemigrapsus</i> sp.	1	1		
<i>Ilyoplax</i> sp.	1	1		
Macrophthalmus abbreviatus	1	1		
Amphipoda	2	1		
<i>Orchestia</i> sp.	2	1		
Philyra pisum	2	1		
Phoxocephalus sp.	3	1		
Adult Mactra veneriformis	4	1		
Actiniaria	5	0.2656	0.67	0.56
Echinodermata Holothuroidea	5	1		
Sinonovacula constricta	5	1		
Odicerotidae	6	1		
Nihonotrypaea japonica	1+2	1		
Stenothyra glabrata	1+2	1		
Bullacta exarata	1+2+3+4+5	1	0.95	0.56
Capitellidae or Maldanidae	1+2+3+4+5	1		
Perioculodes meridichinensis	1+2+3+4+5	1		
Young Potamocorbula laevis	1+2+3+4+5	1		
Lumbrineridae	2+3+4+5	1		
Nephtys caeca	2+3+4+5	0.1353	0.90	0.89
Opheliidae	2+3+4+5	1		
Annelida Polychaeta	2+3+4+5+6	1		
Diastylis tricincta	2+3+4+5+6	1		
Glycera chirori	2+3+4+5+6	0.051	0.97	0.71
Goniadidae	2+3+4+5+6	1		
Young Mactra veneriformis	2+3+4+5+6	1		
Moerella iridescens	2+3+4+5+6	1		
Nemertea	2+3+4+5+6	0.5239	0.95	0.69
Meretrix meretrix	3+4	1		
Diopatra bilobata	4+5	1		
<i>Lingula</i> sp.	4+5+6	1		
Adult Potamocorbula laevis	4+5+6	0.035	0.98	0.67
Nassarius variciferus	5+6	1		



**Appendix 3.4** Contour map of different sediment size classes using local polynomial interpolation, standard search neighbourhood method in ArcGIS 10.0 (ESRI 2010). Dark shading represents low proportions, light shading high proportions.

**DRC 16** 



#### MASSEY UNIVERSITY GRADUATE RESEARCH SCHOOL

#### STATEMENT OF CONTRIBUTION TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Choi Chi Yeung

Name/Title of Principal Supervisor: Dr Phil Battley

#### Name of Published Research Output and full reference:

Journal article

Choi C-Y, Battley PF, Potter MA, Ma ZJ, Liu WL (2014) Factors affecting the distribution patterns of benthic invertebrates at a major shorebird staging site in the Yellow Sea, China. Wetlands. doi:10.1007/s13157-014-0568-4

In which Chapter is the Published Work: 3

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate: 85% and / or
- Describe the contribution that the candidate has made to the Published Work:

I designed the study, conducted the fieldwork, performed the analysis and wrote the article, with assistance from collaborators who are the co-authors of the article.

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Candidate's Signature

28-July-2014
Date

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30-July-2014

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## Chapter 4. How Migratory Shorebird Species Selectively Exploit Prey at a Single-prey-species-dominated Staging Site

Choi C-Y, Battley PF, Potter MA, Ma ZJ, Melville DS & Sukkaewmanee P (In preparation)

#### 4.1 Abstract

Intense competition is expected at staging sites where high concentrations of migratory shorebirds gather to refuel, using the limited resources available. We investigated whether niche differentiation was evident in the diets of the co-existing shorebirds at a major staging site in the northern Yellow Sea during northward migration in 2011 and 2012, as this is one mechanism by which coexistence of potential competitors can be enabled. Great Knots Calidris tenuirostris, Far Eastern Oystercatchers Haematopus ostralegus osculans and Red Knots C. canutus selected mostly the bivalve Potamocorbula laevis while Bar-tailed Godwits Limosa lapponica had a broader diet and selected mostly polychaetes, even though most of their intake was of *P. laevis*. Although all of these shorebirds fed on *P.* laevis, they showed different size preferences and used different feeding methods. Godwits, Great Knots and Red Knots mainly swallowed *P. laevis* whole and they preferred medium-sized P. laevis with relatively high flesh content to shell mass ratio. In contrast, oystercatchers wedged open *P. laevis* and only ingested the flesh, without paying the price for breaking down hard shells and preferred large P. laevis that provide the highest energetic return per prey taken. Despite evidence for niche differentiation in prey selection, the majority of intake between the numerically most abundant godwits and Great Knots overlapped. Their coexistence seems to be enabled by high resource availability rather than niche separation.

#### 4.2 Introduction

Animal migration has been described as a primary adaptation to exploit periodic and temporary resources (Alerstam *et al.* 2003; Dingle & Drake 2007; Harrington *et al.* 2002). About 62% of shorebirds migrate (Warnock *et al.* 2002). Some are long distance transoceanic and transcontinental migrants that require high quality staging sites to refuel before continuing their journeys (Atkinson *et al.* 2007; Battley *et al.* 2012; Choi *et al.* 2009; Hua *et al.* 2013; Warnock 2010). Along the East-Asian Australasian Flyway (hereafter EAAF), migratory shorebirds have a broad distribution in their wintering and breeding areas, but a much narrower range during their stopovers in East Asia. Intense competition for limited resources is expected at staging sites due to the relatively high concentration of shorebirds, limited time for refuelling and limited resources (Newton 2008; Skagen & Oman 1996), and this is particularly applicable to those staging sites in the Yellow Sea, which is located at the heart of the funnel-shaped landmass of the EAAF (Figure 4.1a). However, little is known about the feeding ecology of shorebirds during stopover along

the East Asian-Australasian Flyway, hindering a better understanding of why they migrate and stop at certain places.

One mechanism for coexistence of potential competitors in a stable environment is niche differentiation, in which species- or size-selection of prey minimises dietary overlap (Begon *et al.* 2006). 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 faecal dropping analysis. Many studies have demonstrated prey selection or prey-size preference in shorebirds, but the focus has been biased towards studying a single shorebird species at a time (Moreira 1994; Piersma *et al.* 1994; Tulp & de Goeij 1994; Zwarts & Blomert 1992; Zwarts *et al.* 1996a), missing a community perspective of how closely related predators coexist. In studies that take a community approach, results have been inconsistent. There was little evidence for niche differentiation in prey size in shorebirds in inland wetlands of North America during migration stopovers (Davis & Smith 2001). In contrast, evidence for different prey or preysize selection among shorebirds was found in coexisting shorebirds during southward migration stopovers in Norway (Lifjeld 1984); and during the non-breeding period in the Netherlands (Zwarts & Ens 1999) and Australia (Dorsey 1981). Differences in reported prey selection are probably partly attributable to the different body size or bill lengths of shorebirds, with larger predators generally taking larger prey, which are often buried deeper in the sediment (Zwarts & Ens 1999).

In this study, we evaluate the degree of dietary overlap in the dominant shorebird species during northward migration at the Dandong Yalu Jiang Estuary Wetland National Nature Reserve, in the northern Yellow Sea, China. This is one of the most important 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* (Chapter 2). Given that the diets of the main species overlap in general terms (bivalves are taken by Far Eastern Oystercatchers *Haematopus ostralegus osculans*, Great Knots and godwits, and polychaete worms by oystercatchers, godwits and Dunlins *C. alpina*; Appendix 4.1), there is considerable potential for competition between these species. We hypothesised that the coexisting shorebirds will show evidence of niche differentiation, which may reduce levels of competition. We also explored some of the key properties of the main prey that make it attractive to the shorebirds.

The shorebird species of main interest in this study are the Bar-tailed Godwit, Great Knot and Far Eastern Oystercatcher. They were chosen because they forage in similar areas in high density, may compete for the same prey and use the study area as

#### Chapter 4. Food selection

their most important staging site during northward migration (19,000 and 49,000 of L. l. menzbieri and L. l. baueri godwit, respectively; 44,000 of Great Knots; 2,400 EAAF's Far Eastern Oystercatchers; Chapter 2; Melville et al. 2014), with the godwits and Great Knots comprising more than 50% of total shorebirds in the study area (Riegen et al. 2014). Attention was also paid to Red Knot C. canutus and Dunlin but results of the latter were only presented for reference. All of the studied species have a cosmopolitan distribution except the Great Knot, which is endemic to the EAAF (Piersma et al. 1996). The Bar-tailed Godwit tends to be a generalist feeder that takes a variety of benthos such as bivalves, crustaceans and cumaceans, but predominantly polychaetes on non-breeding grounds (Duijns et al. 2013; McCaffery & Gill 2001; Piersma 1982; Piersma et al. 1993c; Scheiffarth 2001; Zharikov & Skilleter 2002). In contrast, Great Knot and Red Knot are more specialised on bivalves, although other prey such as polychaetes, crustaceans and gastropods are also taken occasionally (Dekinga & Piersma 1993; Piersma et al. 1993c; Tulp & de Goeij 1994; Yang et al. 2013; Zhang et al. 2011). Meanwhile, Far Eastern Oystercatchers seem to have a broad diet like the Bar-tailed Godwit, and are often seen feeding on molluscs, crustaceans, polychaetes and occasionally insects and fish (Melville et al. 2014).

#### 4.3 Materials and methods

#### 4.3.1 Study area

This study was carried out at the Dandong Yalu Jiang Estuary Wetland National Nature Reserve (39°40'–39°58'N, 123°34'–124°07'E). It is located west of the Yalu Jiang estuary in the northern part of the Yellow Sea, on the Chinese side of China-North Korea border (Figure 4.1). The reserve was founded in 1987 and listed 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 at least 29 species listed as 'Threatened' on the IUCN Red List (IUCN 2012; Yan 2008). The reserve and surrounding area is believed to support 250,000 shorebirds during the northward migration (Riegen *et al.* 2014) and is regarded as an 'Important Bird Area' (BirdLife International 2009) but lacks Ramsar recognition (Ramsar 2012).

The reserve extends for about 70 km along the coast, and is comprised mainly of 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 Dayang

River), with aquaculture ponds and paddy fields on the landward side – a typical coastal landscape of the Chinese coast (Barter 2002; Choi *et al.* 2014; Li *et al.* 2013; Ma *et al.* 2009; Yang *et al.* 2011). The extent of tidal flat exposed during ebb tide varies from about 4 km from the seawall in the middle and the west of the reserve (between sites 5 and 11, Figure 4.1), to around 5 km from the seawall in the east (site 2, Figure 4.1).

Focal bird observations and benthos sampling were carried out in a grid in the middle of the reserve between March and May from 2011 to 2012. These areas were chosen as the study area due to the presence of large numbers of foraging shorebirds during northward migration (Chapter 2; Riegen *et al.* 2014) (Figure 4.1c).



**Figure 4.1** Maps showing the locations mentioned in this paper. (*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 and eastern site.

#### 4.3.2 Benthos sampling

We set up a 9 km<sup>2</sup> (3 x 3 km) grid at the middle site and divided it into 36 grid cells, each of which was 0.25 km<sup>2</sup> (0.5 x 0.5 km) (Figure 4.1c). Benthos were sampled at the centre of each grid cell once a month between March and May in 2011 and 2012 (6 times in total).
Another grid with 18 cells from the eastern site was included in 2012 but the benthos data obtained were only used in analysing the burrowing depth of different prey types. The first sampling was done soon after ice-melt and before the peak arrival of migratory shorebirds while the last sampling was carried out at the end of the migratory period (Chapter 2). One benthos core sample (diameter 15.5 cm, area 0.019 m<sup>2</sup>, depth of 30 cm) was taken at each site. 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 at least 72 hours before placing 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, molluscs 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 it contained the head, tail or body segment.

A subset of benthos collected from sampling stations and opportunistically was used to extrapolate the size-biomass (ash-free dry mass, hereafter AFDM) relationship. Dry mass was obtained by drying the samples at 60°C for 60 hours and the ash mass was obtained by incinerating at 560°C for 5 hours. 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 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. Due to its importance to the diet of shorebirds, the size-specific AFDM of the bivalve *Potamocorbula laevis* was investigated separately for each month in 2012. 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 periods and years, as well as the biomass intake rates of shorebirds.

## 4.3.3 Focal sampling of shorebirds

Shorebird focal observations were conducted within the benthos sampling grid at the middle site between March and May from 2011 to 2012 (97 observations were made on Bar-tailed Godwits between March and May in 2010 but these data were only used in analysing the handling time per prey item). A focal bird was chosen randomly from a flock of foraging birds and watched for 5 minutes, using a 20-60 x telescope. All observations

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were carried out by CYC and DSM, with regular exchange on any abnormal findings and effort was made to alternate observations between Great Knots, and male and female Bartailed Godwits, to minimise sampling bias. Individually marked birds were noted to minimise repeated sampling, which was further lowered due to the large number of birds occuping in the reserve relative to the numbers sampled (932 Bar-tailed Godwits in 3 years, 322 Great Knots in 2 years). Observations were initiated for actively foraging birds only but continued even if the focal bird stopped foraging during an observation bout.

Before the start of each 5-minute observation bout, the date, time, estimated location (based on the benthos grid map), breeding plumage score of the focal bird (Piersma & Jukema 1993) and the number of counterparts 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 (see Appendix 4.2 for a detailed explanation of different behaviours). 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 categorised into eight groups, namely bivalve, crab, gastropod, ghost shrimp, razor clam, polychaete, sea anemone and unknown. Bivalve prey were further divided into 'whole' and 'flesh', where the bivalve prey was swallowed whole in the former but only the flesh was taken in the latter. It was sometimes impossible to see ghost shrimps and small worms when they were taken, but the behaviour of predators when consuming these was quite distinctive and their consumption could be confirmed by inspection of faecal droppings afterwards as well as 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 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 with tension compared to ghost shrimps. Any swallowed prey item that was not seen or deduced with confidence was recorded as unknown.

# 4.3.4 Dietary assessment and prey size selection

Diet composition was determined from swallowed prey items recorded during focal observations in Bar-tailed Godwits, Great Knots, Red Knots and Far Eastern Oystercatchers. 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 were treated

as the AFDM obtained when a focal bird swallowed any of these four 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 since 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 relative to the bill length of the focal bird (Appendix 4.2). The average bill length of different shorebird groups were obtained from banding records at the study area (Ma, Z. unpublished data). 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 at least 30 minutes; they were often pooled into one bag (sample sizes are in Table 1). Droppings collected in the field were kept frozen and later oven dried at 60°C for about 2 days before being kept in zip-lock bags for long-term storage. Samples were then sorted and analysed 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 four jaws as equal to one individual *Glycera chirori* (since most of the jaws found in droppings were *G. chirori*, which has four jaws per individual) and six 'plier-shaped' pereopods as one ghost shrimp (since most of the ghost shrimps have three 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 in droppings were used to estimate the length of the ingested shell by regressing shell length on height of left hinge (n=371, R<sup>2</sup>=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 length 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. Then the weighted average AFDM of two size classes (<10 $\geq$ 40 mm) taken by godwits and knots were estimated by month. This gave the biomass contribution of young and adult *P. laevis* to the diet 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 and were assumed to be the same as Dunlin due to their similar bill length. The relationships between AFDM and body size in different benthos groups were summarised in Appendix 4.3. For unidentified prey items, the overall average AFDM per individual benthic item collected in that particular period was used.

# 4.3.5 Data analysis

## 4.3.5.1 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 those observations that lasted for at least 2.5 mins and with all prey items identified were included in this analysis.

Following Manly et al. (2002),  $d_i$  is the difference between the relative use and availability of prey *i* and *j* for *i*<sup>th</sup> individual bird, 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  $\pi_{ai}$  is the available proportion of prey type *i*. Zero values in rare prey type availability or usage were replaced by 0.00001 when calculating  $d_i$  to allow logarithmic calculation to proceed (Aebischer *et al.* 1993; Warton & Hui 2011). Prey types that was unused was excluded in the analysis. Wilk'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).

## 4.3.5.2 Size selection of *Potamocorbula laevis*

In our investigation on *P. laevis* size-selection among different shorebird species, the prey use and availability were compared at the population level because droppings were

pooled during collection (Design 1, Manly *et al.* 2002). The selection ratio for *P. laevis* size class *i* in different shorebirds was calculated as

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

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 standardised selection ratio was calculated as

$$B_i = \widehat{w}_i \left/ \left( \sum_{i=1}^l \widehat{w}_j \right) \right|$$

where *I* is the total number of possible size classes. Selection ratios equal to 1/I denotes the absence of selection, larger than 1/I denotes selection and less than 1/I denotes avoidance (Chesson 1978). The Manly's standardised selection ratio gives an estimated probability for each *P. laevis* size class being 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 for the proportion of use when the null hypothesis was rejected. Bailey's confidence intervals were used instead of other confidence intervals because the former was less sensitive to small sample sizes and had lower error rates (Cherry 1996).

#### 4.3.5.3 Prey quality, handling time and efficiency

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

The successful handling time is the time needed during the handling process that leads to the swallowing of a prey item. We calculated the handling time from focal bird observations between 2010 and 2012 by subtracting the time a prey item was swallowed from the time at the previous foraging peck or probe. In contrast to other researchers who calculated handling efficiency by taking into account negative handling time (handling that led to rejection of prey), we only estimated the handling efficiency for events when 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 (seconds) (Ens *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 was used.

All data from focal observations were used to estimate handling time and profitability, but only those that lasted for at least 2.5 mins were used in estimating the frequency of multiple prey species. Moreover, cases lasting for at least 2.5 mins and with all prey identified were used in prey selection and numerical intake rate analyses. Similarly, only the observations with total foraging time of at least 2.5 mins and with all prey identified were used to estimate the biomass intake rate. All analyses were performed with Microsoft Excel ©. A significance level of ( $\alpha$ ) 0.05 was used for all statistical tests, with means given±SD unless stated otherwise.

# 4.4 Results

# **4.4.1 Prey selection**

Observations of foraging individuals and analysis of droppings confirmed that the bivalve *Potamocorbula laevis* was the dominant prey item in the diet of Bar-tailed Godwits, Great Knots, Far Eastern Oystercatchers and Red Knots (Table 4.1, Table 4.2), constituting 73–99% of the identified prey items during standardised observations (95-99% of prey swallowed by knots and oystercatchers were identified; for godwits 68% were). Individual Great Knots and Oystercatchers typically fed upon just a single prey type during a 5-min observation period whereas godwits more frequently fed upon multiple prey species (Table 4.3). Godwits and knots swallowed *P. laevis* whole whereas oystercatchers prised open the valves and extracted the flesh. Dunlins and occasionally godwits also fed from shells presumably opened by oystercatchers.

Table 4.1 Numerical intake rates (prey per minute) of different shorebirds at Yalu Jiang based on focal observations. Species abbreviations: BAG0=Bar-tailed Godwit, GRKN=Great Knot, FEOY=Far Eastern Oystercatcher and REKN=Red Knot.

YearSpecies (sex)Sample sizeBivalveSea anemonePolychaeteGastropodCrab2011BAG0 (all)77 $11.5\pm11.97$ $0.01\pm0.05$ $0.44\pm0.7$ $3.7\pm0.51$									
2011BAG0 (all)77 $11.5\pm11.97$ $0.01\pm0.05$ $0.44\pm0.7$ BAG0 (female)36 $8.86\pm10.98$ $0.37\pm0.51$ $0.37\pm0.51$ BAG0 (male)35 $13.67\pm12.18$ $0.01\pm0.07$ $0.47\pm0.83$ BAG0 (male)37 $6.93\pm7.13$ $0.01\pm0.07$ $0.47\pm0.83$ CRNN37 $6.93\pm7.13$ $0.01\pm0.06$ $0.6\pm1.02$ BAG0 (all)181 $1.81\pm2.13$ $0.01\pm0.06$ $0.6\pm1.02$ BAG0 (all)84 $1.32\pm1.75$ $0.02\pm0.06$ $0.6\pm1.02$ BAG0 (male)84 $1.32\pm1.75$ $0.01\pm0.07$ $0.56\pm1.02$ BAG0 (male)90 $2.16\pm2.32$ $0.01\pm0.07$ $0.02\pm0.08$ FEOY40 $4.41\pm2.74$ $0.02\pm0.08$ $0.02\pm0.08$ REN14 $1.65\pm0.85$ $0.02\pm0.08$ $0.02\pm0.08$	Year	Species (sex)	Sample size	Bivalve	Sea anemone	Polychaete	Gastropod	Crab	Ghost shrimp
	2011	BAGO (all)	77	$11.5\pm 11.97$	$0.01 \pm 0.05$	$0.44\pm0.7$			$0.23\pm0.81$
		BAGO (female)	36	8.86±10.98		$0.37 \pm 0.51$			0.28±0.95
RKN 37 6.93±7.13 0.01±0.03   2012 BAG0(all) 181 1.81±2.13 0.01±0.06 0.6±1.02 0.01   BAG0 (all) 181 1.81±2.13 0.01±0.06 0.6±1.02 0.01   BAG0 (female) 84 1.32±1.75 0.02±0.06 0.6±1.02 0.01   BAG0 (female) 84 1.32±1.75 0.01±0.07 0.56±1.02 0.01   BAG0 (female) 90 2.16±2.32 0.01±0.07 0.56±1.02 0.02   CRKN 172 1.61±1.09  0.01±0.07 0.05±0.08   FEOY 40 4.41±2.74  0.02±0.08 0.02±0.08   REKN 14 1.65±0.85  0.02±0.08 0.02±0.08		BAGO (male)	35	$13.67 \pm 12.18$	$0.01 \pm 0.07$	$0.47\pm0.83$			$0.21\pm0.71$
2012 BAG0 (all) 181 1.81±2.13 0.01±0.06 0.6±1.02 0.01   BAG0 (female) 84 1.32±1.75 0.02±0.06 0.6±0.95 0.01   BAG0 (female) 84 1.32±1.75 0.01±0.07 0.56±1.02 0.02   BAG0 (male) 90 2.16±2.32 0.01±0.07 0.56±1.02 0.02   BAG0 (male) 90 2.16±2.32 0.01±0.07 0.56±1.02 0.02   FEOY 172 1.61±1.09 1.61±1.09 0.01±0.07 0.01±0.06 0.02   FEOY 40 4.41±2.74 0.01±0.07 0.02±0.08 0.02±0.08   REKN 14 1.65±0.85 0.02±0.08 0.02±0.08 0.02±0.08		GRKN	37	6.93±7.13		$0.01\pm0.03$			
BAG0 (female) 84 1.32±1.75 0.02±0.06 0.6±0.95   BAG0 (male) 90 2.16±2.32 0.01±0.07 0.56±1.02 0.02   BAG0 (male) 90 2.16±2.32 0.01±0.07 0.56±1.02 0.02   CRKN 172 1.61±1.09 1.61±1.09 0.01±0.06 0.02   FEOY 40 4.41±2.74 0.02±0.08 0.02±0.08   REKN 14 1.65±0.85 0.02±0.08	2012	BAGO (all)	181	$1.81\pm 2.13$	$0.01 \pm 0.06$	$0.6\pm 1.02$		0.01	$0.06\pm0.24$
BAG0 (male) 90 2.16±2.32 0.01±0.07 0.56±1.02 0.02   GRKN 172 1.61±1.09 0.01±0.06 0.01 0.01 0.02   FEOY 40 4.41±2.74 0.02±0.08 0.02±0.08 0.02±0.08 0.02±0.08		BAGO (female)	84	$1.32 \pm 1.75$	$0.02\pm0.06$	$0.6\pm 0.95$			$0.08\pm0.29$
GRKN 172 1.61±1.09 0.01±0.06 0.01   FEOY 40 4.41±2.74 0.02±0.08 0.02±0.08   REKN 14 1.65±0.85 0.02±0.08 0.02±0.08		BAGO (male)	60	2.16±2.32	$0.01 \pm 0.07$	$0.56\pm 1.02$		0.02	$0.04\pm0.19$
FEOY 40 4.41±2.74 0.02±0.08   REKN 14 1.65±0.85		GRKN	172	$1.61 \pm 1.09$			$0.01 \pm 0.06$	0.02	
REKN 14 1.65±0.85		FEOY	40	$4.41\pm 2.74$			$0.02\pm0.08$		
		REKN	14	$1.65\pm0.85$					

Prey type	Bar-tailed Godwit 2011-2012	Great Knot	Far Eastern 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
# pooled samples	16	37	1*	5
# droppings	315	692	20	5

**Table 4.2** Diet composition based on analyses of droppings collected in the field in Yalu Jiangcoastal wetland. Values are percentages (weighted average) of all identified prey items.

**Note:** \* This sample contained just two polychaete jaws and one bivalve hinge, reflecting the different feeding method used by oystercatchers when feeding on *P. laevis*.

**Table 4.3** Frequency (percentage of total observations) of multiple prey species being taken during 5-min intake rate observations, after excluding cases with observation time less than 2.5-min, with unknown prey type, or with no prey item swallowed during the observation. Numbers in parentheses represent sample sizes.

Number of	Bar	tailed Go	odwit	Great	Far-Eastern		
prey types taken	Female (275)	<b>Male</b> (308)	Unsexed (25)	<b>Knot</b> (228)	Oystercatcher (41)	<b>Red Knot</b> (15)	Dunlin (6)
1	68	66.2	64	96.9	97.6	100	83.3
2	30.2	30.2	36	3.1	2.4	0	16.7
3	1.8	2.9	0	0	0	0	0
4	0	0.6	0	0	0	0	0

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, Far Eastern Oystercatchers and Red Knots, bivalves and polychaetes by male godwits, and polychaetes by female godwits (Table 4.4).

**Table 4.4** Prey species selection by shorebirds on northward migration in Yalu Jiang coastal wetland in 2011 and 2012. The ranking of six different prey types was based on 5-min focal bird observation (sample size in parentheses) and ash-free dry mass of prey. Prey type that was not taken was 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). "Biv" denotes bivalve, "Cra" for crab, "Gas" for gastropod, "Gho" for ghost shrimp, "Pol" for polychaete and "Sea" for sea anemone.

	Bar	-tailed God	wit			Red
Species	<b>Overall</b> (258)	<b>Male</b> (125)	<b>Female</b> (120)	Great Knot (210)	Far Eastern Oystercatcher (40)	<b>Knot</b> (14)
	Pol <sup>a</sup>	Biv <sup>a</sup>	Pol <sup>a</sup>	Biv <sup>a</sup>	Biv <sup>a</sup>	Biv
	Biv <sup>b</sup>	Pol <sup>a, b</sup>	Gho <sup>b</sup>	Cra <sup>b</sup>	Gas <sup>b</sup>	
Rank order	Gho <sup>b</sup>	Gho <sup>b</sup>	Biv <sup>b</sup>	Pol <sup>c</sup>		
oraci	Cra <sup>c</sup>	Cra <sup>c</sup>	Sea <sup>c</sup>	Gas <sup>d</sup>		
	Sea <sup>d</sup>	Sea <sup>d</sup>				
Wilks'	0.004	0.007	0.446	0.040	0.000	
Lambda	0.294	0.226	0.416	0.048	0.333	N.A.
p value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	N.A.

## 4.4.2 Size-selection of *P. laevis*

The size composition of *P. laevis* was remarkably different between years, with two cohorts present in 2011 but only one in 2012 (Figure 4.2a, Figure 4.2b) and yet there was a 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<sup>-2</sup> in 2011 to 21 m<sup>-2</sup> in 2012 while the adults increased from an average of 337 m<sup>-2</sup> to 781 m<sup>-2</sup>. Knots and the godwits that swallowed *P. laevis* whole preferred mostly 7-14 mm long *P. laevis* based on the standardised selection ratio (Figure 4.2c), while the godwits, oystercatchers and Dunlins that fed only on the flesh of *P. laevis*, preferred those with shell lengths of  $\geq$ 15 mm (Figure 4.2d). Statistically significant differences between the proportions taken and available were found in some *P. laevis* size classes for all the shorebird groups investigated (all with  $\chi^2$ <0.01, Appendix 4.4). Comparison between the available proportions of each

size class relative to its respective 95% Bailey confidence interval of used proportion (Appendix 4.4) were consistent to the preferences observed from the standardised selection ratios (Figure 4.2).



**Figure 4.2** Selection of different sized bivalve *Potamocorbula laevis* by different shorebird groups 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, with white bars representing availability. Standardised 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 line.

# 4.4.3 Prey properties

## 4.4.3.1 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) while 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). Moreover, among the bivalve prey taken by shorebirds, 30% were captured through pecks and 66% through short probes (n=9,466), indicating that most bivalve prey were available near the surface.

## 4.4.3.2 Prey quality

The AFDM per *P. laevis* increased with size and also within season across the monthly samples taken in 2012 (Figure 4.3a). However, as shell mass also increased similarly with length (Figure 4.3b), the quality (energy in relation to shall mass ingested) decreased to c. 11–12 mm length, after which it remained roughly constant across larger sizes (Figure 4.3c). Because of the increase in AFDM through the season, the quality also increased from March to May (Figure 4.3c). The quality of *P. laevis* collected in Bohai was remarkably lower than that collected in Yalu Jiang coastal wetland.

## 4.4.3.3 Handling time and efficiency

Handling time varied substantially between prey types. Godwits took an average of 1–4.5 seconds to handle bivalve prey, about 6 seconds for sea anemone and ghost shrimp, and 9 seconds to handle a long worm (Appendix 4.5). They rarely spent more than 10 seconds handling a prey item. The two knot species had similar diets and took about 2 seconds to handle bivalves. Great Knots occasionally fed on gastropods and rarely on crabs; these took on average 40 seconds to handle. Oystercatchers fed mostly on bivalve flesh, which took on average 5 seconds to handle. Like the Great Knots, oystercatchers occasionally fed on gastropods that took more than 40 seconds 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 the highest among all shorebird groups (Appendix 4.6). The efficiency rank in godwits was followed by polychaetes and ghost shrimps, which are the other selected prey types. Nevertheless, there were high variations in the handling efficiency between focal birds.



**Figure 4.3** Changes in prey quality with length for *Potamocorbula laevis*. (A) AFDM, (B) shell dry mass, and (C) energy in relation to shell mass. Ten samples from Bohai Bay are included to show the contrasts between study areas.

The biomass intake rate of all shorebird groups were dominated by *P. laevis*, which comprised more than 90% of the total intake in knots and oystercatchers (Table 4.5). The contribution of large *P. laevis* to total intake was consistent between years in all shorebird groups despite total intake rates being halved in 2012 (Table 4.5). The disappearance of *P. laevis* in 2012 was, to an extent, replaced in godwits by the uptake of bivalve flesh from opened shellfish.

Table 4.5 Biomass intake rate (AFDM mg s<sup>-1</sup>) of different shorebird groups on different prey types. Numbers in bracket denote the percentage of total intake. Taxa are those listed in Table 4.1.

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)	$0.44\pm0.48$ (22)	1.19±1.3 (60)		$0.28\pm0.59$ (14)	0.03±0.2			$0.04\pm0.14$
	BAGO (female)	34	1.73±1.47	1.34±1.68 (78)	$0.34\pm0.44$ (20)	1±1.31 (58)		0.33±0.64 (19)				$0.05\pm0.16$
	BAGO (male)	34	2.24±1.49	$1.9\pm1.72$ (85)	$0.51\pm0.49$ (23)	$1.39\pm1.31$ (62)		0.27±0.59 (12)	0.05±0.27			$0.04\pm0.12$
	GRKN	29	1.8±1.65	$1.8\pm 1.65$ (100)	0.3±0.32(17)	$1.49\pm1.34$ (83)						
2012	BAGO (all)	170	$1.01 \pm 0.81$	0.77±0.88 (76)	$0.01\pm0.01(1)$	$0.63\pm0.81$ (62)	$0.13\pm0.48$	$0.19\pm0.38$ (19)	$0.04\pm0.17$		$0\pm 0.01$	$0.01 \pm 0.05$
	BAGO (female)	79	0.91±0.69	0.56±0.73 (61)	$0\pm 0.01$ (1)	$0.49\pm0.66$ (53)	0.07±0.38	$0.28\pm0.47$ (31)	$0.05\pm0.18$			0.02±0.07
	BAGO (male)	84	1.06±0.89	0.92±0.95 (87)	$0.01\pm0.01(1)$	$0.71\pm0.88$ (68)	0.2±0.57	$0.1\pm 0.21$ (9)	$0.02 \pm 0.17$		$0\pm 0.01$	$0.01 \pm 0.04$
	GRKN	128	0.81±0.48	0.74±0.48 (92)	0.01±0.01 (1)	$0.69\pm0.47$ (85)	$0.04\pm0.2$			$0.07\pm0.31$		
	REKN	10	0.73±0.44	0.73±0.44 (100)	$0.01\pm0(1)$	$0.64\pm0.36$ (88)	0.08±0.13					
	FEOY	38	2.7±1.5	2.65±1.55 (98)			2.65±1.55			$0.05\pm0.19$		
	DUNL	4	0.77±0.16	0.76±0.17 (99)			0.76±0.17				0.01±0.02	

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# 4.5 Discussion

This study provides evidence for 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 co-existing shorebirds, the numerically most abundant Bar-tailed Godwits and Great Knots rely heavily on similar size ranges of one single bivalve species. This indicates that niche differentiation cannot explain the coexistence of the shorebird community during the two years of study.

# 4.5.1 Food selection

The bivalve *P. laevis* was the most important prey type for the coexisting shorebird species during their stopover. Great Knots, Far Eastern 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 godwits had a broader diet with polychaetes as their most selected prey. Female godwits selected polychaetes more than bivalves but both of these prey were equally selected by males. Meanwhile, ghost shrimps had a higher selection ranking in female than male godwits. The differences between the sexes might stem from the longer bills in females that allow them to reach deeper when feeding on polychaetes and ghost shrimps (mean bill lengths at the study site are 84.7±4.83 mm (n=51) in males and 108.1±7.33 mm (n=46) in females; Ma, Z. unpublished data). This was similar to the usage pattern found in the Bar-tailed Godwits in Europe during northward migration (Scheiffarth 2001); this does not necessarily imply different selection *per se*, as prey availability was not considered.

In addition to the different food selection between species and sexes, the coexisting shorebird groups also differed in their prey-size preference depending on the feeding strategies they used. When *P. laevis* was swallowed whole by godwits, Great Knots and Red Knots, shell lengths of 5–15 mm were preferred; when only flesh was taken by godwits, oystercatchers and Dunlins, shell lengths of 15–20 mm were preferred. Such a difference in prey size preference within the coexisting shorebird community was in accordance to those reported in Australia (Dorsey 1981) and Europe (Lifjeld 1984; Zwarts & Ens 1999). Oystercatchers had the longest handling time when taking flesh out of *P. laevis* compared to other shorebird groups, which may indicate that oystercatchers were

the only group that actively opened up *P. laevis* while other shorebird groups simply scavenged on what remained. The average of 5 seconds handling time was significantly less than those reported for bivalve-feeding oystercatchers in Europe that spent at least 16 seconds when feeding on *Scrobicularia plana* (Wanink & Zwarts 1985).

# 4.5.2 Why Potamocorbula laevis?

P. laevis is clearly the dominant dietary item across a suite of species at Yalu Jiang (Appendix 4.1). This implies that it is accessible, detectable, ingestible, digestible and profitable (Ens et al. 2004). Indeed, the general properties of P. laevis seem to meet all of the requirements listed. They occurred in high densities (mean 597 m<sup>-2</sup>) and could reach up to 11,270 m<sup>-2</sup> in some areas (Chapter 3). They were mostly distributed within 5 cm of the surface and their siphons left clear traces of holes on sediment surface (C.-Y. Choi, pers. obs.), making them both accessible and detectable for the shorebirds studied. P. laevis in our study area seldom reached a length of more than 23 mm, which allowed most of them to be swallowed by even Red Knots (Tulp & de Goeij 1994), the second smallest shorebird in this study. The force required to crush the shell of small *P. laevis* was found to be within range for other bivalves fed on by shorebirds in the Dutch Wadden Sea (Yang et al. 2011). Finally, the relatively short handling time with high energy gain compared to other prey types made *P. laevis* a profitable prey to shorebirds. The short handling time also presumably lowers the chance of interference and kleptoparasitism (van Gils & Piersma 2004), which were not uncommon between Bar-tailed Godwits and other species such as Black-headed Gull Chroicocephalus ridibundus and between godwits themselves (Boyle & Slaymaker 2010; Dann 1987; Choi pers. obs.).

# 4.5.3 Why medium-sized Potamocorbula laevis?

Most of the energy intake of Bar-tailed Godwits, Great Knots and Red Knots came from large bivalves ingested whole, even though small ones were taken preferentially. Nevertheless, taking *P. laevis* as the main food source came with some costs, which included the cost of digesting the hard shells if *P. laevis* is to be swallowed whole. It was demonstrated that Red Knots in Europe selected high quality prey (high meat to shell ratios) (van Gils *et al.* 2005b) and interestingly, prey quality also explained the different size selection of *P. laevis* between birds with different feeding strategies. Although the energy content in *P. laevis* increased with shell length, the prey quality did not and this

might explain why birds that swallowed *P. laevis* whole preferred larger small *P. laevis* and smaller large *P. laevis* (shell lengths of 7–14 mm), which was consistent in both years despite the different size ranges available. This upper prey size limit related to prey quality is in contrast to studies that suggested the upper prey size limit was set by accessibility (deeper burying depth in larger bivalves) or handling ability (gape size of the predators) (Baird *et al.* 1985; Zwarts & Wanink 1989). On the other hand, when birds did not have to pay the price for processing the hard shells, they preferred the large *P. laevis* that contained higher energy content. It should also be noted that the mean arrival time of Bar-tailed Godwits and Great Knots were end of March and early April (Chapter 2), which was two to three weeks after the first benthos sample taken, coinciding with an increase in the quality of *P. laevis*.

The selection for different prey types and preference for different prey sizes by the coexisting shorebirds studied fit with that expected from optimal foraging theory. However, such differences might also be inevitable when the morphological limitation of these birds were considered. In addition to the different bill length already discussed, the fact that most *P. laevis* are equally accessible to those shorebirds studied seems to suggest that other limiting factors may be in play. Red Knots have specialised sensory organs in their bill tips to detect hidden prey more efficiently than oystercatchers (Cunningham et al. 2013; Ens et al. 2004; Piersma et al. 1998). The Red Knots and Great Knots also have a much heavier stomach relative to their body mass compared to oystercatchers and godwits (Great Knots 44% heavier than average, Red Knots 89% heavier, godwits and oystercatchers have stomach mass lower than would be expected for their body mass; Piersma et al. 1993c). This may explain why Great Knots and Red Knots have a diet dominated by *P. laevis* and how the birds could ingest their prey whole. The relatively standard stomach-to-body mass ratio in godwits means that they are not as specialised as the two knots species to a solely bivalve diet, and hence, they have a broader diet and actually select polychaetes and ghost shrimps. However, it was interesting that the oystercatchers fed solely on *P. laevis* despite the availability of polychaetes and ghost shrimps, and given their bill length. In the oystercatchers, there is evidence that their bill tips may have a larger horny layer of keratin than the Bar-tailed Godwits and Red Knots (Cunningham et al. 2013; Piersma et al. 1998), which may make them more suited than godwits in opening the *P. laevis* and only ingesting the flesh than godwits, but less suited to detecting prey buried deep in the mud.

# 4.5.4 Future direction

This study demonstrated prey niche partitioning in a coexisting shorebird community at a staging site during northward migration. Such partitioning may reduce direct competition among these closely related and coexisting shorebird groups, yet there was evidence of direct competition between the numerically most abundant godwits and knots, as reflected by their similar prey size preference and biomass intake rate. Their coexistence was enabled by the high resource availability rather than by niche differentiation. It is therefore important to control any commercial or unsustainable harvest of *P. laevis*, which is a common practice along the Chinese coast because *P. laevis* can be used to feed prawns in aquaculture and poultry and are also used to produce fertilizer (Wei 1984; Wei & Guan 1985a). Studies on the life history and habits, especially natal dispersal, of *P. laevis* will assist in the development of a more thorough conservation plan for shorebirds in the Yellow Sea. Long term monitoring on how the studied shorebirds respond to changes in P. laevis abundance will be interesting. Investigations on the foraging ecology of Red Knots and other shorebirds such as Far Eastern Curlews Numenius madagascariensis, Eurasian Curlews Numenius arguata and Grey Plovers Pluvialis squatarola will create a more complete picture of how these shorebirds coexist in this important staging site during their migration and the possible role of competitive exclusion in shaping the differential use of staging grounds in Red Knots and Great Knots. Given the rapid intertidal habitat loss in Yellow Sea (Murray et al. 2014), there is an urgent need not only to identify important staging sites, but also critical feeding areas within staging sites to prioritise conservation efforts.

(γίπο dsəft) (γίπο dieseli) (γίπο dieseli)	S											S				S
snomens sed	S					Γ				G						S
Potamocorbula laevis (flesh only)	S	s								S		S		S		
Potamocorbula laevis	S	s	S			S				S, G	S	S	L	S	Г	S
Polychaeta	S	s	S		S			S	S	S		S		L, G*		S
unsid pıAjiya	S								S	S				S		
οριασί συστλουσικα	S			S					S	G						
Nemertean	S															
Mactra veneriformis (flesh only)	S															
Aacrophthalmus sp.	S															
Nacrophthalmus ababreviatus	r															
avlia gilva	r													S		
.qs nugaid	L									S						
Laridae or Sternidae																
stoesni																
Grey-backed Тhrush																
epodoatsed	S, G											S, G		S, G		
Decapoda (shrimps not ghost Drimp)	S															
(qminda) sboqaə	Ī													S		
Decapoda (Mantis shrimp)				Γ												
Decapoda (crab)																S
ΒυίΙαςτα ecarata	S								S					S		
៣ព្រិ០រៀ							Γ									
sboqidqmA																
					L							cher				
ĥa	vit	ull	dwit	1	ndpipe	shank	ıck	er			lew	tercato				
Ě	d Gody	aded G	led Go	led Gu	lled Sa	Green.	Sheldı	andpip	b.		ern Cur	ern Oys	7	ot	caup	ver
edator	ur-taile	ack-he	ack-tai	ack-tai	id-bao	mmon	mmon	Irlew S	Irlew s	ulin	Ir Easte	Ir Easte	Irganey	eat Kn	eater 5	vold Va.
L I	B	BI	BI	BI	BI	3	S	C	C	õ	Fa	Fa	ß	5	3	5

Appendix 4.1 Casual records of predation and prey between 2010 and 2012 on the intertidal flat. "S" denotes seen eaten; "L" denotes likely to be eaten; "G" denotes predator handled prey but gave up. Cases were regarded as "likely" when the swallowed items were not distinguishable but the behaviour of birds was distinctive to the ordinary tide-following movement. In the insect example, the birds were seen feeding on abandoned and dried shells outside a shellfish processing factory. These shells did not have much flesh on them but attracted many flies and birds were seen feeding for a substantial amount of time and in several occasions. Similarly for the biofilm, a big flock of shelducks and some Red-necked Stints were seen foraging on soft sediment near seawall. They continued to forage in the area even the tide retreated to more

than 1 km from the seawall. The shelducks were clearly sieving through the mud surface for unknown prey types, which might be biofilm.

Chi-Yeung Choi- July 2014

selection
4. Food
Chapter

	S S	S	S	Л	S		S	S	S S	S	S S	S,G S S	S S S S	S S	J	S	S
-	-					SS			Γ	G	Г						L
d Trattler	ull	over	udplover			Falcon	uns		ed Stint L		rnstone	Т	s Gull	ed Sandpiper		edshank	dpiper L

Note: \* There was an occasion (2-May-2012) when a long polychaete about 4 times of the full bill length of a Great Knot, was picked up by 3 different Great Knots but all of

them eventually gave up and rejected the prey.

**Appendix 4.2** Definitions of different behaviours and prey items during focal bird observation. Different prey size was noted only in polychaetes.

Behaviour	Definitions
Preening	Any maintenance behaviour, mostly preening feathers but also included scratching and leg-stretch
Resting	Rest, often standing with one leg and bill tucked in the back feathers
Vigilant	Often standing still, the head elevated higher above the trunk, bill directed to horizontal level
Flushed	Take off
Out of sight	Out of sight
Interaction	Interaction (note down the species that the focal object interacted with)
Foraging	On the move, trunk inclined slightly downwards, bill directed downward and apparently looking at the ground rather than being alert
Peck	Bill only touched the surface of the substrate
Short probe	Less than half of the bill inserted into the substrate
Deep probe	More than half of the bill probed into the substrate
Swallow	Clear bill opening and closing followed by neck retraction or prey item being seen before being swallowed
Defecate	Dropping seen
Short worm	Worm shorter than half of the bill length
Medium worm	Worm longer than half bill but shorter than full bill length
Large worm	Worm longer than full bill length
Bivalve whole	Whole bivalve was swallowed
Bivalve flesh	Only the flesh of bivalve was swallowed

**Appendix 4.3** The relationship between AFDM (*A*, g) and body size (*L*, mm) in different benthos groups. The length of short, medium and long polychaetes taken by Bar-tailed Godwits were estimated to be 23.92, 71.8 and 116.9 mm in unsexed birds (n=102); 21.18, 63.53, and 111.35 mm in males (n=51); 27.03, 81.08 and 123.05 mm in females (n=46). The length of short polychaetes were estimated to be ¼ of a bird's average bill length, and medium polychaetes to be ¾ of average bill length. The length of long polychaetes was estimated by dividing the difference between average full bill length and longest polychaete (from benthos grids sampling) by two. The AFDM values for *Potamocorbula laevis* flesh was estimated to be 72% of a complete *P. laevis* if taken by a Bar-tailed Godwit, 93% by a Far Eastern Oystercatcher and 61% by a Dunlin (based on measuring the AFDM left in the *P. laevis* remains collected). Great Knot and Red Knot were assumed to have taken the same proportion as Dunlin due to their similar bill length.

Benthos group	Relationship	<b>R</b> <sup>2</sup>	N
Potamocorbula laevis 2011	<i>A</i> =0.00001 x <i>L</i> <sup>2.9421</sup>	0.98	324
Potamocorbula laevis 2012 March	<i>A</i> =0.00003 x <i>L</i> <sup>2.2956</sup>	0.91	75
Potamocorbula laevis 2012 April	<i>A</i> =0.00001 x <i>L</i> <sup>2.745</sup>	0.91	64
Potamocorbula laevis 2012 May	$A$ =0.000003 x $L^{3.3071}$	0.95	50
Potamocorbula laevis 2012 April & May	A=0.000008 x L <sup>2.9302</sup>	0.92	114
Polychaete 2011	$A$ =0.00002 x $L^2$ - 0.0008 x $L$ + 0.0094	0.99	20
Polychaete 2012	<i>A</i> =0.000002 x <i>L</i> <sup>2.3568</sup>	0.85	35
Razor Clam			
Sea anemone 2011			
Sea anemone 2012			
Gastropod 2011	Based on the average AFDM of		
Gastropod 2012	those specimens collected from		
Crab 2011	particular year		
Crab 2012			
Shrimp 2011			
Shrimp 2012			

**Appendix 4.4** The *Potamocorbula laevis* size selection by different shorebird species. n<sub>1</sub> denotes sample size of used proportion based on either droppings or prey remains measurements, n<sub>2</sub> denotes sample size of *Potamocorbula laevis* used to estimate availability. Successive size classes with expected counts fewer than 5 individuals were combined for analysis and were indicated by having only one set of data. The three most preferred *Potamocorbula laevis* size classes for each shorebird species were in bold and shaded, as indicated by their high standardised selection ratio. Available proportion that falls below the Bailey 95% confidence interval of used proportion indicate statistical significant preference while those that are higher than the interval indicate statistical significant avoidance, those within the confidence interval indicate neutral selection. Summary based on this confidence interval can be found in preference, "NS" denotes no significant difference between usage and availability.

Species	Size class (mm)	Available proportion	Used proportion	Bailey 9 Confider interval proport	5% 1ce of used ion	Preference	Selection Ratio w <sub>i</sub>	Standardised Ratio
		$\pi_{i}$	0i	Lower	Upper		$w_i=o_i/\pi_i$	Bi
	1-2	0.009	0	0	0	А	0	0
	2-3	0.057	0	0	0	А	0	0
	3-4	0.14	0.029	0.028	0.03	А	0.207	0.005
	4-5	0.203	0.143	0.141	0.144	А	0.703	0.018
	5-6	0.154	0.201	0.199	0.202	Р	1.305	0.034
	6-7	0.087	0.19	0.188	0.191	Р	2.192	0.057
	7-8	0.038	0.126	0.124	0.127	Р	3.266	0.084
	8-9	0.012	0.066	0.065	0.068	Р	5.338	0.138
	9-10	0.011	0.034	0.033	0.035	Р	3.058	0.079
Bar-tailed Godwit 2011.	10-11	0.003	0.017	0.016	0.018	Р	5.071	0.131
	11-12	0.003	0.015	0.014	0.016	Р	4.564	0.118
n <sub>1</sub> =1210.	12-13	0.006	0.018	0.018	0.019	Р	3.099	0.08
n <sub>2</sub> =1534.	13-14	0.011	0.028	0.027	0.029	Р	2.536	0.066
-	14-15	0.025	0.019	0.018	0.02	А	0.767	0.02
$\chi^2 = 1229.$	15-16	0.028	0.026	0.025	0.027	А	0.914	0.024
df=21. p<0.001	16-17	0.052	0.026	0.026	0.028	А	0.507	0.013
	17-18	0.071	0.021	0.02	0.022	А	0.291	0.008
	18-19	0.053	0.022	0.022	0.024	А	0.417	0.011
	19-20	0.02	0.008	0.008	0.009	А	0.409	0.011
	20-21	0.011	0.006	0.005	0.007	А	0.522	0.014
	21-22	0.003	0.002	0.002	0.003	NS	0.951	0.025
	22-23	0.001	0.002	0	0.004	NC	2 526	0.0((
	23-24	0.001	0.003	0	0.004	NS	2.536	0.066
	24-25			Size	e class not	available		
	25-26			Size	e class not	available		
Bar-tailed Godwit 2012.	1-2 2-3	0.01	0.003	0.002	0.006	А	0.263	0.012

	3-4							
n <sub>1</sub> =368,	4-5							
n <sub>2</sub> =775.	5-6							
	6-7							
$\chi^2 = 167.$	7-8							
df = 14  n < 0.001	8-9							
ar 1), p (01001	9-10	0.006	0.038	0.035	0.042	р	5 897	0 278
	10-11	0.022	0.054	0.051	0.059	р	2 478	0.117
	11-12	0.041	0.087	0.082	0.001	D	2.176	0.000
	12.12	0.041	0.007	0.117	0.127	D	2.100	0.104
	12-13	0.033	0.122	0.141	0.127	D	1.204	0.104
	15-14	0.121	0.147	0.141	0.151	P	1.21	0.057
	14-15	0.126	0.144	0.138	0.148	P	1.139	0.054
	15-16	0.155	0.09	0.085	0.094	A	0.579	0.027
	16-17	0.175	0.095	0.09	0.1	A	0.542	0.026
	17-18	0.112	0.057	0.053	0.061	А	0.508	0.024
	18-19	0.077	0.076	0.072	0.081	NS	0.983	0.046
	19-20	0.044	0.041	0.038	0.045	NS	0.929	0.044
	20-21	0.019	0.03	0.027	0.034	Р	1.544	0.073
	21-22	0.022	0.014	0.012	0.017	А	0.619	0.029
	22-23							
	23-24	0.012	0.003	0.002	0.006	А	0.234	0.011
	24-25							
	25-26			Size	class not availa	ble		
	1-2	0.008	0	0	0	А	0	0
		0.000	0	0	0			
	2-3	0.053	0.005	0.004	0.007	A	0.095	0.001
	2-3 3-4	0.053 0.138	0.005 0.026	0.004 0.025	0.007 0.028	A A	0.095 0.19	0.001 0.002
	2-3 3-4 4-5	0.053 0.138 0.203	0.005 0.026 0.07	0.004 0.025 0.068	0.007 0.028 0.072	A A A	0.095 0.19 0.345	0.001 0.002 0.004
	2-3 3-4 4-5 5-6	0.053 0.138 0.203 0.156	0.005 0.026 0.07 0.106	0.004 0.025 0.068 0.104	0.007 0.028 0.072 0.108	A A A A	0.095 0.19 0.345 0.683	0.001 0.002 0.004 0.009
	2-3 3-4 4-5 5-6 6-7	0.053 0.138 0.203 0.156 0.09	0.005 0.026 0.07 0.106 0.101	0.004 0.025 0.068 0.104 0.099	0.007 0.028 0.072 0.108 0.103	A A A A P	0.095 0.19 0.345 0.683 1.123	0.001 0.002 0.004 0.009 0.014
	2-3 3-4 4-5 5-6 6-7 7-8	0.053 0.138 0.203 0.156 0.09 0.037	0.005 0.026 0.07 0.106 0.101 0.136	0.004 0.025 0.068 0.104 0.099 0.133	0.007 0.028 0.072 0.108 0.103 0.138	A A A A P P	0.095 0.19 0.345 0.683 1.123 3.701	0.001 0.002 0.004 0.009 0.014 0.048
	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b>	0.053 0.138 0.203 0.156 0.09 0.037 0.011	0.005 0.026 0.07 0.106 0.101 0.136 0.138	0.004 0.025 0.068 0.104 0.099 0.133 0.135	0.007 0.028 0.072 0.108 0.103 0.138 0.14	A A A A P P P	0.095 0.19 0.345 0.683 1.123 3.701 13.072	0.001 0.002 0.004 0.009 0.014 0.048 0.168
Great Knot	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084	0.007 0.028 0.072 0.108 0.103 0.138 0.14 0.088	A A A A P P P P	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123
Great Knot 2011.	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b>	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057	0.007 0.028 0.072 0.108 0.103 0.138 0.138 0.14 0.088 0.061	A A A A P P P P P P	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202
Great Knot 2011.	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b>	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048	0.007 0.028 0.072 0.108 0.103 0.138 0.14 0.088 0.061 0.052	A A A A P P P P P P P P	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202 0.214
Great Knot 2011. n <sub>1</sub> =800,	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b> 12-13	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003 0.005	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05 0.03	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048 0.029	0.007 0.028 0.072 0.108 0.103 0.138 0.138 0.14 0.088 0.061 0.052 0.032	A A A A P P P P P P P P P P	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638 5.704	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202 0.214 0.074
Great Knot 2011. n <sub>1</sub> =800, n <sub>2</sub> =1331.	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b> 12-13 13-14	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003 0.005 0.011	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05 0.03 0.033	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048 0.029 0.031	0.007 0.028 0.072 0.108 0.103 0.138 0.14 0.088 0.061 0.052 0.032 0.034	A A A A P P P P P P P P P P P P P	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638 5.704 2.884	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202 0.214 0.074 0.037
Great Knot 2011. n <sub>1</sub> =800, n <sub>2</sub> =1331.	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b> 12-13 13-14 14-15	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003 0.005 0.011 0.021	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05 0.03 0.033 0.013	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048 0.029 0.031 0.012	0.007 0.028 0.072 0.108 0.103 0.138 0.138 0.14 0.088 0.061 0.052 0.032 0.032 0.034 0.014	A A A A P P P P P P P P P P P P P A	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638 5.704 2.884 0.594	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202 0.214 0.074 0.074 0.037 0.008
Great Knot 2011. n <sub>1</sub> =800, n <sub>2</sub> =1331. χ <sup>2</sup> =3599,	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b> 12-13 13-14 14-15 15-16	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003 0.004 0.003 0.005 0.011 0.021 0.029	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05 0.05 0.03 0.033 0.013 0.019	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048 0.029 0.031 0.012 0.018	0.007 0.028 0.072 0.108 0.103 0.138 0.138 0.14 0.088 0.061 0.052 0.032 0.032 0.034 0.014 0.021	A A A A P P P P P P P P P P P A A	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638 5.704 2.884 0.594	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202 0.214 0.074 0.037 0.008
Great Knot 2011. n <sub>1</sub> =800, n <sub>2</sub> =1331. χ <sup>2</sup> =3599, df=20, p<0.001	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b> 12-13 13-14 14-15 15-16 16-17	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003 0.005 0.011 0.021 0.029 0.05	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05 0.03 0.033 0.013 0.013 0.019 0.026	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048 0.029 0.031 0.012 0.018 0.025	0.007 0.028 0.072 0.108 0.103 0.138 0.138 0.14 0.088 0.061 0.052 0.032 0.032 0.034 0.014 0.021 0.028	A A A A P P P P P P P P P P P A A A	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638 5.704 2.884 0.594 0.64	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202 0.214 0.074 0.074 0.037 0.008 0.008 0.008
Great Knot 2011. n <sub>1</sub> =800, n <sub>2</sub> =1331. χ <sup>2</sup> =3599, df=20, p<0.001	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b> 12-13 13-14 14-15 15-16 16-17 17-18	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003 0.005 0.011 0.021 0.029 0.05 0.073	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05 0.05 0.03 0.03 0.033 0.013 0.013 0.019 0.026 0.03	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048 0.029 0.031 0.012 0.018 0.025 0.029	0.007 0.028 0.072 0.108 0.103 0.138 0.138 0.14 0.088 0.061 0.052 0.032 0.032 0.034 0.014 0.021 0.028 0.032	A A A A P P P P P P P P P P A A A A	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638 5.704 2.884 0.594 0.64 0.521 0.412	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202 0.214 0.074 0.037 0.008 0.008 0.008 0.007 0.005
Great Knot 2011. n <sub>1</sub> =800, n <sub>2</sub> =1331. χ <sup>2</sup> =3599, df=20, p<0.001	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b> 12-13 13-14 14-15 15-16 16-17 17-18 18-19	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003 0.005 0.011 0.021 0.029 0.05 0.073 0.059	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05 0.05 0.03 0.033 0.013 0.013 0.019 0.026 0.03	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048 0.029 0.031 0.012 0.018 0.025 0.029 0.02	0.007 0.028 0.072 0.108 0.103 0.138 0.14 0.088 0.061 0.052 0.032 0.034 0.014 0.021 0.028 0.032	A A A P P P P P P P P P A A A A A	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638 5.704 2.884 0.594 0.64 0.521 0.412 0.363	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202 0.214 0.074 0.074 0.037 0.008 0.008 0.008 0.007 0.005
Great Knot 2011. n <sub>1</sub> =800, n <sub>2</sub> =1331. χ <sup>2</sup> =3599, df=20, p<0.001	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b> 12-13 13-14 14-15 15-16 16-17 17-18 18-19 19-20	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003 0.005 0.011 0.021 0.029 0.05 0.073 0.059 0.023	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05 0.05 0.03 0.033 0.013 0.013 0.019 0.026 0.03 0.021	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048 0.029 0.031 0.012 0.018 0.025 0.029 0.02	0.007 0.028 0.072 0.108 0.103 0.138 0.138 0.14 0.088 0.061 0.052 0.032 0.032 0.034 0.014 0.021 0.021 0.028 0.032 0.032 0.032	A A A A P P P P P P P P P A A A A A A A	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638 5.704 2.884 0.594 0.64 0.521 0.412 0.363 0.912	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202 0.214 0.0214 0.074 0.037 0.008 0.008 0.008 0.008 0.007 0.005 0.005
Great Knot 2011. n <sub>1</sub> =800, n <sub>2</sub> =1331. χ <sup>2</sup> =3599, df=20, p<0.001	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b> 12-13 13-14 14-15 15-16 16-17 17-18 18-19 19-20 20-21	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003 0.005 0.011 0.021 0.021 0.029 0.05 0.073 0.059 0.023 0.013	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05 0.05 0.03 0.033 0.013 0.013 0.013 0.019 0.026 0.03 0.021 0.021	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048 0.029 0.031 0.012 0.018 0.025 0.029 0.02 0.02 0.02	0.007 0.028 0.072 0.108 0.103 0.138 0.14 0.088 0.061 0.052 0.032 0.034 0.014 0.021 0.021 0.028 0.023 0.023 0.023	A A A A P P P P P P P P P A A A A A A A	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638 5.704 2.884 0.594 0.64 0.521 0.412 0.363 0.912 1.174	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202 0.214 0.074 0.074 0.037 0.008 0.008 0.008 0.008 0.005 0.005 0.012
Great Knot 2011. n <sub>1</sub> =800, n <sub>2</sub> =1331. χ <sup>2</sup> =3599, df=20, p<0.001	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b> 12-13 13-14 14-15 15-16 16-17 17-18 18-19 19-20 20-21 21-22	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003 0.005 0.011 0.021 0.021 0.029 0.05 0.073 0.059 0.023 0.013	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05 0.03 0.03 0.03 0.033 0.013 0.013 0.019 0.026 0.03 0.021 0.021 0.021 0.021	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048 0.029 0.031 0.012 0.018 0.025 0.029 0.02 0.02 0.02 0.02	0.007 0.028 0.072 0.108 0.103 0.138 0.138 0.14 0.088 0.061 0.052 0.032 0.032 0.032 0.034 0.021 0.021 0.028 0.023 0.023 0.023 0.023 0.023	A A A A P P P P P P P P P A A A A A A A	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638 5.704 2.884 0.594 0.64 0.521 0.412 0.363 0.912 1.174	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202 0.214 0.074 0.074 0.037 0.008 0.008 0.008 0.008 0.007 0.005 0.005 0.012 0.015
Great Knot 2011. n <sub>1</sub> =800, n <sub>2</sub> =1331. χ <sup>2</sup> =3599, df=20, p<0.001	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b> 12-13 13-14 14-15 15-16 16-17 17-18 18-19 19-20 20-21 21-22 22.22	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003 0.005 0.011 0.021 0.021 0.029 0.05 0.073 0.059 0.023 0.013	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05 0.03 0.033 0.033 0.013 0.013 0.019 0.026 0.03 0.021 0.021 0.021 0.021	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048 0.029 0.031 0.012 0.018 0.025 0.029 0.02 0.02 0.02 0.02	0.007 0.028 0.072 0.108 0.103 0.138 0.14 0.088 0.061 0.052 0.032 0.032 0.034 0.014 0.021 0.028 0.023 0.023 0.023 0.017	A A A A A P P P P P P P P P P P A A A A	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638 5.704 2.884 0.594 0.64 0.521 0.412 0.363 0.912 1.174	0.001 0.002 0.004 0.009 0.014 0.048 0.168 0.123 0.202 0.214 0.074 0.037 0.008 0.007 0.008 0.008 0.007 0.005 0.005 0.005 0.012 0.012
Great Knot 2011. n <sub>1</sub> =800, n <sub>2</sub> =1331. χ <sup>2</sup> =3599, df=20, p<0.001	2-3 3-4 4-5 5-6 6-7 7-8 <b>8-9</b> 9-10 <b>10-11</b> <b>11-12</b> 12-13 13-14 14-15 15-16 16-17 17-18 18-19 19-20 20-21 21-22 22-23 22-23 22-23	0.053 0.138 0.203 0.156 0.09 0.037 0.011 0.009 0.004 0.003 0.005 0.011 0.021 0.029 0.05 0.073 0.059 0.023 0.013 0.005	0.005 0.026 0.07 0.106 0.101 0.136 0.138 0.086 0.059 0.05 0.03 0.033 0.013 0.013 0.013 0.019 0.026 0.03 0.021 0.021 0.021 0.021 0.021	0.004 0.025 0.068 0.104 0.099 0.133 0.135 0.084 0.057 0.048 0.029 0.031 0.012 0.018 0.025 0.029 0.02 0.02 0.02 0.02	0.007 0.028 0.072 0.108 0.103 0.138 0.138 0.14 0.088 0.061 0.052 0.032 0.032 0.034 0.014 0.021 0.021 0.028 0.023 0.023 0.023 0.023 0.023	A A A P P P P P P P A A A A A A A A A A	0.095 0.19 0.345 0.683 1.123 3.701 13.072 9.567 15.639 16.638 5.704 2.884 0.594 0.64 0.521 0.412 0.363 0.912 1.174 3.328	0.001 0.002 0.004 0.009 0.014 0.048 0.123 0.202 0.214 0.214 0.074 0.037 0.008 0.007 0.008 0.008 0.007 0.005 0.005 0.012 0.012 0.015

	24-25							
	25-26							
	1-2							
	2-3							
	3-4							
	4-5	0.006	0.012	0.012	0.014	Р	2.133	0.065
	5-6							
	6-7							
	7-8							
	8-9	0.006	0.027	0.026	0.028	Р	4.595	0.14
	9-10	0.004	0.038	0.037	0.04	Р	8.752	0.267
Great Knot	10-11	0.02	0.096	0.094	0.098	Р	4.689	0.143
2012.	11-12	0.039	0.095	0.093	0.097	Р	2.407	0.073
n1042	12-13	0.057	0.122	0.12	0.124	Р	2.138	0.065
m=-694	13-14	0.121	0.125	0.123	0.126	Р	1.028	0.031
112-004.	14-15	0.123	0.117	0.115	0.119	А	0.953	0.029
	15-16	0.161	0.09	0.089	0.092	А	0.561	0.017
$\chi^{2}=955$ , df=17 p < 0.001	16-17	0.174	0.088	0.087	0.09	А	0.507	0.015
ui=17, p<0.001	17-18	0.102	0.075	0.073	0.076	А	0.731	0.022
	18-19	0.086	0.048	0.047	0.05	А	0.556	0.017
	19-20	0.042	0.03	0.029	0.031	А	0.702	0.021
	20-21	0.019	0.022	0.021	0.023	Р	1.161	0.035
	21-22	0.025	0.009	0.008	0.01	А	0.348	0.011
	22-23	0.007	0.002	0	0.003	А	0.263	0.008
	23-24	0.003	0.004	0.003	0.005	Р	1.313	0.04
	24-25	0.003	0	0	0	А	0	0
	25-26			Size	class not availa	ble		
	1-2			Size	class not availa	ble		
	2-3			Size	class not availa	ble		
	3-4							
	4-5							
	5-6							
Far Eastern Ovstercatcher	6-7							
on P. laevis	7-8	0.044	0	0	0	А	0	0
flesh 2012.	8-9							
	9-10							
n <sub>1</sub> =121,	10-11							
n <sub>2</sub> =608.	11-12	0.051	0	0	0	А	0	0
	12-13	0.067	0	0	0	А	0	0
χ²=149,	13-14	0.141	0.008	0	0.019	А	0.058	0.006
df=9,	14-15	0.137	0.033	0.026	0.045	А	0.242	0.023
p<0.001	15-16	0.178	0.091	0.078	0.104	А	0.512	0.049
	16-17	0.163	0.273	0.251	0.283	Р	1.675	0.161
	17-18	0.087	0.306	0.283	0.315	Р	3.508	0.338
	18-19	0.066	0.165	0.148	0.178	Р	2.512	0.242
	19-20	0.066	0.124	0 109	0.137	р	1 884	0 181

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			1					
	20-21							
	21-22							
	22-23							
	23-24							
	24-25							
	25-26			Siz	e class not av	ailable		
	1-2			Siz	e class not av	ailable		
	2-3			Siz	e class not av	ailable		
	3-4							
	4-5							
	5-6							
	6-7							
	7-8	0.042	0.018	0.014	0.027	Р	0.44	0.041
	8-9							
Dunlin on D	9-10							
laevis flesh	10-11							
2012.	11-12	0.049	0.006	0	0.014	А	0.124	0.011
	12-13	0.07	0.018	0.014	0.027	А	0.262	0.024
n <sub>1</sub> =164,	13-14	0.144	0.03	0.025	0.039	А	0.212	0.02
n <sub>2</sub> =529.	14-15	0.132	0.116	0.105	0.126	А	0.876	0.081
	15-16	0.191	0.22	0.205	0.228	Р	1.15	0.106
χ²=84,	16-17	0.157	0.207	0.193	0.216	Р	1.321	0.122
df=10, p<0.001	17-18	0.074	0.213	0.199	0.222	Р	2.895	0.267
	18-19	0.076	0.116	0.105	0.126	Р	1.532	0.141
	19-20	0.023	0.037	0.031	0.046	Р	1.613	0.149
	20-21							
	21-22							
	22-23	0.043	0.018	0.014	0.027	А	0.421	0.039
	23-24							
	24-25							
	25-26			Siz	e class not av	ailable		
	1-2							
	2-3							
	3-4							
Bar-tailed Godwit on <i>P.</i>	4-5							
<i>laevis</i> flesh	5-6							
2012.	6-7							
n -60	7-8	0.135	0.017	0	0.041	А	0.123	0.015
$n_1 = 00,$	8-9							
$n_2 = 775.$	9-10							
	10-11							
χ <sup>2</sup> =41,	11-12							
ar=/,	12-13							
p=0.004	13-14	0.121	0.033	0.02	0.058	А	0.275	0.033
	14-15	0.126	0.067	0.047	0.093	Α	0.527	0.063

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16-17	0.175	0.2	0.165	0.224	NS	1.14	0.137
17-18	0.112	0.15	0.12	0.176	Р	1.336	0.161
18-19	0.077	0.117	0.09	0.143	Р	1.507	0.181
19-20							
20-21							
21-22	0.007	0.400	0.45	0.000	P	4.004	0.000
22-23	0.097	0.183	0.15	0.208	Р	1.894	0.228
23-24							
24-25							
 25-26			Size	class not availa	ıble		

selection	
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Chapter	

Appendix 4.5 The mean and standard deviation of successful handling time (in seconds) that different shorebird groups spent on different prey types in Yalu Jiang coastal wetland between 2011 and 2012. Numbers in parentheses represent sample size (number of individuals) and the range of handling time.

Species Bivalv (flesh	BAGO (overall)	BAGO 2011 (female)	BAGO (male)	GRKN	BAGO 2.07±1 (overall) (56)	<b>BAGO</b> 2.2±2. (female) (21)	<b>BAGO</b> 1.99±( (male) (35)	<b>2012 GRKN</b> 2.77±2 (16) (16)	FEOY 5.25±2 (37)	<b>REKN</b> 2.08±1 (4)	DUNL 2.69±1
ve Bi J (w	0.6	1.( (4-	0.6 (6	$\frac{1.5}{(2)}$	$1.49 1.^{2}$	.15 1.4	0.92 1. <sup>2</sup> (9)	2.24 2.2 (90	2.95 2.9 (3)	1.04 1.8 (10	1.94 2.3
valve 'hole)	€±0.63 16)	)4±0.69 4)	}2±0.61 4)	26±0.39	47±0.99 73)	49±1.2 8)	45±0.84 7)	2±2.11 8)	)3±1.32 )	31±0.7 6)	35 (1)
Razor Clam					4.46 (1)	4.46 (1)					
Crab	11.32±14.76 (2)	11.32±14.76 (2)			9.76±6.29 (2)	14.21 (1)	5.31 (1)	44.39(1)			7.07 (1)
Gastropod					10.29 (1)		10.29 (1)	42.03±53.64 (9)	46.41±3.02 (2)		
Ghost shrimp	6.65±6.84 (58)	7.08±4.44 (27)	6.27±8.45 (31)		6.29±5.11 (32)	7.97±5.48 (18)	4.13±3.74 (14)				
Sea anemone	4.64±3.77 (8)	6.99±5.68 (2)	4.32±3.38 (5)		6.37±12.14 (36)	7.21±15.08 (22)	5.35±5.22 (13)				
Unknown	2.52±1.97 (200)	2.86±2.28 (83)	$2.27\pm1.7$ (110)		2.46±2.98 (256)	2.71±3.3 (118)	2.29±2.75 (129)	4.37±6.49 (22)	2.93 (1)	2.05 (1)	0.82±0.2
Polychaeta (all)	4.94±3.64 (165)	5.88±3.7 (71)	4.29±3.45 (84)		3.68±4.59 (264)	3.89±2.9 (124)	3.51±5.84 (131)				
Polychaeta (long)	9.46±9.69 (36)	11.85±14 (14)	7.54±5.17 (21)		9.02±10.97 (47)	9±8.54 (22)	8.53±13.28 (23)				
Polychaeta (medium)	6.35±4.43 (84)	6.62±3.44 (39)	$6.09\pm5.34$ (40)		5.6±6.17 (147)	6.51±7.83 (72)	4.92±3.95 (69)				
Polychaeta (small)	3.53±2.94 (130)	4.57±3.69 (53)	2.84±2.04 (68)		2.3±1.18 (205)	2.4±1.12 (95)	2.24±1.26 (102)				

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Appendix 4.6 The mean and standard deviation of profitability (amount of ash-free dry mass mg taken per second of handling) for different shorebird groups spent on different prey types in Yalu Jiang coastal wetland between 2011 and 2012. Numbers in parentheses represent sample size (number of individuals).

Year	Species	Bivalvia	Bivalvia	CL	ab	ab Gastropod	ab Gastropod Ghost shrimn	ab Gastropod Ghost Razor chrimn clam	ab Gastropod Ghost Razor Sea shrimn clam anomono	ab Gastropod Ghost Razor Sea Unknown shrimn clam anomona	ab Gastropod Ghost Razor Sea Unknown Polychaeta chrimn clam anomono (211)	ab Gastropod Ghost Razor Sea Unknown Polychaeta Polychaeta shrimn clam anomono GID (Jone)	ab Gastropod Ghost Razor Sea Unknown Polychaeta Polychaeta Polychaeta دارس دراعی میمسمیه (عال) (امین) (میرو)
2011	BAG0 (all)	(mont)	13.19±8.72 (116)	2.53±3.3 1 (2)			2.86±2.77 (58)	2.86±2.77 [58]	2.86±2.77 93.89±63.96 (58) (8)	2.86±2.77 93.89±63.96 7.15±4.36 (58) (200)	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	2.86±2.77 93.89±63.96 7.15±4.36 7.69±11.51 37.77±27.74 13.98±11.12 (58) (8) (200) (165) (36) (84)
	BAGO (female)		13.02±10.76 (44)	2.53±3.3 1 (2)			2.36±2.46 (27)	2.36±2.46 (27)	2.36±2.46 64.65±52.53 (27) (2)	2.36±2.46 64.65±52.53 6.46±4.01 (27) (23)	2.36±2.46 64.65±52.53 6.46±4.01 9.51±12.49 (27) (2) (83) (71)	2.36±2.46 64.65±52.53 6.46±4.01 9.51±12.49 39.42±27.81 (27) (2) (83) (71) (14)	2.36±2.46 64.65±52.53 6.46±4.01 9.51±12.49 39.42±27.81 16.77±13.14 (27) (2) (83) (71) (14) (39)
	BAG0 (male)		13.47±7.52 (64)				3.3±2.98 (31)	3.3±2.98 (31)	3.3±2.98 93.06±71.14 (31) (5)	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	3.3±2.98 93.06±71.14 7.77±4.61 6.64±11.09 37.92±28.43 (31) (5) (110) (84) (21)	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
	GRKN		11.48±4.22 (2)										
2012	BAG0 (all)	$15.11\pm6.9$ (40)	20.12±8.79 (171)	3.36±2.1 7 (2)	14.93(1)		3.85±3.34 (32)	3.85±3.34 77.44 (32) (1)	3.85±3.34 77.44 68.65±48.27 (32) (1) (35)	3.85±3.34 77.44 68.65±48.27 11.04±6.3 (32) (1) (35) (255)	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	3.85±3.34 77.44 68.65±48.27 11.04±6.3 8.3±9.37 33.51±23.7 (32) (1) (35) (255) (263) (47)	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
	BAG0 (female)	$14.8\pm6.93$ (14)	21.1±9.58 (66)	1.83 (1)			2.68±2.61 (18)	2.68±2.61 77.44 (18) (1)	2.68±2.61 77.44 69.54±54.5 (18) (1) (21)	2.68±2.61 77.44 69.54±54.5 10.33±6.04 (18) (1) (21) (117)	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	2.68±2.61 77.44 69.54±54.5 10.33±6.04 9.91±10.35 35.68±25.62   (18) (1) (21) (117) (123) (22)	2.68±2.61 77.44 69.54±54.5 10.33±6.04 9.91±10.35 35.68±25.62 15.89±10.33   (18) (1) (21) (117) (123) (22) (72)
	BAGO (male)	15.28±7.02 (26)	19.61±8.39 (97)	4.9 (1)	14.93 (1)	2:: (1	35±3.66 4)	35±3.66 4)	35±3.66 61.22±32.96 4) (13)	35±3.66 61.22±32.96 11.36±6.24 4) (13) (129)	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
	GRKN	12.91±9.47 (15)	15.23±7.06 (98)	0.14(1)	13.65±13.1 7 (8)					13.05±13.84 (19)	13.05±13.84 (19)	13.05±13.84 (19)	13.05±13.84 (19)
	FEOY	7.51±2.54 (37)			2.08±1.54 (2)					4.59 (1)	4.59 (1)	4.59 (1)	4.59 (1)
	REKN	$11.88\pm9.23$ (4)	11.54±4.57 (16)							7.71 (1)	7.71 (1)	7.71 (1)	7.71 (1)
	DUNL	$10.41\pm7.71$ (8)		0.86 (1)						20.44±3.77 (2)	20.44±3.77 (2)	20.44±3.77 (2)	20.44±3.77 (2)

# Chapter 5. Biotic and Abiotic Influences on Shorebird Foraging Patterns and Intake Rates at an Intertidal Staging Site in the Yellow Sea, China

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# 5.1 Abstract

Migratory shorebirds require staging sites to rest and refuel to complete their migration. Identifying areas with ample food supply and other suitable conditions is therefore of critical importance to prioritise conservation efforts for shorebirds. This study explored the potential biotic and abiotic factors that may affect the foraging patterns and intake rates of Bar-tailed Godwits Limosa lapponica and Great Knots Calidris tenuirostris feeding on tidal flats at their most important staging site in the East Asian-Australasian Flyway during northward migration. In contrast to our expectation that foraging patterns and intake rates would relate strongly to prey availability, we found that abiotic factors such as tidal range, time relative to low tide and distance to seawall, played more important roles. The two study species differed markedly in foraging activity patterns, with godwits foraging at high rates (i.e. most individuals in scans were foraging) throughout the low tide period whereas there was always a high proportion of Great Knots that were not foraging during the same period. Spatially, godwits fed fairly evenly across the entire study area while knots showed high variation and fed more at some patches than others. These differences probably relate to the differing dietary selection of the two species, with Great Knots feeding almost solely on the bivalve Potamocorbula laevis (which occurred mainly >1 km out from the seawall) whereas godwits had a broader diet that also included large numbers of polychaete worms (which were common near to shore). Consequently their prey availability differed markedly and godwits could forage throughout the tidal cycle and across all the tidal flats. Measured intake rates were high, and this study indicated that the study area provided Bar-tailed Godwits and Great Knots with ample food resources. The species differences in how their foraging patterns related to environmental factors stress the need to take species-specific tide-related abiotic factors into account when studying shorebird stopover ecology.

# **5.2 Introduction**

Benthic food resources often correlate strongly with the survival and distribution of migratory shorebirds (Baker *et al.* 2004; Colwell & Landrum 1993; van Gils *et al.* 2006a; Zwarts & Wanink 1993). Benthic prey density was found to be an important factor that affects the intake rate, which was often used as a surrogate for fitness (Scheiner & Willig 2011), in shorebirds (Goss-Custard 1977; Sutherland 1982). However, benthic resources may not be evenly distributed and a vast area of tidal flats does not necessarily support a large number of shorebirds (Rogers *et al.* 2011). Identifying productive areas with ample

food supply is therefore of critical importance to prioritise conservation efforts, especially in regions where migratory shorebirds are in rapid decline and relatively little is known. Migratory shorebirds along the East-Asian Australasian Flyway (hereafter EAAF) are among the most poorly known of the different flyways (Stroud *et al.* 2006), with many species declining partly due to habitat loss (Amano *et al.* 2010; Gan *et al.* 2009; Murray *et al.* 2014; Rogers *et al.* 2011; Wilson *et al.* 2011).

Long distance migratory shorebirds require stopping sites to rest and refuel. Some of these sites are described as staging sites, which are "sites with abundant, predictable food resources where migratory birds prepare for an energetic challenge requiring substantial fuel stores and physiological changes without which significant fitness costs are incurred" (Warnock 2010). Studying the foraging patterns and intake rates of migratory birds at stopping site therefore helps to determine what makes certain sites more attractive than others. Recent studies along the EAAF indicated that some migratory shorebirds congregated at one staging site for a lengthy period during their northward migration (e.g. Bar-tailed Godwits *Limosa lapponica* and Great Knots *Calidris tenuirostris* at Yalu Jiang coastal wetland, Red Knots *Calidris canutus* at Bohai Bay; Battley *et al.* 2012; Chapter 2; Ma *et al.* 2013b; Rogers *et al.* 2010).

In this study, we aimed to investigate the importance of prey density in relation to other abiotic factors in determining the intake rate and foraging patterns of two shorebird species staging in the northern Yellow Sea during northward migration. We predicted that foraging activity patterns and intake rates would depend heavily on prey availability. Moreover, given the different diets of Bar-tailed Godwits and Great Knots (Chapter 4), similar model sets may perform differently in explaining the variations in foraging patterns and intake rates between the two species.

# 5.3 Materials and methods

## 5.3.1 Study area

This study was carried out at the Dandong Yalu Jiang Estuary Wetland National Nature Reserve (39°40'–39°58'N, 123°28'–124°09'E). It is located west of the Yalu Jiang estuary in the northern part of the Yellow Sea, on the Chinese side of China-North Korea border (Figure 5.1a). The reserve was founded in 1987 and listed 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 at least 29 species listed as 'Threatened' on the

IUCN Red List (IUCN 2012; Yan 2008). The reserve supports more than 250,000 shorebirds during the northward migration (Riegen *et al.* 2014) and is regarded as an 'Important Bird Area' (BirdLife International 2009) but lacks Ramsar recognition (Ramsar 2012). The reserve extends for about 70 km along the coast, and comprises mainly bare intertidal mudflat on the seaward side of a seawall, with aquaculture ponds and paddy fields on the landward side, which is typical along the Chinese coast (Barter 2002; Choi *et al.* 2014; Li *et al.* 2013; Ma *et al.* 2009; Yang *et al.* 2011). Aquaculture ponds were used for cultivating sea cucumber, jellyfish, shellfish, prawn and fish while the bare intertidal mudflat immediately on the seaward side of the seawall was used for farming shellfish. There were extensive fishnets (erected up to 2 m high) that ran parallel to the coastline on the intertidal mudflat at the low neap tide water line, catching mostly fishes, crabs and prawns that were brought near the shore during the flood tide. Shallow water further away in the subtidal zone was also used for farming shellfish (C. –Y. Choi, pers. obs.; Figure 5.1b).

Tides are semidiurnal and macrotidal in range (two high and two low tides per day, average tidal range of 4.48 m, maximum range 6.92 m: Davies 1980; Wang *et al.* 1986). Tidal flats extend up to 4 km from the seawall in the middle and the west of the reserve, and 5 km in the east (Figure 5.1b). The supratidal zone in the study area has been converted to aquaculture ponds and therefore extreme high spring tides inundate the entire mudflat completely. The upper tidal flats at some areas with a relatively high elevation do not get inundated during high neap tide.

In order to relate the availability of benthic organisms to the foraging patterns and intake rates of migratory shorebirds, benthos sampling, shorebird behaviour scans and focal bird observation were carried out between March and May in 2011 and 2012. The intertidal flat in the middle of the reserve was chosen as the study area due to the presence of large numbers of foraging shorebirds during northward migration (Chapter 2; Riegen *et al.* 2014) (Figure 5.1c).

# 5.3.2 Benthos sampling

The detailed methods and results of benthos sampling, energy content estimation and biomass distribution were presented in Appendix 1. In brief, a 9 km<sup>2</sup> (3 x 3 km) study area was set up in the middle site and divided into 36 grids, each of which was 0.25 km<sup>2</sup> (0.5 x 0.5 km) with a sampling station at the centre (Figure 5.1c). Benthos samples were taken once a month from these 36 stations between March and May in 2011 and 2012, using a corer with a diameter of 155 mm and to 300 mm deep. The sample was then divided into



the top (50 mm) and bottom layers (250 mm) that were sieved separately through a 0.5 mm sieve.

**Figure 5.1** Maps showing the locations mentioned in this paper. (*a*) The Yellow Sea. (*b*) The Dandong Yalu Jiang Estuary Wetland National Nature Reserve (within the area bounded by the dotted lines). (*c*) The 36 sampling stations in the middle site.

124°0'0"E

123°40'0"E

# 5.3.3 Behavioural scans and focal observations of shorebirds

Foraging patterns were determined from behavioural scans of Bar-tailed Godwits and Great Knots. These were carried out on an opportunistic basis within the benthos sampling grids at the middle site between March and May from 2011 to 2012. Date, time, location, and the numbers of foraging and resting birds were recorded in each scan. Birds that were walking, probing, pecking or handling prey were regarded as foraging while those preening or motionless were treated as resting.

Instantaneous intake rates were derived from focal bird observations, conducted at the same location and timeframe as the behaviour scans. A focal bird was chosen randomly from a flock of foraging birds within watching distance and was watched for 5

124°20'0"E

#### Chapter 5. Foraging patterns and intake rates

minutes, using a 20-60 x telescope. The date, time, location (based on the sampling grids), sex (of the dimorphic Bar-tailed Godwits) and breeding plumage score of the focal bird and the number of conspecifics within 50 m were noted. Given that the aim of focal observation was to investigate the intake rate, foraging birds were selected while resting ones were avoided. However, observations continued even when the focal bird stopped foraging after the start of an observation bout. Detailed description of the methods used in focal observations can be found in Chapter 4.

Swallowed prey items were categorised into seven groups, namely bivalve, crab, gastropod, ghost shrimp, polychaete, sea anemone and unknown. The size-biomass relationships extrapolated in Chapter 4 were used to estimate the ash-free dry mass (hereafter AFDM) of samples that were not incinerated. The average AFDM per prey item sampled per year in crabs, gastropods, ghost shrimps and sea anemones were treated as the AFDM obtained when focal bird swallowed any of these four prey types. More precise AFDM estimates were obtained when birds took polychaetes and bivalves (dominated by *Potamocorbula laevis*). Detailed description of the procedures used in AFDM estimation in prey can be found in Chapter 4.

The tide-related information during behaviour scans and focal observations were extrapolated based on the recorded time and the local tide table (National Marine Data and Information Service 2010, 2011).

# 5.3.4 Data analysis

## 5.3.4.1 Foraging pattern

To minimise the problems of non-independent, double-counting and biases in behaviour scans, in analysis we excluded scans from the same quadrat that were conducted within 30 minutes, and scans of fewer than 10 individuals. The proportion of foraging birds was treated as the outcome variable while 13 biotic (biomass of amphipod, Anthozoa, Bivalvia, Cumacea, Gastropoda, Lingula, Polychaeta, shrimp) and abiotic (minutes relative to low tide, tidal direction, tidal range, time of day and Julian day) factors were treated as predictors. The proportion of foraging birds was logit-transformed before analysis, with proportions equal to 0 and 1 replaced by 0.025 and 0.975, respectively to avoid transformation to undefined values (Warton & Hui 2011). The transformation was carried out using the 'transform' function in R's *car* package (Fox & Weisberg 2011). Biotic (prey) factors for Great Knots only included the benthic biomass in the top 5 cm while it was 30 cm for Bar-tailed Godwits due to their different bill lengths and, therefore, accessibility.

A model selection criteria approach was adopted to investigate how the biotic and abiotic factors affect the foraging patterns of Bar-tailed Godwits and Great Knots (Johnson & Omland 2004). We defined 20 candidate model sets and excluded all other variable combinations based on ecological plausibility (Appendix 5.1). Linear models were then fitted to the data. Due to the large number of predictors relative to the sample sizes, the second order Akaike's Information Criterion (AICc) was used (Burnham & Anderson 2004). The delta AICc was calculated and models with the delta AICc $\leq$ 6 retained within the confidence set (Richards *et al.* 2011). Akaike weights were calculated to reveal the probability of the model being the best among the whole set of candidate models, and the sum of the Akaike weights for each variable was also calculated to assess their relative importance (Burnham & Anderson 2002). Finally, model averaging was used to estimate robust parameters, standard errors, and their confidence intervals (Burnham & Anderson 2002). All the model selection analyses were carried out using the 'aictab' and 'modavg' functions in *AICcmodavg* package (Mazerolle 2013), using R v3.0.1 (R Core Team 2013).

#### 5.3.4.2 Intake rate

The model selection criteria approach described above was used again to investigate how the biotic and abiotic factors affected the intake rates (mg AFDM per second of foraging time) of Bar-tailed Godwits and Great Knots. We defined 46 and 30 candidate model sets for Bar-tailed Godwits and Great Knots (Appendix 5.2); the different numbers between species arose as sex could not be distinguished in the field in Great Knots and their diet (i.e. food availability) was also narrower than for Bar-tailed Godwits (Chapter 4).

To minimise biases and uncertainties arising from unidentified prey items, only observations with at least 2.5 minutes total foraging time and with all prey items identified were included in the intake rate analysis. The intake rate of focal birds was treated as the outcome variable while 13 biotic (biomass of bivalve in preferred size, bivalve larger than preferred size, Polychaeta, shrimp) and abiotic factors (distance to seawall, water, Julian days, minutes relative to low tide, number of counterparts within 50 m, sexes, tidal direction, tidal range and year) were treated as predictors. The intake rate was log<sub>e</sub> transformed in Great Knots and square-root transformed in Bar-tailed Godwits before analysis to meet the assumptions of homoscedasticity and normality. The variance inflation factors were calculated among the variables to test for collinearity. Determination of prey available was limited to those collected in the top 5 cm for Great Knots and 30 cm for Bar-tailed Godwits. Polychaetes and ghost shrimps were also
included in the model for the godwits. The sex of focal individual godwits was determined mainly by the bill length, supplemented by breeding plumage score (Conklin *et al.* 2011). Among individually marked birds observed in the field, 91% of our sexing results agreed with those determined at banding (14/14 in 2010; 35/40 in 2011-12). Distance to water was estimated as the nearest water body to the focal bird, which was zero if the bird was feeding in the water.

## **5.4 Results**

## 5.4.1 Foraging pattern

The 13 biotic and abiotic factors considered in this study together explained 8% and 13% of the foraging patterns of Bar-tailed Godwits and Great Knots, respectively (based on the adjusted  $R^2$  for global model). In both the Bar-tailed Godwits and Great Knots, no single model was clearly superior to the others (w $\geq$ 0.9) (Table 5.1 and Table 5.2). Results from model averaging indicated that time relative to low tide was the most important variable that affected foraging patterns in Bar-tailed Godwits, with a decrease in time relative to low tide leading to a higher proportion of foraging godwits (Table 5.3). In addition, tidal direction and tidal range were also important variables that affected foraging patterns in Great Knots (Table 5.4). Flood tide, spring tide and a decrease in time relative to low tide led to a higher proportion of foraging Great Knots. In both studied species, abiotic factors played more important roles than food availability.

Bar-tailed Godwits and Great Knots differed substantially in how their foraging patterns varied in relation to low tide. Most of the godwits foraged throughout the low tide period while there was always a high proportion of non-foraging knots throughout any stage of the low tide (Figure 5.2). On a broader spatial scale, the foraging pattern of Great Knots were more variable, with a high foraging proportion in some patches but not others while godwits were more consistent, foraging almost across the entire tidal flat (Figure 5.3).

In both species, the proportions of foraging birds at either end of the low tide cycle were substantially lower and started earlier during neap than spring tides, indicating that spring tides restricted the availability of the tidal flat on the falling tide (Figure 5.2). Great Knots showed a higher proportion of foraging in flood than ebb tide, and during spring than neap tides (Table 5.4).

**Table 5.1** 100% Confidence set of best-ranked regression models examining the effect of 13 biotic and abiotic factors on foraging patterns of Bar-tailed Godwits.

Candidate models	К	AICc	Delta AICc	AICcwt	Cum.Wt
MR	3	1514.39	0	0.28	0.28
TI + TD + MR + TR + JD + AN	8	1515.40	1.01	0.17	0.45
TI + TD + MR + TR + JD	7	1516.02	1.62	0.12	0.57
MR + TR	4	1516.40	2.01	0.10	0.67
TD + MR	4	1516.41	2.02	0.10	0.77
TI + TD + MR + TR + JD + PO	8	1517.56	3.16	0.06	0.83
TI + TD + MR + TR + JD + GA	8	1517.61	3.21	0.06	0.89
TI + TD + MR + TR + JD + BI	8	1517.70	3.31	0.05	0.94
TD + MR + TR	5	1518.43	4.04	0.04	0.98
TI + TD + MR + TR + JD + BI + PO	9	1519.46	5.06	0.02	1

*MR* minutes relative to low tide, *TI* time of the day interacts with minutes relative to low tide, *TD* tidal direction, *TR* Tidal range, *JD* Julian day, *AN* biomass of Anthozoa, *PO* biomass of polychaete, *GA* biomass of gastropod, *BI* biomass of bivalve, *AM* biomass of amphipod, *CU* biomass of Cumacea, *LI* biomass of lingual, *SH* biomass of shrimp.

Candidate models	К	AICc	Delta AICc	AICcwt	Cum.Wt
TD + MR + TR	5	1063.46	0	0.50	0.50
TI + TD + MR + TR + JD	7	1065.88	2.43	0.15	0.65
TI + TD + MR + TR + JD + GA	8	1066.94	3.48	0.09	0.74
TI + TD + MR + TR + JD + BI	8	1067.24	3.78	0.08	0.82
TI + TD + MR + TR + JD + PO	8	1067.25	3.80	0.08	0.89
TI + TD + MR + TR + JD + AN	8	1068.01	4.55	0.05	0.94
TI + TD + MR + TR + JD + BI + PO	9	1068.51	5.05	0.04	0.98
TD + TR	4	1070.38	6.93	0.02	1

**Table 5.2** 100% Confidence set of best-ranked regression models examining the effect of 13 biotic and abiotic factors on foraging patterns of Great Knots. Abbreviations in model as in Table 5.1.

Variable	model averaged estimate	Uncondition al S.E.	95% CI	Variable weight
MR	-0.0048	8.00E-04	-0.0063 to -0.0033	1
TD (flood tide)	-0.0012	0.1147	-0.2261 to 0.2236	0.60
TD (ebb tide)	0.0012	0.1147	-0.2236 to 0.2261	0.62
TR (spring tide)	-0.0607	0.1292	-0.3138 to 0.1925	0.62
TR (neap tide)	0.0607	0.1292	-0.1925 to 0.3138	0.62
TI	0	0	0 to 0	0.48
JD	-0.0021	0.0038	-0.0094 to 0.0054	0.48
AN	-0.7399	0.455	-1.6316 to 0.1518	0.17
РО	1.2142	1.8045	-2.3225 to 4.7509	0.08
BI	0.1427	0.2559	-0.3588 to 0.6442	0.07
GA	0.7311	1.0676	-1.3613 to 2.8235	0.06
AM	85.5803	112.0332	-134.0006 to 305.1613	0
CU	43.2676	30.6176	-16.7417 to 103.277	0
LI	0.9234	1.114	-1.26 to 3.1068	0
SH	4.7007	4.1118	-3.3583 to 12.7596	0

**Table 5.3** Model averaged estimates for the 13 factors predicting the foraging proportion of Bartailed Godwits. Abbreviations in model as in Table 5.1. Variables in bold represents important variable based on the 95% confident interval estimates.

**Table 5.4** Model averaged estimates for the 13 factors predicting the foraging proportion of Great Knots. Abbreviations in model as in Table 5.1. Variables in bold represents important variable based on the 95% confident interval estimates.

Variable	model averaged estimate	Uncondition al S.E.	95% CI	Variable weight
TD (flood tide)	0.929	0.2232	0.4914 to 1.3665	1
TD (ebb tide)	-0.929	0.2232	-1.3665 to -0.4914	1
TR (spring tide)	0.7413	0.2402	0.2705 to 1.2121	1
TR (neap tide)	-0.7413	0.2402	-1.2121 to -0.2705	1
MR	-0.0047	0.0016	-0.0077 to -0.0016	0.99
TI	0.000006	0.000005	-0.000003 to 0.00001.5	0.49
JD	0.00036	0.00779	-0.01491 to 0.01564	0.49
BI	0.4955	0.5583	-0.5988 to 1.5898	0.12
РО	8.1698	9.2869	-10.0323 to 26.3718	0.12
GA	1.1839	1.1591	-1.0878 to 3.4557	0.09
AN	-0.4628	8.6894	-17.4937 to 16.5681	0.05
AM	148.4666	185.629	-215.3595 to 512.2926	0
CU	-29.2287	79.29	-184.6343 to 126.1768	0
LI	179.8315	304.3501	-416.6838 to 776.3468	0
SH	-167.6308	510.7773	-1168.736 to 833.4744	0



**Figure 5.2** Proportion of foraging birds in relation to low tide in 2011 and 2012 under different tidal ranges. Smoothed lines were fitted to show the trend. The average number of Bar-tailed Godwits and Great Knots recorded per scan were 174 and 254, respectively.



Spatial variation in foraging proportion

**Figure 5.3** Spatial variation in foraging patterns among Bar-tailed Godwits and Great Knots within the 36 grids. The layout of sampling station corresponds to those in Figure 5.1c.

## 5.4.2 Intake rates

The 13 biotic and abiotic factors considered together explained 33.7% and 4.5% of the variation in the intake rates of Bar-tailed Godwits and Great Knots, respectively (adjusted  $R^2$  based on the full models). In both species, no single model was clearly superior to the other sets (w≥0.9) (Table 5.5 and Table 5.6). However, it was clear that none of the prey availability variables were involved in the top four candidate models for either species. Results from model averaging indicated that abiotic factors including the year, date, tidal range, time relative to low tide and distance to seawall were important variables that affected the intake rate in godwits (Table 5.7). Their intake rates were higher in 2011, in neap tide, near low tide, with increasing Julian day and distance to seawall. For Great Knots, only year and distance to seawall affected the intake rate (Table 5.8). Their intake rates were higher in 2011 and with increasing distance to seawall, but the factors considered explained relatively little variation (4.5%) in the intake rate of knots. Examining the functional response indicated that the plateau of intake rates were reached quite early as density of bivalve prey increased (Figure 5.4).

**Table 5.5** 100% Confidence set of best-ranked regression models examining effect of 13 biotic and abiotic factors on intake rate (square-root transformed) of Bar-tailed Godwits (full model adjusted R<sup>2</sup> 33.7%, n=181). Only observations with all prey items identified and foraging time exceeding 2.5 minutes were included.

			Delta		
Candidate models	K	AICc	AICc	AICcwt	Cum.Wt
YE + DA + TR + MR + TD	7	141.53	0	0.56	0.56
YE + DA + TR + MR + TD + SE + BP	9	143.37	1.84	0.22	0.78
YE + DA + TR + MR + TD + CP + DS + DW	12	144.43	2.9	0.13	0.91
YE + DA + TR + MR + TD + SE + BP + CP + DS + DW	14	146.46	4.93	0.05	0.96
YE + DA + CP + DS + DW	9	148.76	7.23	0.02	0.98
YE + DA + TR + MR + TD + BI515 + BI15 + PO + SH	11	149.09	7.56	0.01	0.99
YE + DA + TR + MR + TD + SE + BP + BI515 + BI15					
+ PO + SH	13	151.35	9.82	0	0.99
YE + DA + SE + BP + CP + DS + DW	11	151.47	9.94	0	1

*YE* Year, *DA* Days since the end of February, *TR* Tidal range, *MR* minutes relative to low tide, *TD* tidal direction, *CP* number of counterparts within 50m, *DS* distance to seawall, *DW* distance to water, *SE* Sex, *BI515* biomass of bivalve (length 5-15 mm) available, *BI15* biomass of bivalve (length $\geq$ 15 mm) available, *PO* biomass of polychaete available, *SH* biomass of Shrimp available.

**Table 5.6** 97% Confidence set of best-ranked regression models examining the effect of 10 biotic and abiotic factors on intake rate (Log<sub>e</sub> transformed) of Great Knots (full model adjusted R<sup>2</sup> 4.5%, n=111). Only those observations with all prey items identified and foraging time exceeding 2.5 minutes were included.

Candidate models	К	AICc	Delta AICc	AICcwt	Cum.Wt
MR	3	239.16	0	0.18	0.18
DS	3	239.65	0.49	0.14	0.32
DA	3	239.93	0.77	0.12	0.44
DW	4	241.01	1.86	0.07	0.51
BI515	3	241.59	2.44	0.05	0.56
BP	3	241.81	2.65	0.05	0.61
YE + DA	4	241.88	2.73	0.05	0.65
TD	3	241.99	2.83	0.04	0.7
BI15	3	242.03	2.88	0.04	0.74
YE	3	242.06	2.9	0.04	0.78
TR	3	242.07	2.91	0.04	0.82
BI515 + BI15	4	243.11	3.95	0.02	0.85
TR + MR + TD	5	243.34	4.18	0.02	0.87
YE + DA + BP	5	243.36	4.2	0.02	0.89
CP + DS + DW	7	243.44	4.28	0.02	0.91
СР	4	243.62	4.46	0.02	0.93
YE + DA + BI515 + BI15	6	244.29	5.14	0.01	0.94
YE + DA + TR + MR + TD	7	244.44	5.28	0.01	0.96
BP + BI515 + BI15	5	244.95	5.79	0.01	0.97
TR + MR + TD + BP	6	245.14	5.99	0.01	0.97

**Table 5.7** Model averaged estimates for the 14 variables predicting intake rate (square-root transformed) of Bar-tailed Godwits. Variables in bold represents important variable based on the 95% confident interval estimates.

Variable		model averaged estimate	Unconditional S.E.	95% CI	Variable weight	
Year		-0.2215	0.0812	-0.3806 to - 0.0625	0.99	
Date		0.0088	0.0025	0.0038 to 0.0138	0.99	
Distance to seawall		0.0003	0.0001	0.0002 to 0.0004	0.99	
	0-5	-0.0943	0.0872	-0.2652 to 0.0766		
Number of counterparts	6-10	0.02	0.0796	-0.136 to 0.176	0.99	
	>10	0.0943	0.0872	-0.0766 to 0.2652		
	Zero	0.0049	0.0845	-0.1607 to 0.1704		
Distance to water	1-50m	-0.114	0.119	-0.3473 to 0.1193	0.99	
	>50m	0.114	0.119	-0.1193 to 0.3473		
Spring		-0.2218	0.0764	-0.3716 to - 0.072	0.54	
Tidal range	Neap	0.2218	0.0764	0.072 to 0.3716	0.71	
Time relative to low t	tide	0.0001	0.0005	-0.0008 to 0.001	0.71	
Tidal direction	Flood	-0.0889	0.1141	-0.3124 to 0.1347	0.71	
i idai direction	Ebb	0.0889	0.1141	-0.1347 to 0.3124	0.71	
Breeding plumage		0.0191	0.0341	-0.0478 to 0.086	0.36	
Sov	Female	-0.0458	0.1175	-0.276 to 0.1845	0.26	
Sex	Male	0.0458	0.1175	-0.1845 to 0.276	0.30	
Available bivalve (5-15mm)		0.253	0.1914	-0.1221 to 0.6282	0.13	
Available bivalve (>15mm)		-0.0139	0.0501	-0.112 to 0.0843	0.13	
Available Polychaete		-1.0974	0.8283	-2.7207 to 0.526	0.13	
Available ghost shrimp		-5.9643	3.2674	-12.3683 to 0.4397	0.13	

Variable		model averaged estimate	Unconditional S.E.	95% CI	Variable weight
Year		-0.401	0.1867	-0.7668 to -0.0352	0.51
Date		-0.0008	0.0053	-0.0111 to 0.0095	0.25
Distance to seawal	1	0.0002	0.0001	0 to 0.0003	0.19
Breeding plumage		-0.0042	0.0041	-0.0123 to 0.0038	0.17
Distance to water	Zero	0.2756	0.1848	-0.0866 to 0.6379	
	1-50m	-0.0671	0.2385	-0.5345 to 0.4003	0.09
	>50m	0.0671	0.2385	-0.4003 to 0.5345	
	0-5	0.2321	0.2678	-0.2928 to 0.7571	
Number of	6-10	0.0877	0.1648	-0.2354 to 0.4108	0.08
counter put to	>10	-0.2321	0.2678	-0.7571 to 0.2928	
T: 1-1	Spring	0.1132	0.1381	-0.1574 to 0.3838	0.07
i idal range	Neap	-0.1132	0.1381	-0.3838 to 0.1574	0.07
Tidal direction	Flood	0.1143	0.207	-0.2913 to 0.52	0.07
	Ebb	-0.1143	0.207	-0.52 to 0.2913	0.07
Time relative to low	tide	-0.0001	0.0009	-0.0019 to 0.0017	0.06
Available bivalve (5-	-15mm)	0.5027	0.4864	-0.4505 to 1.456	0.06
Available bivalve (>:	15mm)	-0.0227	0.0968	-0.2125 to 0.167	0.04

**Table 5.8** Model averaged estimates for the 11 variables predicting intake rate ( $Log_e$  transformed)of Great Knots. Variables in bold represents important variable based on the 95% confident intervalestimates.



**Figure 5.4** Intake rates of Bar-tailed Godwits and Great Knots in relation to the harvestable density of their main prey in Yalu Jiang coastal wetland in 2011 and 2012. The smoothed curves were generated using loess smoothing method (displayed as mean ± 95% standard error).



**Figure 5.5** The change in foraging patterns and intake rates in Bar-tailed Godwits and Great Knots in relation to the harvestable biomass (AFDM grams per core sample) of their main prey *Potamocorbula laevis*.

## **5.5 Discussion**

In contrast to our prediction that prey availability would play an important role in determining the foraging patterns and intake rates of Bar-tailed Godwits and Great Knots during stopover at Yalu Jiang coastal wetland, we found that abiotic factors such as time relative to low tide, distance to seawall and tidal range, played a more important role. Nevertheless, in accordance with our prediction, similar model sets performed differently in explaining the variations of intake rates between godwits and knots.

Associations between the distribution of shorebirds and their prey may disappear in finer scale analysis (Colwell & Landrum 1993); this could explain our failure to detect any relationship between prey availability and foraging and intake rates of shorebirds. The fact that we selected the most attractive part of the reserve (where most birds foraged) to conduct our study might make it less likely to detect a positive relationship between prey availability and foraging behaviour of birds.

## 5.5.1 Foraging patterns

Time relative to low tide was an important factor that determined the foraging patterns of Bar-tailed Godwits and Great Knots, with the proportion of birds foraging increasing towards low tide. A closer examination revealed a striking contrast in the foraging patterns between godwits and knots, with most of the godwits foraging throughout the low tide whereas there was always a high proportion of non-foraging knots during the same period (Figure 5.2). There were also differences in when godwits and knots started feeding during spring tides and neap tides (Figure 5.2). The tidal flats became available about 250 minutes before low tide on spring tides, but around 300 minutes before on neap tides. On spring tides, virtually all godwits started feeding immediately whereas on neaps there was a more gradual, and earlier, initiation of feeding. Great Knots also started feeding earlier on neaps, but still showed a wide range in foraging proportions, even on spring tides. The difference between these patterns likely arises from the difference in diet between godwits and knots. The latter fed almost exclusively (92–100% of their biomass intake) on the shellfish *P. laevis*, which had a patchy distribution, and was mostly found more than 1,000 m out from the seawall (Chapters 3, 4 & 10). Consequently, foraging opportunities were low on the upper flats that were the first exposed on the falling tide and knots tended to wait for the tide to drop before moving out to feed. In contrast, godwits had a broader diet that included polychaetes (9–31% of their biomass intake) that dominated near the seawall (Chapters 3, 4 & 10). Godwits could start feeding immediately

once the flats were exposed, and walk out with the falling tide, eventually reaching the shellfish beds where the bulk of their biomass intake (61–87%) was gained. This difference in foraging pattern was also evident in the maps of feeding activity (Figure 5.3), in which the distribution of feeding activity of godwits was more uniform across the entire tidal flats.

The varied foraging pattern during low tide in Great Knots was in contrast to that reported in their wintering ground, where most Great Knots foraged throughout the low tide (Tulp & de Goeij 1991). The different patterns between godwits and knots also contradicted the pattern from studies in their wintering grounds and in other shorebird studies that smaller shorebird species spend more time feeding in a tidal cycle (Dann 1987; Engelmoer *et al.* 1984; Zwarts *et al.* 1990). These differences may be partly due to the high harvestable prey biomass in this study, which was almost twice as much as those reported in wintering grounds and other important stopover sites for shorebirds (Appendix 1; Tulp & de Goeij 1994). High prey levels might enable high enough intake rates that birds do not need to feed continuously across the low tide period (Stienen *et al.* 2008). Alternatively, the difference could imply that Great Knots suffered a digestive bottleneck that required them to take digestive pauses (van Gils *et al.* 2005c; Zwarts & Dirksen 1990).

Tidal direction and tidal range also affected the proportion of individuals foraging in Great Knots. The proportion of foraging knots was higher in flood than ebb tide, which could be a result of the flood tide pushing birds regularly towards the seawall and giving birds less time to rest. Alternatively, the birds may anticipate a fasting period over high tide and therefore forage more. The higher proportion of foraging knots during spring than neap tide cycle could be the result of the reduced tidal flat exposure time during spring (18.58±0.99 h per day) than neap tide (21.01±1.61 h per day), as reflected in Figure 5.2. The tidal flats became available about 250 minutes before low tide on spring tides, but around 300 minutes before on neap tides; this difference evidently, forces birds to feed as quickly as possible. This imposed further feeding restriction to Great Knots during spring tide that were already restricted by their narrower diet.

## 5.5.2 Intake rates

In contrast to foraging patterns, the performance of similar models on intake rates of godwits was substantially different to knots. The full model explained 33.7% of variation in the intake rates of godwits but only 4.5% of knots. The relatively poor results in knots may partly stem from digestive pauses that slow down the foraging activity as the birds

become satiated, adding further variation to the intake rates. For both species, the intake rates decreased from 2011 to 2012 but increased as the birds moved further away from the seawall. These seem to be related to the availability and distribution of their main prey *Potamocorbula laevis*, which was mainly distributed further than 1,000 m from the seawall and had a different size composition between years (Chapters 3 & 4). Functional response plots (Figure 5.4) between intake rates and harvestable bivalve prey density indicated that intake rates reached a plateau when prey density was still relatively low. This indicates that prey availability might be higher than the birds can handle and process, which may also explain the relatively poor performances of prey availability in explaining the variations in intake rates and foraging patterns of godwits and knots (Figure 5.5).

Estimated intake rates for Bar-tailed Godwits (1.99±1.5 mg AFDM/s in 2011, 1.01±0.81 in 2012) were within the upper range of those reported during fuelling in wintering grounds (1.45-2.13 mg DM/s based on diet dominated by crabs and the use of DM may over-estimate the intake by twice as much as it would have been in AFDM: Zharikov & Skilleter 2002); Great Knot intake rates (1.8±1.65 mg AFDM/s in 2011, 0.81±0.48 in 2012) were substantially higher (0.24 mg AFDM/s: Tulp & de Goeij 1994). This provided another line of evidence that the harvestable prey biomass at Yalu Jiang coastal wetland during northward migration was reasonably high for shorebirds to refuel and prepare for their next flight towards their breeding grounds. In other words, the ample food resources partly explained why the study site is the most important staging site along the flyway for both Bar-tailed Godwits and Great Knots during northward migration (Chapter 2).

Despite prey availability not being an important factor in the models, the fact that different foraging patterns and intake rates observed between Bar-tailed Godwits and Great Knots could partly be attributed to their different dietary selections indicate that food is important but may occur in densities too high to explain the variation.

## 5.5.3 Implications for future studies

Our results show that the intertidal ecosystem is a dynamic environment and tide-related abiotic factors such as tidal ranges and exposure time play important roles in determining the foraging patterns and intake rates of shorebirds. Comparative studies to date have focused on relating food availability to the distribution of shorebirds while abiotic factors such as those related to the tidal cycle, including inundation time, have received less attention (Piersma *et al.* 1993b). The latter is of critical importance for shorebirds at

staging sites where they have to refuel within a limited amount of time constrained both by the tidal cycle and the migration schedule of the birds. These tide-related factors, in addition to food availability, may play an important role in staging site selection by shorebirds (van Gils *et al.* 2006b) and should be reported more often in similar studies to allow comparison.

**Appendix 5.1** The twenty candidate model sets used to test the factors that may affect foraging patterns of Bar-tailed Godwits and Great Knots in this study.

Candidate models
TI + TD + MR + TR + JD + AM + AN + BI + CU + GA + LI + PO + SH
TI + TD + MR + TR + JD
TD + MR + TR
TD + MR
MR + TR
TD + TR
TD
MR
TI + JD
JD
TI
TI + TD + MR + TR + JD + BI
TI + TD + MR + TR + JD + PO
TI + TD + MR + TR + JD + BI + PO
TI + TD + MR + TR + JD + GA
TI + TD + MR + TR + JD + AN
AM + AN + BI + CU + GA + LI + PO + SH
BI
PO
BI + PO

*TI* time interacts with minutes relative to low tide, *TD* tidal direction, *MR* minutes relative to low tide, *TR* Tidal range, *JD* Julian day, *AM* biomass of amphipod, *AN* biomass of Anthozoa, *BI* biomass of bivalve, *CU* biomass of Cumacea, *GA* biomass of gastropod, *LI* biomass of lingual, *PO* biomass of Polychaeta, *SH* biomass of Shrimp.

Appendix 5.2 The 46 candidate model sets used to test the factors that may affect intake rate of
Bar-tailed Godwits.

Species	Candidate models
-	YE + ID + TR + MR + TD + SE + BP + CP + DS + DW + BI515 + BI15 + PO + SH
	YE
	ID ID
	שן תיד
	IR MD
	MR
	SE
	BP
	CP
	DS
	DW
	BI515
	BI15
	PO
	CH CH
	SE + BP + BISIS + BIIS
	SE + BP + PO + SH
	YE + JD + SE + BP
	TR + MR + TD + SE + BP
	SE + DS + DW + BP + CP
	SE + BP + BI515 + BI15 + PO + SH
Day tailed Codurit	YE + JD + TR + MR + TD + SE + BP
Bar-talled Godwit	YE + ID + SE + BP + CP + DS + DW
	YE + ID + SE + BP + BI515 + BI15 + PO + SH
	TR + MR + TD + BP + SE + CP + DS + DW
	TR + MR + TD + SE + BP + BI515 + BI15 + PO + SH
	SF + BP + CP + DS + DW + BI515 + BI15 + PO + SH
	VE + ID + TD + MD + TD + SE + BD + CD + DC + DW
	IE + JD + IR + MR + ID + SE + DI + CI + DS + DW $VE + ID + TD + MR + TD + CE + DD + DI + CI + DO + CI$
	IE + JD + IR + MR + ID + SE + BP + BISIS + BIIS + PO + SH
	YE + JD + SE + BP + CP + DS + DW + BIS15 + BI15 + PO + SH
	TR + MR + TD + SE + BP + CP + DS + DW + BI515 + BI15 + PO + SH
	YE + JD
	TR + MR + TD
	CP + DS + DW
	BI515 + BI15 + PO + SH
	YE + ID + TR + MR + TD
	YE + ID + CP + DS + DW
	YE + ID + BI515 + BI15 + PO + SH
	TR + MR + TD + CP + DS + DW
	TD + MD + TD + BI515 + BI15 + DO + CH
	III + MII + III + DIJJ + DIJJ + IO + JII
	$\Gamma_{L} + \Gamma_{D} + \Gamma_{M} + \Gamma_{D} + \Gamma_{D} + \Gamma_{D} + \Gamma_{D} + \Gamma_{D} + 2\Gamma$
	YE + JD + IK + MK + ID + CP + DS + DW
	YE + JD + TR + MR + TD + BI515 + BI15 + PO + SH
	YE + JD + CP + DS + DW + BI515 + BI15 + PO + SH
	TR + MR + TD + CP + DS + DW + BI515 + BI15 + PO + SH
	YE + JD + TR + MR + TD + BP + CP + DS + DW + BI515 + BI15
	YE
	JD
	TR
Great Knot	MR
ar out mildt	тр
	RD
	US

```
DW
BI515
BI15
YE + JD
TR + MR + TD
CP + DS + DW
BI515 + BI15
YE + JD + BP
TR + MR + TD + BP
BP + CP + DS + DW
BP + BI515 + BI15
YE + JD + TR + MR + TD
YE + JD + BP + CP + DS + DW
YE + ID + BI515 + BI15
TR + MR + TD + BP + CP + DS + DW
TR + MR + TD + BI515 + BI15
BP + CP + DS + DW + BI515 + BI15
YE + JD + TR + MR + TD + BP + CP + DS + DW
YE + JD + TR + MR + TD + BI515 + BI15
YE + BP + ID + CP + DS + DW + BI515 + BI15
TR + MR + TD + BP + CP + DS + DW + BI515 + BI15
```

YE Year, JD Julian day, TR Tidal range, MR minutes relative to low tide, TD Tidal direction, SE Sexes, BP breeding plumage score, CP number of counterparts within 50m, DS Distance to seawall, DW Distance to water edge, BI515 Ash-free dry mass (AFDM) of bivalve between 5 and 15mm, BI15 AFDM of bivalve larger than 15mm, PO AFDM of Polychaeta, SH AFDM of Shrimp.

# Chapter 6. How Bivalve Size and Quality Interact to Limit Intake Rates of Bar-tailed Godwits and Great Knots in the Northern Yellow Sea

Choi C-Y, Battley PF, Potter MA, Ma ZJ & Melville DS (In preparation)

# 6.1 Abstract

Intake rate is commonly used as a surrogate for fitness and therefore is an important currency in the study of foraging ecology. It is often positively related to the biomass and density of harvestable prey. In this study, we report an exception found in the Bar-tailed Godwits and Great Knots during northward migration stopover on the intertidal flats in the north Yellow Sea. We found clear behavioural evidence for a digestive bottleneck in the bivalve-feeding shorebirds during our study. In accordance to our predictions, the species with the greatest reliance on ingesting bivalves whole (Great Knot and Red Knot) had more frequent and longer pauses in their foraging than the species with mixed diets (Bar-tailed Godwit) or that ingested only the flesh of bivalves and not the shell (Far Eastern Oystercatcher). Such differences were also found at the population level between Great Knots and godwits. Godwits which fed mostly on hard prey also had more frequent and longer pauses than those feeding on soft prey. Such digestive constraints on hardshelled prey could partly explain the substantial decline in the numerical and biomass intake rates of godwits and Great Knots in 2012 compared to 2011, despite similar numerical and biomass density of their most important bivalve prey Potamocorbula laevis. In addition, decrease in prey quality, increase in handling time and possibly searching time were other potential factors that might contribute to the decline in total biomass intake rate in 2012. We conclude it is important to take digestive constraints and the possible length of foraging period into account when studying the foraging ecology of shorebirds to allow meaningful comparisons between studies and reliable estimates, especially for shorebirds that may face digestive bottlenecks at sites with very high food availability.

# 6.2 Introduction

The intake rate of an animal is commonly defined as "the speed at which food is eaten during foraging" (Ens *et al.* 2004). It is an interaction between density (Wanink & Zwarts 1985), size distribution (Zwarts *et al.* 1996a) and quality of harvestable prey (van Gils *et al.* 2005b; van Gils *et al.* 2003). The intake rate is commonly used as a surrogate for fitness and therefore, is an important currency in the study of foraging ecology (Scheiner & Willig 2011). The intake rate is often positively related to prey biomass and density, with the peak being constrained by searching and handling time (Goss-Custard *et al.* 2006). Additionally, digestive constraints can also limit processing capacity (and hence intake rates), for example in large grazing herbivores where intake rates decline despite high grass biomass being available (Wilmshurst *et al.* 1999). The same constraint has been

surmised to limit intake rates (Wilson 1990) and be the reason for digestive pauses in shorebirds (Ens *et al.* 2004).

Digestive constraints on intake rate are particularly applicable to shorebirds that feed on hard-shelled prey. Red Knots *Calidris canutus* are bivalve-specialists capable of ingesting hard-shelled prey whole and crushing the shell with their large gizzards (Piersma *et al.* 1993c). Their daily energy intakes in captive experiments were constrained by their ability to process the shells ingested (van Gils *et al.* 2005b; van Gils *et al.* 2003). Similarly, studies on Far Eastern Curlews *Numenius madagascariensis* in Australia (Zharikov & Skilleter 2003), Whimbrels *Numenius phaeopus* in the Banc d' Arguin (Zwarts & Dirksen 1990) and Gull-billed Terns in *Gelochelidon nilotica* in Guinea-Bissau (Stienen *et al.* 2008), all of which had a crab-dominated diet, also found evidence for a digestive bottleneck effect. However, all of these studies were conducted in the wintering grounds while little evidence has been found for digestive bottlenecks in birds on migratory stopping sites.

On an intertidal flat in the north Yellow Sea, we found a potentially analogous situation in the refuelling of a large generalist forager (Bar-tailed Godwit Limosa *lapponica*) and a medium-sized bivalve-specialist (Great Knot *Calidris tenuirostris*) during their northward migration stopover. At least 60% of the biomass intake of godwits and 90% of Great Knots during their stopovers was composed of a single bivalve prey Potamocorbula laevis (Chapter 4). Paradoxically, the numerical and biomass intake rates of both species declined substantially in 2012 compared to 2011 despite similar numbers and biomass of *P. laevis* being present between years (Chapters 3, 4 & 10). However, the size-structure of the *P. laevis* population was different in the two years, with young *P. laevis* (length<10 mm) dominating in 2011 but adult *P. laevis* (length≥10 mm) dominating in 2012. Although godwits and Great Knots were capable of taking almost all the possible sizes of *P. laevis*, they preferred intermediate-sized shellfish, which were the least available size-classes (Chapter 5). Intake rates of godwits were fairly well explained by biotic and abiotic factors, but these same factors were poor at explaining variation in Great Knot intake rates (Chapter 6). We hypothesise that Great Knots are subject to similar digestive constraints as documented in other shorebird species mentioned above. Given the unusually high reliance of godwits upon bivalves at our study site, and the fact that the species does not have a particularly large gizzard for their body mass (as opposed to mollusc-specialists including the Great Knot; Battley & Piersma 2005a), it is possible that Bar-tailed Godwits are also constrained to some degree by digestive factors.

The aim of this study was therefore to explore how the foraging activity and intake rates of Bar-tailed Godwits and Great Knots differ and to evaluate the potential impacts of digestive bottlenecks on these species. Documenting digestive bottlenecks in the wild is difficult, so we used several lines of indirect evidence to investigate likely bottleneck effects (Stienen *et al.* 2008; Zwarts & Dirksen 1990). We predicted that if bivalve-foraging leads to digestive constraints in the field, then comparing species with the greatest reliance on bivalves ingested whole (Great Knot and Red Knot) to those with mixed diets (Bar-tailed Godwit) or that ingested only the flesh (Far Eastern Oystercatcher *Haematopus ostralegus osculans*), the former should (a) spend higher proportion of time not foraging, (b) have more frequent and longer foraging pauses, and (c) within a single species, individuals feeding on hard prey should have more frequent and longer foraging pauses than those feeding on soft prey.

# 6.3 Materials and methods

## 6.3.1 Study area

This study was conducted at the Dandong Yalu Jiang Estuary Wetland National Nature Reserve (39°40′–39°58′N, 123°34′–124°07′E), located on the Chinese side of China-North Korea border. The reserve and surrounding area supports more than 250,000 shorebirds during northward migration and is the most important northward migration staging area for Bar-tailed Godwits, Great Knots and Far Eastern Oystercatchers (Chapter 2; Melville *et al.* 2014; Riegen *et al.* 2014). A 9 km<sup>2</sup> (3 x 3 km) study site in an area of high bird use was set up on the intertidal flat in the middle of the reserve for detailed benthos sampling and shorebird observations. More detailed descriptions of the study area can be found Chapters 3 and 4.

## 6.3.2 Behaviour scan and focal observation of shorebirds

Foraging activity at the population level was determined from behaviour scans of Bartailed Godwits and Great Knots. These were conducted on an opportunistic basis within the study area between March and May in 2011 and 2012. Date, time, location, and the numbers of foraging and resting birds were recorded in each scan. Birds that were walking, probing, pecking or handling prey were regarded as foraging while those preening or motionless were treated as resting.

Focal bird observations were carried out at the same location and time-frames as the behaviour scans to determine foraging patterns and intake rates of individuals. Complete descriptions of the methods can be found in Chapter 4. In brief, a randomly chosen focal bird from a flock of foraging birds was watched for 5 minutes, during which all swallowed prey items were recorded on a digital voice recorder, as were all other activities, events and interactions with other birds during the observation bout (Appendix 4.2). Our main focus was the numerically-dominant Bar-tailed Godwits and Great Knots, with the maximum number of at least 4,800 and 19,000, respectively were recorded within the study site (C.-Y. Choi unpublished data). Observations were also made where possible on Far Eastern Oystercatchers (maximum count=1,288) and Red Knots (maximum count=84) when they were present in the study area. All of these four species fed on *P. laevis*, godwits and the two knots species predominantly swallow the *P. laevis* whole and only occasionally picked the flesh out while oystercatchers predominantly took only the flesh without swallowing the shell (Chapter 4). Given that the aim of the focal bird observations was to investigate the diet and intake rate, resting birds were not selected, but observations continued if focal birds stopped foraging after the start of an observation bout. Data were transcribed using JWatcher (Blumstein et al. 2006), recording all activity states, feeding actions and prey captures. From these, handling times could be generated (apart from when Great Knots were 'sewing' for small prey in 2011 and the feeding action resulting in an individual prey swallow could not be determined), and the frequency and duration of pauses in foraging bouts could be extrapolated.

Numerical intakes were multiplied by prey- and size-specific biomass relationships (Chapters 4 & 5) to give biomass intake rates (in mg ash-free dry mass per second) across a foraging bout, excluding non-foraging time. Individuals were categorised as having a hard-bodied diet if hard-bodied prey (bivalves swallowed whole) contributed more than soft-bodied prey to the total biomass intake, and vice versa.

### 6.3.3 Statistical analysis

Bivalve prey quality was defined as the amount of energy content per dry mass of shell that a bird processed (van Gils *et al.* 2005a). The prey quality in different sized *P. laevis* was calculated as  $Q=d \times a \times AFDM_{flesh} / DM_{shell}$ , where *Q* is the prey quality (defined as flesh-to-shell ratio, presented as kJ g<sup>-1</sup> shell dry mass; van Gils *et al.* 2005a), *d* is the energetic density of flesh (22 kJ g<sup>-1</sup> AFDM) (Zwarts & Wanink 1993) and *a* is the assimilation efficiency (0.8) (Kersten & Piersma 1987). The amount of *P. laevis* shell eaten by focal birds was estimated using the same method as the *P. laevis* ash-free dry mass estimates described in Chapter 4.

Analysis of covariance with permutations was used to test the null hypothesis that there was no difference in (1) the proportion of time spent foraging between species groups, after controlling for the effect of year; (2) the proportion of time spent foraging between godwits feeding mainly on soft-bodied and hard-bodied prey, after controlling for effects of year and sex; (3) the frequency of digestive pauses between species, after controlling for year; (4) the frequency of digestive pauses between birds feeding mainly on soft-bodied and hard-bodied prey, after controlling for year and species; (5) the handling time between 2011 and 2012 in godwits per bivalve prey that was swallowed whole, after controlling for sex. These tests were conducted using "aovp" function in the *ImPerm* package (Wheeler 2010), performed with R v3.0.1 (R Core Team 2013). A significance level of ( $\alpha$ ) 0.05 was used for all statistical tests, with means given±SD unless stated otherwise.

## **6.4 Results**

#### 6.4.1 Foraging patterns

Striking differences in foraging patterns were found between Bar-tailed Godwits and Great Knots at the population level. The proportion of godwits foraging was generally high across the entire low-tide period (Figure 6.1). In contrast, the proportion of foraging Great Knots ranged from almost all to virtually no birds foraging at any time of the tide. Similarly, at the individual level, godwits and oystercatchers spent significantly more time within observation bouts foraging than did Great Knots and Red Knots (5,000 iterations, controlling for year, p<0.0001, Table 6.1). There was an effect of year, with the proportion of time spent foraging being consistently higher in 2011 than 2012 in godwits and Great Knots (5,000 iterations, p=0.0024, Table 6.1). Godwits feeding predominantly on hard-bodied prey spent 5-7% less time foraging than those foraging on soft-bodied prey (5,000 iterations, controlling for year and sex, p<0.0001, Table 6.2).

The frequency of pauses within foraging bouts was significantly higher in Great Knots and Red Knots than in godwits and oystercatchers (5,000 iterations, controlling for year, p<0.0001, Table 6.3). Consequently, the two knot species spent 18–28% of the time not foraging, whereas godwits and oystercatchers spent only 1–8% of the time not actively foraging (Table 6.3). There was an effect of year, indicating that pauses were more frequent overall in 2012 than in 2011 (5,000 iterations, p<0.0001). Finally, pauses were

more frequent in birds with hard-bodied prey than those with soft-bodied prey (5,000 iterations, controlling for year and species, p<0.0001, Table 6.3).



**Figure 6.1** The population-level proportion of foraging Bar-tailed Godwits and Great Knots (based on behaviour scans) in relation to time relative to low tide during two northward migrations at Yalu Jiang coastal wetland. Smoothed lines were fitted to show the trend and on average, 174 Bar-tailed Godwits and 254 Great Knots were included per scan.

**Table 6.1** Activity budgets of different shorebirds in the Yalu Jiang coastal wetland based on focalobservation. Values are average proportions of time±SD. Species abbreviations: BAGO=Bar-tailedGodwit, GRKN=Great Knot, FEOY=Far Eastern Oystercatcher and REKN=Red Knot.

Species	Year (n)	Foraging	Preening	Vigilant	Resting
BAGO	2011 (134)	0.95±0.12	0.03±0.1	0.02±0.05	0
female	2012 (221)	0.93±0.15	0.03±0.11	0.03±0.08	0±0.06
BAGO male	2011 (158)	0.96±0.1	0.02±0.09	0.02±0.05	0
	2012 (245)	0.94±0.15	0.03±0.11	0.02±0.06	0.01±0.06
	2011 (45)	0.78±0.23	0.13±0.2	0.07±0.1	0.01±0.05
GRKN	2012 (252)	0.75±0.25	0.15±0.2	0.08±0.11	0.02±0.09
FEOY	2012 (43)	0.92±0.14	0.01±0.03	0.06±0.13	0.01±0.04
REKN	2012 (18)	0.72±0.2	0.15±0.18	0.11±0.12	0.02±0.06

Sexes	Year	Prey type (n)	Foraging	Preening	Vigilant	Resting
		Soft (61)	0.98±0.05	0.01±0.02	0.01±0.04	0
	2011	Hard (29)	0.91±0.17	0.05±0.15	0.04±0.06	0
Female		Soft (107)	0.95±0.13	0.03±0.12	0.02±0.06	0±0.01
	2012	Hard (54)	0.9±0.17	0.04±0.12	0.06±0.12	0±0.01
		Soft (48)	0.99±0.03	0±0.01	0.01±0.03	0
	2011	Hard (50)	0.94±0.11	0.03±0.09	0.02±0.04	0±0.01
Male		Soft (89)	0.96±0.12	0.02±0.08	0.01±0.02	0.01±0.05
	2012	Hard (77)	091+015	0.05+0.13	0 04+0 07	0+0.02

**Table 6.2** Activity budgets of Bar-tailed Godwits with different diets, determined by the dominant prey type in biomass intake during observation. Values are mean proportions of time±SD. Cases in which focal bird did not take anything or bird's diet dominated by unknown prey were excluded.

**Table 6.3** The frequency (number per minute) and duration of digestive pauses (seconds) and proportion of non-foraging time during focal bird observation for different species, diets and years, at Yalu Jiang coastal wetland. Species codes as per Table 6.1. F=female, M=male.

Year	Species	Prey type (n)	Frequency of foraging pause	Average duration of foraging pause	Proportion of non- foraging time
	BAGOF	All (151)	0.38±0.64	3.89±11.14	0.04±0.11
2011	BAGOM	All (174)	0.39±0.54	3.90±12.87	0.04±0.10
	GRKN	All (67)	1.13±0.74	9.25±10.51	0.18±0.20
	BAGOF	All (226)	0.46±0.76	8.17±27.09	0.07±0.15
	BAGOM	All (251)	0.43±0.63	5.38±17.86	0.06±0.14
2012	GRKN	All (255)	1.55±1.23	11.01±16.60	0.25±0.24
	FEOY	All (43)	0.58±0.69	7.48±17.82	0.08±0.14
	REKN	All (18)	1.43±0.84	14.64±19.21	0.28±0.20
	DAGOD	Soft (61)	0.27±0.38	3.00±8.76	0.02±0.05
0011	BAGOF	Hard (37)	0.68±0.83	4.93±8.38	0.08±0.15
2011	DACOM	Soft (48)	0.22±0.41	1.40±2.03	0.01±0.03
	BAGOM	Hard (56)	0.59±0.51	5.06±10.74	0.06±0.11
	DACOE	Soft (107)	0.37±0.46	7.00±23.09	0.05±0.13
	BAGOF	Hard (54)	0.78±1.22	7.93±23.26	0.10±0.17
0.04.0	DAGON	Soft (89)	0.28±0.39	4.02±12.03	0.04±0.12
2012	BAGOM	Hard (80)	0.57±0.69	5.41±9.39	0.08±0.15
	CDUN	Soft (8)	0.58±0.71	4.49±5.69	0.10±0.15
	GKKN	Hard (203)	1.62±1.16	11.76±17.14	0.27±0.24

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## 6.4.2 Intake rate

The biomass intake rate of bivalve prey that were swallowed whole in male and female Bar-tailed Godwits and Great Knots in 2012 was 62%, 63%, and 61% lower, respectively, than in 2011, despite bivalve availability being similar both numerically and in terms of biomass between years (Table 6.4 and Chapter 4). The size structure of *P. laevis* changed substantially, however, with a marked decrease in small *P. laevis* in 2012. Consequently, almost no small *P. laevis* were taken by godwits and Great Knots in 2012. Biomass intake rates on large *P. laevis* by both shorebird species also decreased in 2012, despite there being twice as many large *P. laevis* present. The loss of small bivalves in 2012 was partly compensated by an increase in taking bivalve flesh in godwits, and bivalve flesh and other prey in Great Knots (Figure 6.2), but the total biomass intake rate (all prey combined) in male, female Bar-tailed Godwits and Great Knots in 2012 still declined by 53%, 47%, and 55% respectively, when compared to 2011 (Table 6.4).

The numerical intake rate of large *P. laevis* in godwits and Great Knots declined by 28.8 and 35.3%, respectively, while the prey quality in all size classes declined by 22.1% on average. In other words, 57–61% of the decline in total biomass intake rate could be explained by the decline in numerical intake of large *P. laevis*, and 39–43% by decline in prey quality.

Chapter 6. Constraints on intake rates

Table 6.4 Summary of different biomass intake rates, biomass intake compositions, prey availability, prey quality and behaviour of shorebirds between years in Yalu Jiang coastal wetland.

Species	Year	Biomass in	itake rate		Numerical	density		Total <i>P. laevis</i> biomass density	Percentage of time spent	Dry mass of shell ner <i>P.</i>
		(AFDM mg	S <sup>-1</sup> )		(number m	-2)		(AFDM g m <sup>-2</sup> )	foraging	<i>laevis</i> taken
		Total	Small P. laevis	Large <i>P.</i> laevis	Total <i>P.</i> <i>laevis</i>	Small <i>P.</i> laevis	Large <i>P.</i> Iaevis		D	(g)
Bar-tailed	2011	$1.73 \pm 1.47$	$0.34\pm0.44$	$1\pm 1.31$	452±604	568±865	337±663	14±28.6	95±12	0.052
female	2012	$0.91\pm0.69$	$0\pm 0.01$	0.49±0.66	402±807	21±75	783±1593	15.5±31.2	93±15	0.139
Bar-tailed	2011	2.24±1.49	$0.51\pm0.49$	$1.39\pm 1.31$	452±604	568±865	337±663	14±28.6	96±10	0.052
Godwit male	2012	$1.06\pm0.89$	$0.01 \pm 0.01$	$0.71\pm0.88$	402±807	21±75	783±1593	$15.5\pm31.2$	94±15	0.139
Great Knot	2011	$1.8\pm 1.65$	0.3±0.32	$1.49\pm 1.34$	452±604	568±865	337±663	14±28.6	78±23	0.079
	2012	$0.81 \pm 0.48$	$0.01 \pm 0.01$	$0.69 \pm 0.47$	402±807	21±75	783±1593	15.5±31.2	75 ±25	0.143



**Figure 6.2** The biomass intake rate composition in Bar-tailed Godwits and Great Knots during northward migration at Yalu Jiang coastal wetland.

## 6.4.3 Prey quality

The quality of *P. laevis* decreased with shell length and the quality for each size class in March was considerably lower than in April and May (Figure 6.3). The weighted average of shell mass per *P. laevis* taken was substantially higher in 2012 than 2011 for godwits (0.14 g in 2012 versus 0.05 g in 2011) and Great Knots (0.14 g versus 0.08 g). Intake rates of both species were higher when the ingested shell mass was lower (Figure 6.4).



**Figure 6.3** Availability, usage and quality of *Potamocorbula laevis* in relation to size. Sizes available and taken by Bar-tailed Godwits and Great Knots in 2011 and 2012 are shown in the upper and middle plots, respectively (bars represent availability). Prey quality (energy content per gram of dry mass of shell) in relation to shell length is shown in the bottom plot, for April and May combined in 2011 and by month (March–May) in 2012.



**Figure 6.4** The biomass intake rate of Bar-tailed Godwits, Great Knots and Red Knots in relation to shell mass of *Potamocorbula laevis* during northward migration at Yalu Jiang coastal wetland.

## 6.4.4 Handling time

The handling time for individual *P. laevis* swallowed whole by Bar-tailed Godwits was significantly longer in 2012 (female:  $1.49\pm1.2$ , n=68; male:  $1.45\pm0.84$ , n=97) than 2011 (female:  $1.04\pm0.69$ , n=44; male:  $0.92\pm0.61$ , n=64) (5,000 iterations, controlling for sex, p<0.0001).

## 6.5 Discussion

#### 6.5.1 Digestive bottleneck

There was clear behavioural evidence supporting the proposition that a digestive bottleneck existed in the bivalve-feeding shorebirds at the Yalu Jiang coastal wetland during our study. In accordance to our predictions, at the population level, foraging activity levels were routinely much lower in Great Knots, whose diet consisted almost entirely of bivalves swallowed whole, than in Bar-tailed Godwits, which had a broader diet that included soft prey. This was matched by the individual foraging data, in which the species with the greatest reliance on bivalves ingested whole (Great Knot and Red Knot) had more frequent and longer pauses in their foraging than the species with mixed diets (Bar-tailed Godwit) or that ingested only the flesh (Far Eastern Oystercatcher). Just as compelling is the finding that within Bar-tailed Godwits, individuals feeding mostly on hard prey also had more frequent and longer pauses than individuals feeding on soft prey. These pauses resulted in 4–7% less time being spent foraging – this is evidently the digestive 'penalty' godwits pay when swallowing and processing *P. laevis*. Given that both Great Knots and Red Knots spent 18–28% of the time within foraging observation periods not actually foraging, it seems that the more exclusively bivalve-derived diet of those species, and/or lower functional capacities of their gizzards, result in a much greater loss of potential foraging time (note that as observations excluded birds that were not foraging, the true proportion of time spent not foraging would be higher for all species).

In accordance with our prediction on the effect of digestive bottleneck, we found that in year when prey quality was poor, the proportion of foraging time was significantly shorter and the occurrence of digestive pauses was significantly more frequent. Given the evidence of digestive constraints, it was not surprising that the foraging patterns observed in our study (godwits and oystercatchers foraged longer than the Great and Red Knots) was counter to the general belief that larger shorebirds forage for shorter than smaller shorebirds in a tidal cycle (Dann 1987; Engelmoer et al. 1984; Ens et al. 2004; Zwarts et al. 1990). Our findings hinted that the smaller species in our study might be constrained by factors that were often overlooked or uncommon. The Great Knots and Red Knots (both were bivalve specialists) were forced to take digestive pauses when their digestive organs were filled with shells. On the other hand, the larger species, Bar-tailed Godwits was more a generalist with a broader diet (Chapter 4), and may be capable of prey switching when their digestive organs were nearly full, thus avoiding the digestive pauses found in the knots. It is interesting to note that the Far Eastern Oystercatcher, the largest species in the study and a specialist feeder that fed almost exclusively on P. laevis (Chapter 4), fit into the body size- foraging time belief as they tended to forage less than godwits (Table 6.1, Table 6.3). However, the impact of bottleneck was less obvious in oystercatchers than other bivalve specialists (Great and Red Knots), probably because the oystercatchers managed to take only flesh out of the bivalves and therefore, avoid paying the price for shell processing in Great and Red knots.

#### 6.5.2 Constraints on intake rate

Shorebirds usually attain higher intake rates when eating large prey compare to small prey (Ens *et al.* 1996; Zwarts *et al.* 1996a). However, our results indicated that exception could arise when birds were feeding on prey that imposes digestive constraints, such as

bivalves. In the absence of apparent decline in the numerical and biomass density of their main prey, the decrease in intake rates of Bar-tailed Godwits and Great Knots and their different foraging patterns in both population- and individual-level could partly be explained by the digestive constraint.

In the absence of small *P. laevis* in 2012, godwits and Great Knots compensated their loss partly by taking more flesh *P. laevis* and other prey types, but their total biomass intake rate were still only about half of that in 2011 (Table 6.4). The birds could not increase their intake of large *P. laevis* probably due to the limits in processing rate and they did not prefer *P. laevis* larger than 15 mm perhaps due to the lower energy return per dry mass of shell processed (Figure 6.3) and the potentially higher crushing force (Yang *et al.* 2013). The birds would have to forage for longer in 2012 to meet their net energy gain in 2011.

Further evidence for digestive constraints might limit intake rate was found when a decrease in prey quality in 2012, thus amount of energetic gain per shell mass consumed, regularly (almost consistently) led to a lower proportion of foraging time and more frequent digestive pauses in godwits and Great Knots. In addition, godwits with hard prey-dominated diet had a significantly lower proportion of foraging time and took digestive pauses more frequently than those with soft prey-dominated diet. These indicated that the decrease in prey quality might lead to the decline in intake rate through more digestive pauses (Figure 6.4), in accordance to experiments on captive Red Knots that showed intake rates on hard-prey decreased with shell mass per prey (van Gils *et al.* 2003). Strictly speaking, digestive pauses should have no effect on intake rate because intake rate only takes foraging time into account. However, digestive pauses may slow down the way that birds forage and might therefore, lower the intake rate.

In addition to digestive constraints, an increase in handling time and possibly searching time were two other reasons that might contribute to the decline in total biomass intake rate in godwits and Great Knots in 2012. Larger *P. laevis* took the godwits significantly longer time to handle and it would not be surprising if the same applied to Great Knots. Moreover, the presence of more than a thousand flesh-eating oystercatchers within the study area in 2012 meant lots of partly-opened shells were left on the tidal flat, which might lead to longer search time for godwits and Great Knots in order to select the intact ones. These factors might lower the instantaneous biomass intake rate in 2012.

This study confirmed that the intake rates of shorebirds reached a plateau at relatively low prey density (Goss-Custard *et al.* 2006) for *P. laevis* but not necessarily for polychaetes (Figure 6.5). These might suggest that the processing rate and handling time of birds were limiting the intake of bivalve prey. Based on the study of ruminants, it was

stated that "Measures of instantaneous intake only tell us how quickly an individual will reach its daily dry matter intake limit, not what this limit will be" (Wilmshurst *et al.* 1999). In analogous to that statement and the use of *long-term* intake rate in other studies (van Gils *et al.* 2003; Zwarts & Dirksen 1990), it is important to take digestive constraints and the possible length of foraging period into account when studying the foraging ecology of shorebirds to allow meaningful comparison between studies and reliable estimates, especially for shorebirds that may face digestive bottleneck at sites with very high food availability.

## 6.5.3 Stopover site quality

This study is probably one of the first that demonstrates a possible bottleneck effect at a migratory staging site from a multi-species perspective. Previous reports on shorebirds were mostly in wintering grounds focusing on single species (Zharikov & Skilleter 2003; Zwarts & Dirksen 1990). The fact that bivalve prey were found and handled faster than could be processed by Godwits and Great Knots, while taking into account the relatively high bivalve quality and biomass availability in Yalu Jiang coastal area compared to other stopover and wintering sites for shorebirds (Appendix 1; Escudero et al. 2012; van Gils et al. 2005a), suggested that there may be more food available than the birds can take and therefore, may possibly support more birds than currently present, at least in the two years of study. Nonetheless, little is known about the life history of *P. laevis*. Their highly clumped distribution could be an adaptation to shorebird predation through dilution effect of predation risk (Hamilton 1971; Krebs & Davies 1993). Moreover, the remarkably low availability of the most "preferred" size range of *P. laevis* to the numerically most abundant shorebirds (Bar-tailed Godwits and Great Knots) at Yalu Jiang could be another product of the predator-prey evolutionary arm race – the most profitable size range of P. laevis for shorebirds were present mostly in the boreal mid-summer and autumn when predation pressure by migratory shorebirds was lowered, while environmental conditions for growth and reproduction remained favourable. It would be interesting to conduct experiments to determine how the life history of P. laevis was affected by episodic shorebird predation.

Given the remarkable impact of *P. laevis* on the intake rates of shorebirds during their migration stopover, Bar-tailed Godwits may be less affected than Great Knots by the fluctuations in the availability of *P. laevis* because the former had a broader diet while the latter is a bivalve-specialist (Chapter 4). In years when the availability of *P. laevis* are low, the availability of other naturally occurring bivalve species are unlikely to be adequate for

Great Knots (Chapters 3 & 10), which may have to turn their attention to the young cultivated Razor Clams that local fishermen put on the intertidal flat during boreal spring, thus increasing the potential of human-wildlife conflicts which deserve more attention in the future studies.



**Figure 6.5** The functional responses of Bar-tailed Godwits and Great Knots on bivalves and polychaetes during northward migration at Yalu Jiang coastal wetland, using loess smoothing method (displayed as mean ± 95% standard error).

# Chapter 7. Impacts of Shorebird Predation on the Numbers and Sizestructure of the Bivalve Potamocorbula laevis at an Important Shorebird Staging Site in the Northern Yellow Sea

Choi C-Y, Battley PF, Potter MA & Ma ZJ (In preparation)

## 7.1 Abstract

Long-distance migratory shorebirds often congregate in a small number of staging sites to refuel and likely have significant impacts on their prey, but such predation impact has often proved difficult to detect. We used exclosures to investigate the impact of shorebird predation on a bivalve species *Potamocorbula laevis* at a staging site in the north Yellow Sea during northward migration. We predicted that the number of *P. laevis* in plots that were accessible by shorebirds would show a greater decline than plots that excluded shorebirds. Fifteen and twelve pairs of experimental plots (open and closed) were set in 2011 and 2012, respectively, and core samples were taken once a month for 3 months that coincided with the early, middle and late shorebird migration periods. Our results indicated that shorebird predation had a significant impact on the number of *P. laevis* in one of the years in our study. In accordance to our prediction, the decline in numbers of P. *laevis* was significantly more rapid in open plots (accessible by shorebirds) than in closed plots (shorebirds excluded). The size classes taken heavily by shorebirds also showed greater declines in open than closed plots. The absence of *P. laevis* recruitment in 2012, coupled with significant shorebird predation impact could lead to a decline in food availability in the following year. Long-term monitoring effort is needed to ensure that we are informed about whether adequate food supplies remain for shorebirds during the northward migration staging period in this internationally important staging site.

# 7.2 Introduction

Shorebirds are ephemeral predators that congregate in large numbers on migration at staging sites where they refuel and prepare for the next flight (Warnock 2010). According to Warnock (2010), staging sites often have high quantities of high quality and predictable prey to support the energy requirements of shorebirds. The availability of prey at staging sites is therefore of critical importance for migratory shorebirds. Given their congregative nature and high energy demands, shorebirds have the potential to have significant impacts on their prey (Sewell 1996; Wilson 1991b). However, such impacts have not always been detectable (Hamer *et al.* 2006; Kalejta 1993; Lopes *et al.* 2000) although some have reported 49–90% mortality of prey (Lewis *et al.* 2007; Weber & Haig 1997) and changes in size structure in prey that were attributed to predation by waterbirds (Sanchez *et al.* 2006; Wilson 1991b). Most studies on predation impacts by shorebirds were conducted in Europe and North America, with very little done in East Asia (but see Melville *et al.* 1997), where the number of shorebirds and their coastal intertidal habitats have been declining

rapidly (Murray *et al.* 2014; Rogers *et al.* 2011; Wilson *et al.* 2011). A better understanding of the impact of predation by shorebirds on benthos at staging sites in the Yellow Sea in East Asia during northward migration is not only important for estimating the carrying capacity of those sites (Goss-Custard & West 1997) and understanding the function of shorebirds within the wetland ecosystem (Bauer & Hoye 2014), but also for providing insights into how prey availability may lead to competition and affect the migration timing and route choice among shorebird species (Schneider & Harrington 1981).

There are four common ways to investigate the impact of shorebird predation on benthos prey (Baird *et al.* 1985). The first two methods are direct measurements of the changes in the density of prey before and after the predation event, either within the same general area or by excluding birds from feeding in certain areas. The other two methods are indirect estimates based on the daily food requirements of birds, either through foraging observations or converting daily energy requirements to food requirements, after taking daily activity budgets, energetic costs of different activities and food assimilation efficiency into account (Baird *et al.* 1985). All of these methods have their shortcomings. Exclosures may alter the physical conditions (Hulberg & Oliver 1980) while foraging observations can be labour-intensive and intake rates at night are very difficult to estimate (Szekely & Bamberger 1992). Nevertheless, the use of exclosures is a powerful method by which to study interactions between species (Underwood 1981) and is the most frequently used method when attempting to directly detect impacts of predation on benthic prey (Stevens *et al.* 2006).

In this study, we investigated the impact of shorebird predation on a major bivalve prey species at the Dandong Yalu Jiang Estuary Wetland National Nature Reserve in the northern Yellow Sea, China. This is a site used intensively by shorebirds during northward migration from March to May (Chapter 2; Riegen *et al.* 2014), where the benthic biomass and shorebird diets are dominated by the bivalve *Potamocorbula laevis* (Chapters 3 & 10). Several factors make the reserve a likely site where predation impact by shorebirds can be detected (See Sewell 1996): sediments in the area are relatively stable, and there is intense feeding by shorebirds ( $\geq$  250,000 shorebirds in the general area, Riegen *et al.* 2014); shorebirds have high energy demands during the study period (Ma *et al.* 2013b); shorebird predation is largely focused on a single prey species (Chapter 4); and that prey species occur in high enough densities that differences may be detectable (Choi *et al.* 2014). In addition to using exclosures to directly test for an impact of bird predation we also undertook large-scale shellfish surveys to enable comparisons between the experimental and broader-scale prey abundances and size-structures. We measured both prey density and size to test for size-selective impacts of predation by shorebirds
(Chapter 4; Zwarts & Blomert 1992; Zwarts *et al.* 1996a) and interaction between age classes in the prey (Kent & Day 1983; Sewell 1996; Wilson 1991b). We predicted that patterns of change in numbers and size-structure of *P. laevis* would differ in plots with and without shorebird predation during the northward migration period.

## 7.3 Materials and methods

### 7.3.1 Study site

The Dandong Yalu Jiang Estuary Wetland National Nature Reserve (hereafter the 'reserve') is located at the Yalu River estuary, which borders North Korea to the east and China to the west (39°40'-39°58'N, 123°34'-124°07'E). The Yalu River has a low sediment load compared to other rivers in China (Zhang & Liu 2002) and the growth of the river delta has slowed down since the construction of reservoirs in the 1970s (Cheng 1988). This reserve is an estuarine wetland with a semidiurnal tidal rhythm of two high and two low tides per day. The reserve extends in an east-west direction along the coast for about 70 km and has a total area of 814.3 km<sup>2</sup>, within which about 360 km<sup>2</sup> is intertidal flat (Ministry of Environmental Protection The People's Republic of China 2013). Bare intertidal flats extend up to 5 km offshore along the reserve, and range from muddy to sandy sediments. The reserve is the most important region within the Yellow Sea for shorebirds during northward migration, supporting at least 250,000 shorebirds, or about 700 shorebirds per km<sup>2</sup> of intertidal area. These are mostly Bar-tailed Godwits *Limosa* lapponica, Great Knots Calidris tenuirostris, Dunlins C. alpina, Eurasian Curlews Numenius arguata, Far Eastern Curlews N. madagascariensis and Grey Plovers Pluvialis squatarola (Barter 2002; Riegen et al. 2014). Despite its importance to shorebirds, little is known about shorebird feeding ecology and the benthic fauna in the reserve (Barter & Riegen 2004; Melville 2010).

Like other coastal areas in China, the reserve is subject to significant human activities. Areas to the landward side of the seawall in the reserve are aquaculture ponds cultivating sea cucumbers, jellyfish, razor clams, shrimps and fishes. The bare intertidal flats on the seaward side of the seawall are leased to fishermen for rearing shellfish. In areas 3–4 km further off the seawall, there are extensive fishnets that run parallel to the seawall that are used for catching fishes, crabs and shrimps (Figure 7.1c). In the subtidal zone, there is another shellfish farming area. Little is known about the impact of these human activities to the local ecosystem and the shorebirds.

### 7.3.2 Study species

The bivalve *Potamocorbula laevis* (family Corbulidae) was the most popular food source for shorebirds in the study area during northward migration during our study (Chapters 4 & 5). They are commonly found in sandy sediments, especially in the river beds and besides channels (Sun 1988; Wei & Guan 1985b). While they are reported to burrow deeper with age (and hence size), 88% of the biomass of *P. laevis* in the study site were in the top 5 cm of sediment; most are therefore considered accessible to shorebirds (bill lengths of Bar-tailed Godwits range from 74–126 mm; Great Knots bills average 44 mm; Z. J. Ma unpublished data).

Studies in the 1980s indicated that *P. laevis* in Shandong, China, spawns once a year mainly between mid September and mid October (Wei & Guan 1985a). However, a more recent study in the reserve found that *P. laevis* spawns twice a year, during early May and the end of September (Liu & She 2003). Young *P. laevis* entering their first winter have shell lengths of about 2–3 mm (Wei & Guan 1985b). The main growing season for *P. laevis* is between late April and mid September, with a peak growth rate of 2–2.5 mm per month when the water is warm (Wei & Guan 1985b). During the northward migration period for shorebirds, therefore, spat from the previous breeding season should be ~ 5 mm in length; older cohorts average c. 11–22 mm (Wei & Guan 1985b).

*P. laevis* tend to show a clumped distribution on tidal flats (Chapter 3; Sato & Azuma 2002; Sun 1988; Yang *et al.* 2007) that may relate to salinity (Yang *et al.* 2007), sediment composition (Sun 1988; Wei & Guan 1985b), inundation period (Chapter 3; Sun 1988) and interspecific interactions (Sato & Azuma 2002). They are capable of reaching very high densities in the boreal spring and summer, e.g. 120,000 ind/m<sup>2</sup> in Shandong (Sun 1988), 15,896 ind/m<sup>2</sup> in Bohai Bay (Yang *et al.* 2013), 8,320 ind/m<sup>2</sup> in Isahaya Bay in Japan (Sato & Azuma 2002), 6,160 ind/m<sup>2</sup> in Fujian Xiamen subtidal zone (Zhou *et al.* 2008), 641 ind/m<sup>2</sup> in the Yellow River delta (Wang *et al.* 2010) and 605 ind/m<sup>2</sup> in our study area (highest density reached $\geq$ 19,290 ind/m<sup>2</sup>) (Chapter 3). Areas with high *P. laevis* density largely contain one- and two-year old individuals (Wei & Guan 1985b).

Before the early 1980s, *P. laevis* was commonly used as poultry feed and fertilizer (Wei 1984). However, due to its high density, high crude protein content and ease of digestion for penaeid shrimps, *P. laevis* was exploited for aquaculture shrimp, crab and fish feed since the early 1980s in Shandong and Fujian (east coast of China), leading to the disappearance of *P. laevis* in some regions (Wei 1984; Wei & Guan 1985a; Yang *et al.* 2007). Nonetheless, recent surveys in this reserve and Bohai Bay found that local fishermen continue to harvest *P. laevis* on the mudflat in summer (Yang *et al.* 2013). *P.* 

*laevis* forms the principle prey at the reserve for Great Knots, Far Eastern Oystercatchers *Haematopus ostralegus osculans* and Red Knots *C. canutus* and a major prey for Bar-tailed Godwits (Chapter 4).



**Figure 7.1** Maps showing the locations mentioned in this paper. (*a*) The Yellow Sea. (*b*) The Dandong Yalu Jiang Estuary Wetland National Nature Reserve in 2012 (within the area bounded by the dotted line). (*c*) The 36 sampling stations in the middle site (in the middle of each grid square), large circles and triangles denote experimental plots used in 2011 and 2012, respectively; black lines on the tidal flat denote fishnets, light polygons denote channel.

### Experimental setup

Fifteen and twelve pairs of 2.5 m x 2.5 m plots were set in 2011 and 2012, respectively, in the middle of the reserve where *P. laevis* was abundant (Figure 7.1c). Precautions were taken to minimise changes to the physical conditions by selecting areas with little human disturbance and visiting the experimental plots regularly to clear algae and debris. In each pair of plots, one was assigned as "closed" (treatment) and the other as "open". In the "closed" plots, a bamboo pole (30 cm above ground, 70 cm underground) was put at each corner of the 2.5 m x 2.5 m square and strands were tied between poles at about 4 cm and 15 cm height. Two additional strands were tied diagonally across and bright-coloured tapes were attached to the strands. The "open" plot was a corresponding control plot set

within 5 m of each closed plot, with one bamboo pole at each corner of the 2.5 m x 2.5 m square (Figure 7.2). In both closed and opened plots, samples were taken from the 1.5 m x 1.5 m area in the middle of the plot (Figure 7.3), leaving at least 0.5 m from the edge to minimise impacts from sedimentation and hydrodynamic alteration, trapped vegetation and edge effects (Kalejta 1993; Wilson 1991a). This 1.5 m x 1.5 m area was subdivided into nine squares (0.5 m x 0.5 m) and core samples were taken from three of these squares during each month, yielding three replicates per plot per month (Figure 7.3). Core samples were taken once a month for 3 months, coinciding with the early, mid and late shorebird migratory periods (March 17–23, April 17–25 and May 18–25 respectively) (Chapter 2; Riegen *et al.* 2014). These gave 90 core samples per month in 2011 (15 pairs x 2 treatments x 3 replicates) and 72 in 2012 ( $12 \times 2 \times 3$ ).



**Figure 7.2** Photo of the experimental plots, with open plots on the left and closed plots to the right.

Chapter 7. Predation impact



**Figure 7.3** The sampling design for closed and open plots. Samples were taken in the nine 0.5 m by 0.5 m squares in the centre of the plot. Three samples were taken from each square in the months indicated by the numbers (1=March, 2=April and 3=May). The upper right of the plot was always the pole nearest to the northeast direction.

Core samples were collected from the top 5 cm using a PVC tube (diameter 0.155 m, area 0.019 m<sup>2</sup>) and washed in the field through a 0.5-mm mesh sieve and counted. Because of the large numbers of *P. laevis* in samples, only a subsample was measured when more than 50 individuals were present per core. In 2011, the initial samples (March) revealed a strongly bimodal size-distribution, so thereafter subsamples of individuals were measured in cohorts<10 mm (representing first-year individuals; n=10 measured) and $\geq$ 10 mm (one-year and older; n=50 measured). In 2012 the smaller cohort was absent and lengths of up to 50 randomly-chosen individuals were measured to the sample square after measurement, except during the final sampling period, to minimise potential movements of bivalves from high density squares (un-sampled squares) to low density squares (sampled squares).

Grid samples were also collected in 36 sampling stations across the study area (Figure 7.1c). These stations were evenly distributed and 500 m apart from each other, providing a more general picture of the whole study area and could be used as a reference to the findings inside experimental plots. Single samples from grids were taken up to 30 cm deep and all *P. laevis* measured and counted. Sampling covered the same time periods as for the experimental plots. During the two years of study (2011 and 2012), the maximum number of Bar-tailed Godwits and Far Eastern Oystercatchers foraging within

the experimental grids were 4,800 and 1,288 respectively, while 19,000 Great Knots and 84 Red Knots were estimated at the roost near the grids (C.-Y. Choi unpublished data).

### 7.3.3 Statistical analysis

A mixed design general linear model with multilevel model approach was used to analyse how the three main factors (treatment, month, year) and their interactions affected the numbers of *P. laevis*. This multilevel model is a regression or linear model that differs from the mixed ANOVA by taking dependency in the data into account. The former handles dependent data by modelling the dependency, which allows us to look at the analysis as a linear model, despite violating one of the assumptions of regression (non-independent residuals) (Field *et al.* 2012). Sampling year was treated as a between-group independent variable while the treatment and month were the repeated-measures independent variables. Contrast was set for month between March and April, and between March and May. This was not necessary for treatment and year because both of these variables only have two levels. The test was conducted using "lme" function in the *nlme* package (Pinheiro *et al.* 2013), performed with R v3.0.1 (R Core Team 2013). A significance level of ( $\alpha$ ) 0.05 was used for all statistical tests, with means given±SD unless stated otherwise. Effect size was calculated using Pearson's correlation coefficient *r*, with 0.1, 0.3 and 0.5 denoting small, medium and large effects respectively (Cohen 1992).

### 7.4 Results

### 7.4.1 Predation impact

The main effects of treatment, month and year could not be interpreted alone due to significant interaction effects. All three possible 2-way interactions between three factors were significant while the 3-way interaction was not significant ( $\chi^2(2)=2.519$ , p=0.284). The patterns of change in numbers of *P. laevis* differed between 2011 and 2012 (interaction for month and year,  $\chi^2(2)=8.236$ , p=0.016). The numbers of *P. laevis* between March and April decreased in 2012 but increased slightly in 2011 (b=-57.190, t(48)=-2.732, p=0.009, *effect size* r=0.367). The numbers between March and May declined in both years but more rapidly in 2012 than in 2011 (b=-49.012, t(48)=-2.34, p=0.0234, *effect size* r=0.320, Figure 7.4). There was an effect of the bird exclusions, but not across both years (interaction of treatment and year,  $\chi^2(1)=4.556$ , p=0.033). In 2011, the open and

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closed plots showed similar changes, whereas in 2012 the decline in numbers from March to May was substantially greater in the plots open to birds (b=-17.238, t(74)=-2.24, p=0.0281, *effect size r*=0.252, Figure 7.4). The magnitudes of decline in the number of *P. laevis* from March to May between closed and open plots were 27% and 38% respectively in 2011, and 51% and 78% respectively in 2012. In other words, shorebird predation accounted for at least 11–27% of the decline in *P. laevis*.



**Figure 7.4** Changes in numbers of *Potamocorbula laevis* from March to May in 2011 and 2012 in open (dotted lines) and closed plots (solid lines). Points represent mean and error bars show 95% pointwise confidence intervals of 45 and 36 cores in 2011 and 2012, respectively.

### 7.4.2 Size distribution

Two cohorts of *P. laevis* were present in 2011, with small individuals increasing numerically from March to May in the large-scale grid survey (Figure 7.5). In the experimental plots, the smaller cohort was also present but was less frequent than the larger cohort. A shift in the size-structure of the larger cohort in both experimental plots and the grid survey suggests growth of about 2 mm per month. In 2012 the small cohort was absent and there was no evidence of growth from March to April, especially for *P. laevis* $\geq$ 17 mm. A shift in size-structure in the closed plots from April to May suggests

growth of about 3 mm. In the open plots and grid survey, numbers of virtually all size classes reduced substantially from March to May; in the closed plots the reductions were less extreme.



**Figure 7.5** Frequency distribution of *Potamocorbula laevis* in the grids (36 core samples per month), open and closed plots during 2011 (45 per month in open plots and another 45 in closed plots) and 2012 (36 per month in open and another 36 in closed). The frequencies shown in the grid figures were a direct reflection of what was measured in the field. In both opened and closed plots, the length of up to 60 (10 young and 50 adults) *P. laevis* were measured per sample. The frequency distribution was estimated differently in these cohorts by first pooling the length measurement data from different samples together, separated by month and treatment. Then the proportion of each size class was calculated separately in young (<10 mm) and adults ( $\geq$ 10 mm). These proportions were then multiplied by the total number of young and adults counted to give the frequency distribution per sample in 2011. In the absence of young *P. laevis* in 2012, the same method was used without dividing the calculation into two groups.

# 7.5 Discussion

*Potamocorbula laevis* was the dominant prey species for the most numerous shorebirds in our study area in the reserve in 2011 and 2012, and the data from the exclosures indicate that bird predation had a demonstrable impact on numbers of *P. laevis* in one of the two years in our study (2012). The decline in numbers of *P. laevis* was significantly more rapid in plots that were accessible by shorebirds than plots that were not, and the size classes preferred by shorebirds showed marked declines in the general area.

The two years differed in a number of ways. There was widespread spatfall in 2011 and none in 2012. Predation by Bar-tailed Godwits and Great Knots in 2011 was focused on *P. laevis* of 5–10 mm length, which had more favourable flesh to shell mass ratios than larger individuals (Chapter 4). In 2012, in the absence of small *P. laevis*, godwits and knots took individuals 12–17.5 mm long. More than 1,300 Far Eastern Oystercatchers were also foraging in 2012 but not in 2011. They fed largely on sizes larger than 17 mm, which was right at the cut-off point at which growth was not detected between months (in grids and open plots), implying a high predation rate on those sizes (Figure 7.5). The predation pressure on large shellfish was presumably greater in 2012 than in 2011 when an abundance of small individuals (which were evidently settling on the tidal flats through the migration period) formed the main target of the two most numerous avian predators.

However, the locations of the experimental plots were also different in the two years of study (Figure 7.1c). They were set up in 2011 before the main arrival of shorebirds, low on the tidal flats and fairly close to tidal channels. It turned out that these areas were little-used by shorebirds, and the high tidal flows may have inhibited the settlement of young shellfish. The presence of high adult densities may also have inhibited young *P. laevis* from settling, which has been shown to occur in bivalves, polychaetes and amphipods (Kent & Day 1983; Peterson 1982; Wilson 1989). Consequently, the size distribution of shellfish in 2011 differed between the grid survey and the experimental plots, with far fewer spat present in the experimental plots. In effect, we had a set-up in which neither experimental plot type was subject to substantial bird predation pressure in 2011; it is not surprising then that there was no difference in the patterns of change between the two plot types. In 2012, the plots were established at slightly higher elevation tidal flats that did have substantial shorebird feeding activity. Under those conditions, of high bird use and a lack of spatfall, an impact of bird predation was clearly detectable. But it is therefore not clear whether it is the absence of spat, or the increase in predation pressure, that resulted in the significant impact of bird predation we found in 2012. Additionally, the quality of *P. laevis* as prey was lower in 2012 (lower flesh to shell mass

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ratios). This could cause birds to increase their intake rates to compensate (and hence increasing the predation pressure), though intake rate measurements in both years suggest that the instantaneous intake rate did not increase in 2012, possibly due to digestive constraints, increase in handling time and searching time (Chapter 6).

Numbers of larger *P. laevis* decreased over time in both years in both open and closed plots. The exclosures were designed to exclude birds but not other predators and it is possible that other taxa such as fishes, shrimps, gastropods or crabs were responsible for some of the declines in *P. laevis*. However, the numbers of gastropods and crabs found in the study area were negligible compared to those of *P. laevis*, and the local fish population is probably lowered by the intensive catching effort along the intertidal flat (Figure 7.1c) (Chapter 3). Fishes, shrimps and crabs may also feed on bivalves through 'siphon nibbling', which is not fatal for the shellfish (Ens et al. 2004). It may be that P. *laevis* is highly mobile, even as older individuals, and declines in closed plots result from movement from high-density plots into surrounding areas that were subject to intense bird predation and therefore had lowered densities. Both inter- and intra-specific competition have been reported to lead to emigration (Lee 1996; Peterson 1982). Given the high densities *P. laevis* reached in our experimental plots (highest density reached  $\geq$  19,290 m<sup>-2</sup> in 2011 and  $\geq$  14,250 in 2012), such density-dependent compensation is possible, and would result in an underestimate of the true impact of predation on the populations of *P. laevis*. This could be the reason for the consistent decline in open and closed plots between April and May in 2011, when shorebird predation was unlikely to have taken place within either type of plot. Natural mortality of *P. laevis* may also have been occurring over the study period.

The 11–27% decline of *P. laevis* due to shorebird predation in this study was considerably lower than those reported in exclosure studies that investigated how amphipods, chironomid larvae, oligochaetes and polychaete worms were affected by shorebird predation (43–62%) (Bengtson *et al.* 1976; Goss-Custard 1977; Szekely & Bamberger 1992; Weber & Haig 1997). This might reflect the high *P. laevis* availability in the study area (Chapters 4 & 10) and the payoff from defensive investment by bivalve through imposing additional digestive constraints on predators (Chapter 6). The latter was reinforced by the apparent lack of growth in the larger *P. laevis* cohort in 2012 in open plots and grids, where oystercatchers prey heavily on these larger size classes by taking flesh out without taking the shell (Chapter 4). Despite there being 20-fold fewer oystercatchers than Bar-tailed Godwits and Great Knots combined, the predation impact by oystercatchers was more noticeable than godwits and Great Knots (Figure 7.5). In line with this, the numerical intake rate of bivalve prey in oystercatchers (4.41±2.74 per min)

was almost three times higher than that achieved by godwits (1.81±2.13) or knots (1.61±1.09). Such a difference means the total number of *P. laevis* taken by oystercatchers was only 7-fold fewer than godwits and knots combined.

To conclude, this study confirmed that the impact of bird predation on intertidal benthos can be highly variable (Wilson 1991a). Multi-year studies can increase the likelihood of detecting significant predation impacts, due to the high variability in benthos recruitment (presence of spat in 2011 but absence in 2012), different predatory responses (oystercatchers fed extensively in 2012 within the grids in 2012 but outside in 2011), and emigration of studied species (general decline in the number of *P. laevis* in both open and closed plots in both years). The absence of *P. laevis* recruitment, combined with significant shorebird predation in 2012 would mean a decline in food availability afterwards. Therefore, it is of critical importance to continue to monitor the shorebird population and benthos abundances to see how shorebirds respond to the change in food availability, and to investigate factors that affect the recruitment success of *P. laevis*.

# 8.1 Key findings

In this thesis, my aim was to study the stopover ecology of Bar-tailed Godwits *Limosa lapponica* and Great Knots *Calidris tenuirostris*, to describe the type, amount and characteristics of their benthos resources, to investigate their diets, foraging patterns and mechanisms of coexistence and finally, their predation impact on their prey, at the Yalu Jiang coastal wetland.

In *Chapter 2*, repeated counts of the two shorebird species were incorporated with Thompson's modelling approach to provide estimates of the total number of birds transiting and their passage times. Bar-tailed Godwits were further divided into two groups based on the photographs taken in the field that revealed how proportions of different subspecies change through time. We estimated an annual average of over 68,000 Bar-tailed Godwits and 44,000 Great Knots used the area on northward migration from 2010–2012. These were equivalent to at least 42% of the East Asian-Australasian Flyway's northward migrating *L. l. baueri* godwits, 19% of *L. l. menzbieri* godwits, and 22% of the Great Knots, thereby confirming that the study area remains the most important northward migration staging site for Bar-tailed Godwits and indicating that it has become the most important for Great Knots along the flyway.

Results from *Chapter 3* indicated that polychaetes and bivalves dominated the benthic communities, with the former dominating upper tidal flats and the latter, *Potamocorbula laevis* in particular, dominating intermediate and lower tidal flats. Two

sites approximately 10 km apart showed substantial differences in benthic species abundance and distribution, indicating high spatial variability, which was correlated with both exposure time during the tidal cycle and sediment particle size. Benthic communities showed substantial annual and within season variation. Two of the frequent prey for migratory birds, namely ghost shrimps *Nihonotrypaea japonica* and young *P. laevis*, were relatively common in 2010 and 2011, respectively, but not in 2012.

In *Chapter 4*, the dietary composition of four shorebird species in our study area and the mechanism for their coexistence were investigated. Great Knots, Red Knots *C. canutus* and Far Eastern Oystercatchers *Haematopus ostralegus osculans* selected mainly the bivalve *P. laevis* while Bar-tailed Godwits had a broader diet and selected polychaetes, even though most of their intake was of *P. laevis* (Figure 8.1). Although all of these shorebirds fed on the same prey, they showed different size preferences and used different feeding methods. Godwits, Great Knots and Red Knots mainly swallowed *P. laevis* whole and they preferred medium-sized *P. laevis* with relatively high flesh content: shell mass ratio. Oystercatchers wedged open *P. laevis* and only ingested the flesh, without paying the price for breaking down hard shells and preferred large *P. laevis*. Despite evidence for niche differentiation in prey selection, the majority of intake for godwits and Great Knots, the two most numerically abundant migrant species, overlapped. Their coexistence seems to be enabled by high resource availability rather than niche separation.



Figure 8.1 A Bar-tailed Godwit feeding on *Potamocorbula laevis* (Photo by Phil Battley).

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After determining the diet of Bar-tailed Godwits and Great Knots, the macrobenthic biomass in the study area was quantified (*Appendix 1*). The average macrobenthic biomass (15.4 g AFDM m<sup>-2</sup>) is within the range of other intertidal flats worldwide. The macrobenthic biomass composition in the study area was dominated by the bivalve species *P. laevis*, which comprised more than three quarters of total macrobenthic biomass during the study period (11.8 g AFDM m<sup>-2</sup>). There was also evidence for large spatial variation in benthos biomass between sites a mere 10 km apart.

In *Chapter 5*, results from behaviour scans and focal bird observations indicated that the variation in the foraging patterns of Bar-tailed Godwits and Great Knots were explained mainly by abiotic factors such as tidal range, time relative to low tide and distance to seawall, rather than by prey availability. Additionally, the performance of similar explanatory models on intake rates of Great Knots was substantially poorer than in Bar-tailed Godwits, and there was always a high proportion of non-foraging knots throughout the low tide period. These differences in foraging patterns and modelling results between the two species could partly be explained by their different dietary selections and, therefore, distribution of selected prey. The results also hinted that food availability in the study area was higher than the birds could process, which was supported by the generally higher intake rate and prey availability in the studied area when compared to those in wintering grounds. In other words, the study area provided Bar-tailed Godwits and Great Knots with ample food resources during our study and it is important to take tide-related abiotic factors into account when studying the foraging ecology of shorebirds.

Results from *Chapters 3 and Appendix 1* indicated that the numerical and biomass intake rates of both Bar-tailed Godwits and Great Knots declined substantially in 2012, compared to 2011, despite similar numerical and biomass density of their most important bivalve prey *P. laevis. Chapter 6* investigated potential explanations for the observed differences. We found clear behavioural evidence that a digestive bottleneck existed in the bivalve-feeding shorebirds. It is probably the first study that quantifies the impact of a bottleneck on shorebirds in field activity terms. Such a digestive constraint on hard-shelled prey, decreased prey quality (amount of energy per dry mass of shell taken), and increased handling and searching time were potential reasons behind the decline in total biomass intake rate in the two shorebird species in 2012.

In *Chapter 7*, the impact of shorebird predation on the bivalve *P. laevis* was investigated using exclosure plots. Shorebird predation had a significant impact on the number of *P. laevis* in one of the years. The decline in number of *P. laevis* was significantly more rapid in open plots (accessible by shorebirds) than closed plots (shorebirds

excluded). The size classes taken heavily by shorebirds also showed greater decline in open and closed plots. The significant predation impact and lack of *P. laevis* recruitment would mean a decline in food availability afterwards.

In short, the Yalu Jiang coastal wetland is the most important northward migration staging site for Bar-tailed Godwits and Great Knots along the EAAF. Their staging numbers exceeded 100,000 and they staged for 34-40 days on average between 2010 and 2012. The benthic community in the study area displayed high spatial and temporal variation and was dominated by one bivalve species (*P. laevis*). Given the contrasting body size, bill length and published knowledge on diets of Bar-tailed Godwits and Great Knots, they seem to be two species that could co-exist through niche differentiation (Figure 8.2). It was, therefore, surprising to find the strong overlap in their main prey type (P. laevis) and sizes taken, which implies intense competition during staging. They showed different foraging patterns which might reflect the digestive constraints imposed on the smaller-sized Great Knots. There was evidence that Bar-tailed Godwits and Great Knots paid the price of taking hard-shelled prey by having more frequent foraging pauses; Far Eastern Oystercatchers avoid this by taking only flesh out of the bivalve (Figure 8.3). Such a difference in cost and benefits between these shorebird species when taking *P. laevis* was possibly one of the reasons that led to the different *P. laevis* size preference among them. The shorebird community in the study area as a whole imposed significant predation impact on *P. laevis* during their stopover in one of the two years tested. Long term monitoring effort is needed to see how the changes in the availability of their main bivalve prey affect the diet and distribution of shorebirds.



**Figure 8.2** Coexistence of multiple shorebird species at Yalu Jiang coastal wetlands: Bar-tailed Godwits, Dunlins *C. alpina*, Great Knots and Red Knots feeding alongside with each other (Photo by Chi-Yeung Choi).



**Figure 8.3** A mixed flock of Far Eastern Oystercatchers and Dunlins foraging in area with high density of *Potamocorbula laevis* (Photo by Chi-Yeung Choi).

# 8.2 Stopover ecology at Yalu Jiang coastal wetland

Variability is omnipresent in nature and shorebirds have been shown to be flexible in their diet (Skagen & Oman 1996; van Gils et al. 2005b; Zwarts & Wanink 1993) and internal organs (Dekinga et al. 2001; Piersma et al. 1993c; van Gils et al. 2003). The findings of this thesis should not be over-generalised until more data becomes available. Nonetheless, it is revealing to see some interesting contrasts such as the reliance on one single bivalve prey in the Bar-tailed Godwits in my study, which is unexpected given their generalist feeding habits in Europe where they take mostly polychaetes (Duijns et al. 2013; Scheiffarth 2001). Given the generally higher annual biomass variation in bivalves than polychaetes (Beukema et al. 1993), these raise the question of what benefits may Red Knots and Great Knots have in being bivalve-specialists, which would put them at greater risk of starvation during bivalve-poor years, when godwits are less-impacted due to their broader diet (Chapters 4 & 5). Alternatively, one may also ask what price godwits pay by taking so many bivalve prey. During the course of my study, "bloody" droppings (Figure 8.4) from godwits were encountered from time to time. It remains to be determined whether these represent blood from damaged digestive organs in a generalist feeder that was not specialised in breaking down hard-shelled prey, or incomplete digestion of worms.

Chapter 8. Synthesis



**Figure 8.4** Droppings with reddish appearance in Bar-tailed Godwit (top) and unknown shorebird species (bottom) (Photos by Chi-Yeung Choi).

The intensive focal bird observation, behaviour scan and benthos sampling work in my study were carried out in the middle site of the reserve, where a large number of shorebirds chose to forage. However, the eastern site (Figure 1.2c) also holds a significant number of shorebirds, especially during the early migratory season and at high tide. I demonstrated that very different benthos communities exist at the middle and eastern sites (Chapter 3) but the diets of shorebirds in the eastern site have not been quantified yet. It would be revealing to document how shorebirds change their diet and foraging range through the season in relation to differences in prey availability. More specifically, do shorebirds forage in the eastern site more when they first arrive, due to the availability of more digestible prey and a poor knowledge of other areas, then slowly spread towards the middle site for more profitable prey as they rebuild their digestive apparatus and gain a better understanding of the general area? Despite the general westward movement in the foraging range through time, the birds still preferred to roost in the eastern site after foraging in the middle site. It would be interesting to investigate the relative importance of safe roost, prey availability and competition level in determining the home range of staging shorebirds at Yalu Jiang coastal wetland.

This study hinted that food density can alter flocking behaviour of the shorebirds. Bar-tailed Godwits in Europe fed mostly on polychaetes (Scheiffarth 2001) and were regarded as solitary (Folmer *et al.* 2010). However, the Bar-tailed Godwits that fed on *P. laevis* in this study behaved like the gregarious Great Knots and Red Knots (Figure 8.2). This could be driven by high prey density (Goss- Custard 1984) with a lower price of flocking (Colwell 2010) as the sessile nature of *P. laevis* means the prey do not elicit evasive responses, which would otherwise occur in more mobile prey such as lugworms *Arenicola marina* (Duijns & Piersma 2014). In other words, the tendency to flock in the same species might vary according to prey density, nature of prey and perhaps handling time, which deserve further study.

# 8.3 Functions of stopping sites

My study confirmed that the Yalu Jiang coastal wetland is the most important northward migration staging site for Bar-tailed Godwits along the EAAF, and showed that the area has become the most important for Great Knots (Chapter 2). Other studies further showed that this area is also the most important to Eurasian Curlews *Numenius arquata*, Far Eastern Curlews *N. madagascariensis* and Far Eastern Oystercatchers during their northward migrations (Barter & Riegen 2004; Melville *et al.* 2014; Moores 2012). The estimate of more than 250,000 shorebirds using the area during northward migration is equivalent to more than 700 individuals km<sup>-2</sup>, a density that is higher than many of the important shorebird sites reported along the East Atlantic flyway, except Banc d' Arguin in Mauritania (4,160 individuals km<sup>-2</sup>) and west Iceland (833 individuals km<sup>-2</sup>) (Barter & Riegen 2004; Riegen *et al.* 2014). Nonetheless, such comparisons may not be valid because different studies were conducted in different times and scales (Rehfisch 1994), and overemphasis on very high maximum shorebird densities may overlook other important aspects such as the function of wetland to shorebirds and the duration or intensity of usage by shorebirds.

The stopover duration estimates generated from Thompson's modelling approach based on 3 years of count data (Chapter 2) indicated that Bar-tailed Godwits and Great Knots staged for more than a month on average, which was consistent with satellite and radio-tracking results (Battley *et al.* 2012; Ma *et al.* 2013b). This also indicated that the staging role of the study area was fairly consistent between years. Concurrent studies on refuelling rate based on the analysis of body mass and plasma metabolites of Great Knots, Red Knots and Red-necked Stints *C. ruficollis* indicated that these species deposited fuel more rapidly in Yalu Jiang coastal wetland and Bohai Bay, than in Chongming Dongtan (Hua 2014). Taking prey availability and quality into account (Chapters 3, 4 & 10; Yang *et al.* 2013), this reinforces the staging role that Yalu Jiang coastal wetland plays for shorebirds during northward migration.

Nevertheless, given the diverse migration strategies employed by different shorebird species, it is likely that the same stopping site may serve different purposes depending on the shorebird species, their age, and season. For example, despite the lesser importance of Chongming Dongtan to shorebirds during northward migration, first-year calidrid sandpipers used the site to refuel during southward migration (Choi *et al.* 2009). On the other hand, in addition to the refuelling role that it served during northward migration, at least 13 shorebird species used Yalu Jiang coastal wetland when moulting primary feathers while on southward migration (Q. Q. Bai pers. comm.). Therefore, more field observations or even banding work will help reveal the roles of different stopping sites for different shorebird species, age-classes and in different seasons. This will allow better decisions to be made when prioritising conservation efforts.

Given the similar refuelling role that Yalu Jiang coastal wetland and Bohai Bay play during northward migration (Hua 2014), the dominance of shorebird species such as Red Knots and Curlew Sandpipers *C. ferruginea* in Bohai Bay but not Yalu Jiang coastal wetland (Hassell *et al.* 2013; Riegen *et al.* 2014) might well be explained by their preferences for a small bivalve diet as small *P. laevis* (1-6 mm) occur in high density in Bohai Bay (Thomas & Dartnall 1971; Yang *et al.* 2013).

### 8.4 Selection of stopping sites

In this study, there was evidence for niche differentiation in terms of the size of *Potamocorbula laevis* preferred by different shorebirds and such differences were related to feeding method. Shorebirds that only take the flesh out of *P. laevis* prefer the larger size classes (>15 mm) that have more flesh per prey item while shorebirds that swallow *P.* 

*laevis* whole prefer smaller size classes (<15 mm) that have higher prey quality (higher energy per dry mass of shell ratio) (Chapter 4). Despite the different preferences, shorebirds were taking the same cohort of *P. laevis* and at least 18 avian species were seen feeding on *P. laevis* in the study area. Taking into account that the two most abundant shorebird species in the study area, Bar-tailed Godwits and Great Knots, preferred the same size range of *P. laevis*, there must be intense competition between shorebird species. Therefore, the coexistence of these shorebirds was enhanced by ample food resources rather than niche differentiation, at least in 2011 and 2012.

Further evidence for ample food supplies included an early peak in functional responses by Bar-tailed Godwits and Great Knots when the density of *P. laevis* was still low (Chapter 5). Digestive pauses in Great Knots and Red Knots, which suggest a higher ingestion rate than process rate, if one assumes that birds would adjust their feeding apparatus depends on prey availability and quality, digestive pauses may indicate that their highest processing capacity had been reached (Chapter 6). Moreover, benthos biomass in the study area was comparable to other productive tidal flats used by shorebirds around the world (Appendix 1).

Despite evidence for the ample food resources, significant predation impact on *P. laevis* by shorebirds was detected in 2012 when little *P. laevis* recruitment occurred, which raises the issue of carrying capacity. Perhaps 2011 and 2012 were 'good' years for shorebirds staging at Yalu Jiang coastal wetland, in terms of food supplies and this led to the observed overlapping in dietary intake between godwits and Great Knots.

The observed dietary overlapping was surprising because niche differentiation has been quite widely accepted as the mechanism that allows coexistence of shorebirds in the same site (Baker & Baker 1973; Jing *et al.* 2007). Nonetheless, Bar-tailed Godwits may switch to other prey sources in years when *P. laevis* are no longer profitable and this may be the time when niche differentiation could enable coexistence. Following down this line and assuming that the highest degree of dietary overlap occurs between coexisting species when food is most abundant (shorebirds in both Baker & Baker 1973; MacLean 1969), and the least dietary overlap occurs when food abundance is low (five titmouse species, Hartley 1953), then the results of dietary study again reflect the high food availability in Yalu Jiang coastal wetlands to shorebirds during our study period. Further studies in their Australian wintering grounds where both species co-exist would provide insight into whether the degree of dietary overlap found at Yalu Jiang is greater than at other times of the year.

It is possible that larger-scale distributions of shorebird species or populations around the Yellow Sea reflect a lack of dietary differentiation between co-existing species

and an avoidance of competition among closely related species. Along the EAAF, there are at least three pairs of shorebird populations that are very similar in their body size, bill shape and diets. The first is the *baueri* and *menzbieri* godwits. These two Bar-tailed Godwit subspecies have different breeding and winter ranges, but they both converge on the Yellow Sea during northward migration (Battley et al. 2012). However, baueri godwits used the eastern part of Yellow Sea more, from Yalu Jiang coastal wetland to the Korean peninsula while menzbieri godwits used the south and west of Yellow Sea more (Battley et al. 2012; Wilson et al. 2007). The distributions around the Yellow Sea could simply reflect birds selecting habitats on the "appropriate" side from which to embark on their next migratory flight (Battley et al. 2012). Alternatively, the earlier arrival of baueri than menzbieri (Battley et al. 2012; Chapter 2) could enable baueri to settle in large numbers at the best site around the Yellow Sea (Yalu Jiang coastal wetland), causing menzbieri to largely select other sites. The second pair is the Great Knot and Red Knot. These two species overlap to some extent in their breeding and wintering distributions and they both feed heavily on bivalve prey during the non-breeding season (Chapter 4; Yang et al. 2013). Like the two godwit subspecies, the distributions of Great Knots and Red Knots in the Yellow Sea are slightly different, with the former more heavily distributed towards Yalu Jiang coastal wetland and the Korean peninsula, while Red Knots favoured the Bohai Bay in the west of the Yellow Sea (Bamford *et al.* 2008; Hassell *et al.* 2013; Rogers *et al.* 2010; Yang et al. 2008). It is worth noting that 1,499 Red Knots were counted in Yalu Jiang coastal wetland in 1999, but the number had dropped to fewer than 100 by 2012 (Barter et al. 2000; C.-Y. Choi unpublished data), showing their failure to establish in Yalu Jiang coastal wetland and perhaps, ample food supply in Yalu Jiang coastal wetland does not occur every year. The last pair/group is the Dunlin, Curlew Sandpiper and Broad-billed Sandpiper Limicola falcinellus, which have very similar body size, bill shape and length. Their breeding ranges overlap to some extent but their wintering distribution is quite different, with Curlew Sandpipers wintering mostly in Australia, Broad-billed Sandpipers in both Australia and southeast Asia, and Dunlins along the east coast of China, and seldom migrating further south than the equator. Like the previous pairs, the staging distribution of Dunlins, Broad-billed Sandpipers and Curlew Sandpipers are quite different during northward migration, with Dunlins mostly distributed at Yalu Jiang coastal wetlands and the Korean peninsula, while Broad-billed Sandpipers and Curlew Sandpipers favour Bohai Bay (Bamford et al. 2008; Hassell et al. 2013; Yang et al. 2008).

In short, overlap in diets between different sized and morphologically structured species may suggest coexistence was enhanced by ample food supply while little overlap may imply coexistence through niche differentiation. It has been claimed that the latter can never be proved or tested satisfactorily (Newton 2008), but studies in food-poor years at Yalu Jiang coastal wetlands may shed light on how niche differentiation may enhance coexistence. On the other hand, insights on the importance of niche differentiation and how it may relieve competition could be found in the selection and use of staging sites by ecologically similar, i.e. competition-prone, species. The distributions of staging shorebird populations during northward migration in the Yellow Sea are very good subjects to study because of the limited refuelling time and concentration of birds from across the flyway into a relatively restricted area during migration. Information on benthos resource availability, quality and diet of shorebirds in less-studied sites in the Yellow Sea will help to understand the decisions and driving forces behind site preferences of different species.



**Figure 8.5** The similar size and shape of the bill in the Broad-billed Sandpiper (top left), Dunlin (top right) and Curlew Sandpiper (bottom) (Photos by Chi-Yeung Choi).

## 8.5 Transit number estimates

Studies thus far showed that the Thompson's modelling approach could provide robust estimates for the number of birds transiting as well as their passage dates in Bohai Bay (Rogers *et al.* 2011) and Yalu Jiang coastal wetland (Chapter 2). Unlike other methods, this approach does not require estimation for length of stay or residence probability that

would require extensive fieldwork in addition to repeated counts, making this potentially a very attractive approach for monitoring migratory birds. The next important step would be testing this approach on stopover sites where more rapid turnover occurs (e.g. Chongming Dongtan) and if it performs well, then this could be promoted to a wider community by making a user-friendly program to allow more count data to be modelled. Such a development is particularly important along the EAAF where count data are accumulating at a more rapid rate than trained researchers can analyse them (China Coastal Waterbird Census Group 2009, 2011). The passage date estimates generated from this approach also broaden the scope of simple counts to investigate age or sex-related migration phenology, as well as correlating passage dates to climate change.

# 8.6 Carrying capacity

One of the key questions in stopover ecology is whether stopping site limits the population size of shorebirds. This is a simple question, but extremely difficult to answer (Zwarts 1996). My results from the predation impact experiments indicated that there is no easy answer. The impact of shorebird predation on Potamocorbula laevis may vary with benthos recruitment success and the behaviour of predators (Chapter 7). It remains unclear whether the significant impact on prey was sufficient to reduce the population size of Bar-tailed Godwits and Great Knots below what they would otherwise achieve. There was no clear sign of prey-switching in Bar-tailed Godwits in 2012, suggesting that despite having an impact on *P. laevis*, the supply of *P. laevis* was probably still sufficient to make it more profitable than other prey types. However, the predation impact in 2012 may be long-lasting, as the trend of *P. laevis* seemed to be on the brink of a massive crash with very few young recruited in 2012. Diets of each shorebird species are unlikely to be restricted to one simple prey type over a period of years; they have to take other prey types in the long run due to high annual variation in their food supply (Zwarts 1996). Therefore, long-term monitoring is needed to understand the trend of *P. laevis* and how shorebirds respond to the change of their most favourable prey, and most importantly, whether the harvestable food supply is always large enough.

Measurements of social dominance, intraspecific kleptoparasitism and interference during feeding are three other important factors that need to be taken into consideration when determining the carrying capacity (Zwarts 1996). Alternatively, along the EAAF, given the large number of individually marked birds and long-term monitoring efforts on wintering grounds (Minton *et al.* 2010), the carrying capacity of a staging site might be determined by comparing the annual juvenile ratio and adult survival rate, after

taking wintering and breeding conditions into account. Analysis of the massive resighting records of individually marked shorebirds in Bohai Bay, Yalu Jiang coastal wetland and other stopping sites would yield interesting outcomes on how 'good' these staging sites are for their users.

Moreover, the fate of shorebirds also depends on their ability to adjust their migratory routes. High site fidelity has been reported but it is unclear if that reflects the inability to switch between sites or the lack of good alternative sites. Evidence thus far seems to favour the latter proposition because shorebirds were found to move inland in Australia and America to colonise suitable sites when opportunities arise in the more dynamic wetland landscapes inland (Kingsford et al. 1999; Warnock et al. 1995). There was also evidence for a shift in migration route of Ruffs *Philomachus pugnax* when their habitats deteriorated in Europe (Verkuil et al. 2012). Nonetheless, shorebirds along the EAAF would probably have more difficulties in changing their routes than shorebirds in other flyways, due to the transoceanic flight and few suitable habitats en route. The loss of an important staging site in the south of Yellow Sea, for example, would test the physiological limit of long-distance migrants by forcing them to fly further without refuelling. Such physiological limits are likely more genetically determined and unlikely to be overcome through behaviour changes. In the end, the ability to shift would be important only if alternative sites are suitable, in terms of prey quality, availability, and competition and predation pressure. Analysis of individually-marked resighting data may shed light on how flexible shorebirds are in switching sites but ground work on resource availability and quality are also crucial.

More long-term data are needed before one can say whether the carrying capacity for shorebirds have been reached at Yalu Jiang coastal wetland. My study seems to suggest that this study site may support more shorebirds than the numbers present during the 3 years of study. However, given the high annual variation in benthos communities, it is perhaps the poor years that ultimately constrain the shorebird populations. Yalu Jiang coastal wetland has been relatively well preserved comparing to other tidal flats in the Yellow Sea, partly because of the effort from the reserve and overseas collaboration, and partly because of its remoteness. However, a lack of large scale reclamation does not necessarily mean the tidal flat is safe, because changes in tidal flat area or condition could still occur. An unconfirmed source suggested that some crabs in Yalu Jiang coastal wetlands failed to reproduce due to the change of sedimentation processes after a new reclamation outside the reserve that may have blocked the transport of sediments from the river to the tidal flat (Han 2002). Finally, information collected such as the prey energy content, their availability during a tidal cycle and the diet

of shorebirds, could potentially be used to parameterise or test the modelling approach that predicts non-breeding shorebird population size or the demographic rates, using an individual-based ecology approach (West *et al.* 2011). Such a modelling approach for non-breeding coastal birds has only been tested using waterbird data within Europe (Stillman & Goss-Custard 2010). This could potentially become a very useful tool for managing the vulnerable wetlands along the EAAF by quantitatively predicting the effect of environmental change on the population size of waterbirds.

# 8.7 Conservation of staging sites along the EAAF

There has been an increasing number of studies showing the potential link between the declining number of shorebirds and the loss of staging habitats along the EAAF and the conservation of staging sites is still of critical importance to safeguard the future of shorebirds along the EAAF (Amano *et al.* 2010; Moores *et al.* 2008; Murray *et al.* 2014; Rogers *et al.* 2011; Wilson *et al.* 2011). Urgent effort is needed to ensure the remaining important staging sites are protected, especially from intertidal flat reclamation.

Unfortunately, the use of shorebirds themselves to promote their conservation has not been very successful (e.g. Saemangeum in South Korea). The aesthetic values and interesting biological insights in the physiological and sensory mechanisms that sustain their journey (Piersma & Baker 2000) were more appreciated by researchers than policy makers, and probably more by the rich than the poor. It is true that shorebirds could be used as an indicator for the health of wetlands and as 'integrative sentinels' of global environmental change (Li et al. 2009b; Piersma & Lindstrom 2004; Sutherland et al. 2012), but there seems to be a lack of understanding on the role of migratory shorebirds in the ecosystem compared to other migrants (Bauer & Hoye 2014). Such information is important to convince decision makers and public to conserve the shorebirds and their habitats. There is evidence for apex consumers playing important roles in maintaining species diversity of the ecosystem and losing apex predators could change the function of the ecosystem (Estes *et al.* 2011). Similarly, given their migratory nature, the local decline of shorebirds may have much broader ecosystem implications that extend to the other sites used by shorebirds during their annual-cycle (van Gils et al. 2012), but such possibilities have yet been very well understood. Given the limited conservation success and uncertainty in the ecological roles that shorebirds play in the ecosystem, it may be worth putting more emphasis on the economic values of natural wetlands when it comes to shorebird conservation. Such an approach is particularly useful in less-affluent societies where the aesthetic values of nature are not appreciated as much as the economic values.

Globally, the most critical threat to coastal ecosystems is habitat loss (Gray 1997). For the staging sites of shorebirds along the EAAF, such loss was mostly through reclamation and to a lesser extent, *Spartina* invasion (Gan *et al.* 2009; IUCN 2012; Li *et al.* 2009a; Murray *et al.* 2014). The coastal habitats used heavily by shorebirds are also important foraging and nursery habitats for fishes (Lotze *et al.* 2006), which in turn support local people. The collapse of such a system would not only reduce the ability of the coastal area to buffer natural disasters such as flood and storm (Lotze *et al.* 2006), but also be detrimental to the livelihoods and traditional east-Asian culture that depends on the coastal fishing activity (Reid *et al.* 2008; Sato & Koh 2004).

The future for shorebirds along the EAAF may seem depressing, given the continued deterioration of shorebird habitats, especially those within the Yellow Sea. Habitats for shorebirds in developed countries also continue to deteriorate, even legally protected areas such as the Wadden Sea in Europe and Delaware Bay in America, leaving more doubts about the effectiveness of the current conservation approach and management regime (van Gils *et al.* 2006a; Walls *et al.* 2002).

Although many of the important staging sites are deteriorating and some have already been lost forever, the decreasing staging options could ironically, make conservation management easier because effort can be more concentrated. Moreover, international cooperation in the conservation of shorebirds along the EAAF has been particularly encouraging, as reflected by the three most studied shorebird sites in China, namely the Yalu Jiang coastal wetlands, Bohai Bay and Chongming Dongtan National Nature Reserve. It was the selfless devotion by experts and volunteers from the Australasian Wader Studies Group and Miranda Naturalists' Trust (New Zealand) with local reserve staff that laid the foundation for shorebird research and conservation in these areas. The rapid increase in the number of bird-watchers in China and environmental awareness also allow shorebird researchers to be positive (Ma *et al.* 2013a).

More importantly, the coastal landscape of staging sites of shorebirds along the EAAF is unique, in terms of the amount and type of anthropogenic activities, compared to those in Europe and America. The use of farmland by waterbirds is well documented and many studies have investigated ways to optimise the farming practices that benefit both farmers and the birds (Elphick 2010). In addition to farmland, the coastal landscape in East Asia is also dominated by aquaculture ponds and inland salt pans, which are less studied compare to farmland. Study on wintering Dunlins in Chongming Dongtan indicated that aquaculture ponds were used more frequently than farmland (Choi *et al.* 2014). In general, a few features of the stopping sites in the EAAF have often been

overlooked: 1) large scale aquaculture ponds or inland salt pans along the East Asia coasts that are not common in Europe and North America (deduced from annual production reported in Waite *et al.* 2014), but might have mitigated the negative effect of coastal intertidal flat reclamation on shorebirds along the EAAF; 2) extensive shellfish farming on tidal flats in China and Korea, with some tidal flats being leased to fishermen, including those in a national nature reserve (C.-Y. Choi pers. obs.; Feng *et al.* 2004; Sato & Koh 2004); 3) extensive fishnets set on the tidal flat to trap fishes, crabs and prawns that are washed ashore with flood tide, a practice that has been reported from both ends of the Chinese coast (from Yalu Jiang coastal wetland between China and North Korea border, to Beilun river estuary between China and Vietnam border) (C.-Y. Choi pers. obs.; Yang *et al.* 2011) and is likely to be a common practice in the country.

Given the bias towards affluent countries in shorebird and waterbird research, very little has been published about the usage of aquaculture ponds or salt pans as habitats for waterbirds and how they could be managed to benefit both fishermen and waterbirds. In 2012, Asia produced nearly 90% of the total aquaculture production in the world, and China alone produced 62% (Waite et al. 2014). Thus, waterbirds along the EAAF face a coastal landscape that their counterparts in other flyways would seldom face - aquaculture ponds. Pleas made back in 1997 for more research on the use of aquaculture ponds by waterbirds have largely been overlooked (Young & Chan 1997). These habitats were frequently used by shorebirds as high-tide roost when the intertidal flat is inundated (Choi et al. 2014). However, it seems to be a common practice to leave some of the ponds completely dry during the boreal winter to sterilise the area, which allows vegetation to grow and makes them less attractive to shorebirds (Choi et al. 2014; K.-W. Cheung pers. comm.; Li et al. 2013). Occasionally they could also be used as supplementary feeding habitat when drained, allowing shorebirds to reach the substrate and obtain food from there (C.-Y. Choi pers. obs.; Young & Chan 1997). Therefore, it is important to understand the factors such as types of substrate, terrain, and proximity to feeding area, that make certain ponds more attractive to shorebirds to facilitate management effort (Rogers et al. 2006a; Rogers *et al.* 2006b). It is also important to document the different practices used in aquaculture ponds or salt pans in different parts of China and for different products because case-by-case studies are required to evaluate the impact of aquaculture on the environment (Godet et al. 2009). Coinciding the harvesting time with low food availability on the tidal flat will create supplemental feeding habitat for shorebirds, while limiting the drained period will allow extended usage by shorebirds. Supplementary feeding schemes in aquaculture ponds based on solid scientific knowledge and justification may be a mean to support those critically threatened shorebird species such as the Spoon-billed Sandpipers *Eurynorhynchus pygmeus* during their stopover along the Chinese coast, when tidal flat conditions deteriorate and become unprofitable for shorebirds to forage on.

On the other hand, understanding the different practices used in aquaculture ponds and salt pans will also help to evaluate the potential impact of antibiotics and other pollutants generated from aquaculture on wildlife (Holmstrom *et al.* 2003; Xie & Yu 2007). Some Aquaculture ponds were abandoned after three or four years of intensive use as they become less productive, which lead to more natural wetlands being converted for new aquaculture ponds (Flaherty & Karnjanakesorn 1995). Therefore, it is important to encourage more sustainable practice such as the use of polyculture of fish and crabs instead of cultivating single species intensively to reduce the pressure for reclamation.

Similarly, shellfish farming on intertidal flat is growing rapidly along coast in many parts of the world but their impacts were less studied (Godet *et al.* 2009). China has the largest mariculture production in the world and such systems usually operate on intertidal flats with water level less than 15 m, but expanded to depths up to 50 m more recently. A total area of 7,520 km<sup>2</sup> coastal areas was used for mariculture in 2001 (Feng et al. 2004). Shellfish alone contributed more than 80% of the mariculture production between 1999 and 2001 (Feng et al. 2004). Studies outside Asia have shown that shellfish harvesting may drive shorebirds away from their preferred habitats (Cayford 1993; deBoer & Longamane 1996) and lower the food availability and quality to shorebirds (Dias et al. 2008; van Gils et al. 2006a). However, the situation in China may be different because fishermen start shellfish farming by seeding spat that were about 2 mm long in high densities on the tidal flat during the boreal spring, coinciding with northward migration of shorebirds. Small prey even with low prey quality, could still be useful for migratory shorebirds if they occur in sufficiently high density (Yang et al. 2013). This can create human-wildlife conflicts when birds feed on the shellfish seeds (Figure 8.6). Nonetheless, during years when natural food availability is low, reserve staff could use such means to provide supplemental food to shorebirds if needed. Therefore, it is important to document the intensity and type of shellfish farming (manually or mechanical) in different staging sites, and evaluate these impacts, especially their competitive interaction with local natural benthic communities, through fieldwork and comprehensive literature reviews.

Finally, there are extensive fishing activities on the tidal flat, in addition to those in the sea, and it is important to understand how they may impact on the trophic relationships on the intertidal flat. Might this actually help the shorebirds by lowering competition for benthic food resources? In short, there may not be any pristine intertidal ecosystem left in East Asia and conservation management in such ecosystem should take anthropogenic activities into considerations.

Despite the potential roles that aquaculture ponds and salt pans may play in shorebird conservation, it is important that the conservation of the most favourable habitat for shorebirds – intertidal flat remains the top priority (Choi et al. 2014; Ens et al. 2004; Ma et al. 2004). Conservation-related research on migratory shorebirds should also put more emphasis on the investigation of how conserving wetlands in the less affluent countries can benefit the local people. It is through the development of sustainable fisheries and regulated anthropogenic activities in wetlands that will guarantee the future of many migratory shorebirds and other wetland species in heavily populated areas (Ens et al. 2004; Lee 2012). Any attempt to conserve the migratory shorebirds requires cooperation between multiple countries based on scientific knowledge of the annual cycles and important habitats used during the breeding, nonbreeding, and migration periods. Effort should also be made to encourage collaboration between experts in different fields such as ornithologists, ecologists, social scientists and physical oceanographers. A comprehensive approach that studies not only the food webs at intertidal wetland systems to disentangle inter-species relationships between major natural and cultivated fauna, but also foresee the changes of the dynamic intertidal flat will allow better conservation decisions to be made. I hope that the results from my thesis, and the concurrent research in Bohai Bay and Chongming Dongtan, manage to provide the scientific knowledge on the stopover ecology of shorebirds along the EAAF that can be used for improving the conservation of shorebirds along the flyway.

Chi-Yeung Choi- July 2014



**Figure 8.6** Intertidal flat in Yellow Sea – shared between local people who harvest shellfish to make a living and the long distance migratory shorebirds that refuel and prepare for their next flight (Photo by Murray Potter).

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# APPENDIX 1. THE MACROBENTHOS BIOMASS DENSITIES AT AN IMPORTANT SHOREBIRD STAGING SITE DURING NORTHWARD MIGRATION

# Abstract

The importance of different wetlands to migratory shorebirds has often been evaluated by the number of birds present while relatively less consideration was given to the critical avian food resources. This study quantified the macrobenthic biomass in one of the most important staging sites for shorebirds in the Yellow Sea – the Yalu Jiang Estuary Wetland National Nature Reserve – during northward migration. The average macrobenthic biomass (15.4 g AFDM m<sup>-2</sup>) is within reasonable range compare to other intertidal flats worldwide. The macrobenthic biomass composition in the study area was dominated by a bivalve species *Potamocorbula laevis*, which composed of more than three quarters of total macrobenthic biomass during the study period (11.8 g AFDM m<sup>-2</sup>). There was also evidence for large spatial variation in benthos biomass within merely 10 km. Given the large spatial variation and dominance of *P. laevis*, more studies should be carried out in the future to investigate its life history and factors that may affect its reproductive success and survival.

# Introduction

Many shorebirds are transoceanic and/or transcontinental long distance migrants that require high quality stopping sites (i.e. staging sites) to refuel before continuing their journeys (Atkinson et al. 2007; Battley et al. 2012; Choi et al. 2009; Hua et al. 2013; Warnock 2010). Shorebird populations along the East Asian-Australasian Flyway (hereafter EAAF) are among the most poorly known of the different flyways (Stroud *et al.* 2006). The importance of different wetlands to migratory shorebirds along the EAAF has been assessed mainly on the number of birds present (Bamford *et al.* 2008; Barter 2002); little consideration has been given to the food resources present for birds, the macrobenthos in the wetlands. The latter deserves more attention because food availability is related to many ecological patterns of the predators such as geographic distribution, community structure and timing of annual cycles (Hutto 1990; Skagen & Oman 1996). The distribution and abundance of Great Knots Calidris tenuirostris, Red Knots C. canutus and Bar-tailed Godwits Limosa lapponica have been shown to relate to food availability (Piersma et al. 1995; Rogers 2005; Yates et al. 1993; Zwarts et al. 1992). Moreover, large areas of intertidal flat do not necessarily support large number of shorebirds (Rogers et al. 2011) and this is particularly important in the conservation of intertidal flats for shorebirds in the Yellow Sea, where 65% of the tidal flats were lost in the last 50 years (Murray et al. 2014).

Previous benthos studies suggested that the North Yellow Sea has a higher benthos biomass and density than the South Yellow Sea and Bohai Sea and echinoderms contributed the highest biomass (Hu *et al.* 2000; UNDP/GEF 2007a). However, these studies either used wet weight as biomass estimates or focused on subtidal and marine areas, with relatively little relevance to the shorebirds. In this study, we aimed to quantify the macrobenthic biomass composition in one of the most important shorebird staging site in the Yellow Sea – the Yalu Jiang Estuary National Nature Reserve in China. We also explored the spatial and temporal variation of different macrobenthic taxonomic groups during the intense shorebird northward migration period.

### **Materials and Methods**

#### Study area

This study was carried out at the Dandong Yalu Jiang Estuary Wetland National Nature Reserve (39°40′–39°58′N, 123°34′–124°07′E) (Figure 1.2). Detailed descriptions on the study area can be found in Chapter 3.

In order to understand the food availability for the migratory shorebirds, benthos sampling was carried out near site 5 between March and May from 2011 to 2012. Additional samples were taken near site 2 in 2012. These areas were chosen due to the presence of large number of foraging shorebirds during northward migration (Chapter 3; Riegen *et al.* 2014) (Figure 1.2).

#### **Benthos sampling**

At site 5, we set up a 9 km<sup>2</sup> (3 x 3 km) study area and divided it into 36 grids, each of which was  $0.25 \text{ km}^2$  (0.5 x 0.5 km) and a sampling station was set at the centre of each grid (Figure 1.2d). Benthos samples were taken once a month between March and May in 2011 and 2012. An addition of 18 grids with similar design was set near site 2 in 2012. The first sampling was done soon after ice-melt and before the peak arrival of migratory shorebirds while the last sampling was carried out at the end of migratory period (Chapter 2). One benthos core sample was taken per station using corer with a diameter of 155 mm (area 0.019 m<sup>2</sup>) and to 30 cm deep. The sample was then divided into the top (5 cm) and the bottom layer (25 cm) and was sieved separately through a sieve with 0.5 mm meshsize in the field. All soft-bodied organisms were either kept in 70% ethanol, or soaked in 5% formalin for at least 72 hours before replacing by 70% ethanol. Hard-bodied organisms were kept frozen until further analysis. All organisms were identified to the finest practicable taxonomic level using dissecting microscope. In general, polychaetes were identified to family level, molluscs and crustaceans to species or genus. Some softbodied organisms were broken during collection but measurements of these specimens were still taken and recorded, with specific notes on whether it contained the head, tail or body segment.

A subset of benthos collected from sampling stations and on random basis was used in estimating the size-specific benthos biomass. Dry mass was obtained by drying the samples at 60°C for 60 hours and the ash weight was obtained by incinerating at 560°C for 5 hours. All masses were weighted to the nearest 0.0001 g and the difference between dry mass and ash mass was the ash-free dry mass (hereafter AFDM). The size-specific values for AFDM of different benthos taxonomic groups were then obtained by regressing AFDM on a body size variable. Flesh was separated from the shell before drying in all bivalves and only the AFDM from flesh was used in relating different sizes to AFDM. Due to its importance to the diet of shorebirds (Chapter 4), the size-specific AFDM of bivalve *Potamocorbula laevis* was investigated separately for each month in 2012. These relationships between body size variable and AFDM in different taxonomic groups were then used to estimate the total AFDM of different taxonomic groups available in different periods and years.

# Results

Two hundred and twenty benthic core samples were taken in 2011 and 2012. Results of the relationships between AFDM and body size variable in different macrobenthic taxonomic groups are presented in Table A1.1. The macrobenthic biomass in the study area was dominated by Bivalvia (79.6%), followed by Anthozoa (7.4%), Gastropoda (5.7%) and Polychaeta (3.2%). Different groups showed different vertical distribution in the substrate: most of the biomass of Bivalvia, Gastropoda and Amphipoda was found within the top 5 cm of the sediment. In contrast, most of the biomass of Anthozoa, Lingulata and shrimps was found below 5 cm, while the biomass of Polychaetes and crabs was more or less equally available on the top or below 5 cm (Table A1.2). Polychaeta (91.5%) and Bivalvia (65.2%) were most frequently found in the sampling stations. Anthozoa, Lingulata and shrimps were found rarely, but they still had a fairly high contribution to the total macrobenthic biomass.

In finer taxonomic terms, the macrobenthos biomass was dominated by one single bivalve species, *Potamocorbula laevis*, which contributed more than three quarters of the total macrobenthic biomass during the study period (76.7%). This was followed by Actiniaria (7.4%), the gastropod *Bullacta ecarata* (5.3%), *Lingula sp.* (2.7%), the polychaete *Glycera chirori* (1.6%) and razor clams *Sinonovacula constricta* (1.3%) (Table A1.3Table ). Capitellidae or Maldanidae and *P. laevis* were frequently sampled but the former had very low contribution to the total macrobenthic biomass (Table A1.3Table ).

Year	Taxonomic group		Body size variable	Power regression	R <sup>2</sup>	N
2011	Perioculodes meridichinensis	Amphipoda	Length	A=0.00002 x V <sup>2.5318</sup>	1	4
2012	Perioculodes meridichinensis	Amphipoda	Length	A=0.000003 x V <sup>3.2137</sup>	1	5
2011	Phoxocephalus sp.	Amphipoda	Length	A=0.000003 x V <sup>3.1633</sup>	0.94	3
2012	Phoxocephalus sp.	Amphipoda	Length	A=0.000008 x V <sup>2.8669</sup>	0.96	6
2011	Anemone	Anthozoa	Length	A=0.015 x V <sup>0.7123</sup>	0.85	7
2012	Anemone	Anthozoa	Volume	A=0.0015 x $V^{0.6176}$	0.93	3
2012	Mactra veneriformis	Bivalvia	Length	A=0.00001 x V <sup>2.7771</sup>	0.97	8
2011	Potamocorbula laevis	Bivalvia	Length	A=0.00001 x V <sup>2.9421</sup>	0.98	324
2012- 3	Potamocorbula laevis	Bivalvia	Length	A=0.00001 x V <sup>2.2956</sup>	0.91	75
2012- 4	Potamocorbula laevis	Bivalvia	Length	A=0.00001 x V <sup>2.745</sup>	0.91	64
2012- 5	Potamocorbula laevis	Bivalvia	Length	A=0.000003 x V <sup>3.3071</sup>	0.95	50
2012	Sinonovacula constricta	Bivalvia	Length	A=0.0000007 x V <sup>3.4104</sup>	0.99	9
2011	<i>Lingulidae</i> sp.	Branchiopoda	Length	A=0.00001 x V <sup>2.908</sup>	0.99	6
2012	Macrophthalmus abbreviatus	Crab	Width	A=0.00006 x V <sup>2.7689</sup>	0.61	4
2011	Macrophthalmus japonicus	Crab	Length	A=0.00002 x V <sup>3.4522</sup>	0.98	10
2012	Philyra pisum	Crab	Length	A=0.000009 x V <sup>3.658</sup>	0.99	3
2011	Diastylis tricincta	Cumacea	Length	A=0.000007 x V <sup>3.6566</sup>	0.98	3
2012	Diastylis tricincta	Cumacea	Length	A=0.000003 x V <sup>2.7061</sup>	0.92	4
2011	Bullacta exarata	Gastropoda	Length	A=0.00002 x V <sup>3.2936</sup>	0.99	5
2012	Bullacta exarata	Gastropoda	Length	A=0.00007 x V <sup>2.9599</sup>	0.63	9
2011	<i>Thais</i> sp. Or <i>Reishia</i> sp.	Gastropoda	Height	A=0.00002 x V <sup>2.7773</sup>	0.95	7
2012	Opheliidae	Opheliidae	Length	A=0.000008 x $V^{1.7924}$	0.99	3
2011	Flabelligerimorpha	Polychaeta	Length	A=0.000002 x V <sup>1.8649</sup>	0.81	7
2012	Flabelligerimorpha	Polychaeta	Length	A=0.000004 x V <sup>1.818</sup>	0.84	7
2011	Glycera chirori	Polychaeta	Length	A=0.000001 x V <sup>2.481</sup>	0.98	8
2012	Glycera chirori	Polychaeta	Length	A=0.000003 x V <sup>2.2947</sup>	0.87	11
2012	Nephtys caeca	Polychaeta	Length	A=0.000002 x V <sup>2.1724</sup>	0.96	8
2011	Polychaete	Polychaeta	Length	A=0.000007 x V <sup>1.8524</sup>	0.97	5
2012	Polychaete	Polychaeta	Length	A=0.000003 x V <sup>2.1902</sup>	0.95	9

**Table A1.1** The relationship between AFDM (*A*, g) and body size variable (*L*, mm) in different benthos groups.

2011	Nihonotrypaea japonica / Callianassa harmandi	Shrimp	Length	A=0.0000005 x V <sup>3.2701</sup>	0.96	13
2012	Nihonotrypaea japonica / Callianassa harmandi	Shrimp	Length	A=0.0000004 x V <sup>3.6204</sup>	0.95	5

**Table A1.2** The main characteristics of macrobenthos taxonomic groups found in the study area between March and May in 2011 and 2012. Samples included 270 core samples taken from site 2 (54 in 2011) and site 5 (108 in 2011 and 108 in 2012), with all samples 30 cm deep and sieved through a 0.5 mm sieve. Biomass was averaged across stations, periods, years and sampling depths summed.

Taxonomic groups	Biomass (g AFDM m <sup>-2</sup> )	Percentage of biomass in top 5cm	Percentage of biomass in bottom 25cm	Frequency of occurrence (percentage of total 270 cores)
Bivalvia	12.29±32.16	88.34	11.66	176 (65.19)
Anthozoa	1.15±4.97	8.59	91.41	19 (7.04)
Gastropoda	0.88±3.51	74.21	25.79	66 (24.44)
Polychaeta	0.5±1.2	57.71	42.29	247 (91.48)
Lingulata	0.42±2.18	5.96	94.04	17 (6.3)
Shrimp	0.11±0.66	3.21	96.79	21 (7.78)
Crab	0.06±0.48	42.39	57.61	12 (4.44)
Cumacea	0.01±0.09	68.05	31.95	24 (8.89)
Amphipoda	0.01±0.04	72.32	27.68	37 (13.7)

Large variations in macrobenthic biomass were found between sampling stations, yielding a high standard deviation (Table A1.4Table ). The spatial variation in the mean biomass between sites was usually larger than the annual variation within site (Figure A1.1Figure) and contrasting patterns were found in the two most frequently sampled taxa. Polychaetes showed noticeable annual variation in biomass but the spatial variation was relatively small between sites (Figure A1.1Figure). In contrast, the biomass of *P. laevis* was remarkably lower in site 2 than site 5 and few were found near the seawall (Figure A1.1).

**Table A1.3** The frequency of occurrence and mean biomass (averaged across stations, periods, years and sampling depths summed) of top twelve macrobenthic taxonomic groups that contributed most to the benthic biomass in the study area between March and May in 2011 and 2012.

Taxonomic groups	Class	Biomass (g AFDM m <sup>-2</sup> )	Frequency (Percentage out of total n=270)		
Potamocorbula laevis	Bivalvia	11.83±32.03	142 (52.6)		
Actiniaria	Anthozoa	1.15±4.97	19 (7)		
Bullacta ecarata	Gastropoda	0.82±3.48	59 (219)		
<i>Lingula</i> sp.	Lingulata	0.42±2.18	17 (6.3)		
Glycera chirori	Polychaeta	0.25±1.15	71 (26.3)		
Sinonovacula constricta	Bivalvia	0.2±1.93	3 (1.1)		
Meretrix meretrix	Bivalvia	0.14±1.35	13 (4.8)		
Nihonotrypaea japonica	Crustacea	0.11±0.66	21 (7.8)		
Moerella sp.	Bivalvia	0.1±0.49	18 (6.7)		
Capitellidae or Maldanidae	Polychaeta	0.08±0.22	164 (60.7)		
Annelida Polychaeta	Polychaeta	0.06±0.18	146 (54.1)		
Nephtys caeca	Polychaeta	0.05±0.08	115 (42.6)		

**Table A1.4** The mean biomass (g AFDM m<sup>-2</sup>, averaged across stations) of the main macrobenthic groups at site 5 in the Yalu Jiang coastal wetland during 2011 and 2012. Data presented were summed between upper and lower layers. The dominant bivalve species *Potamocorbula laevis* was further divided into two groups according to shell length (*P. laevis* 1 with shell length<10 mm, *P. laevis* 2 with shell length>10 mm).

	da	Bivalvia								a		
Period	Amphipoo	Anthozoa	All	P. laevis 1	P. laevis 2	Crab	Cumacea	Gastropoo	Lingula	Polychaet	Shrimp	All benthos
2011-3	0.00	1.29	12.28	0.23	11.27	0.00	0.00	0.07	0.46	0.52	0.05	14.68
2011-4	0.01	1.34	12.76	0.59	11.98	0.02	0.02	0.07	0.59	0.39	0.31	15.49
2011-5	0.04	2.05	18.32	1.58	16.36	0.08	0.06	0.33	0.90	0.35	0.23	22.36
2011 avg												17.51
2012-3	0.01	0.62	19.74	0.20	19.43	0.14	0.00	0.84	0.15	0.24	0.03	21.77
2012-4	0.00	0.52	17.22	0.06	17.11	0.19	0.00	1.36	0.56	1.09	0.23	21.17
2012-5	0.01	2.77	9.77	0.00	9.76	0.01	0.00	2.41	0.51	0.40	0.00	15.89
2012 avg												19.61





**Figure A1.1** The mean (across months) biomass (AFDM m<sup>-2</sup>) of all macrobenthos, Polychaeta and bivalve *Potamocorbula laevis* sampled from the 36 and 54 sampling stations in 2011 and 2012, respectively.

# Discussion

These results demonstrate that the macrobenthic biomass at the Yalu Jiang Estuary National Nature Reserve is highly variable between sites, even merely 10 km apart, and this variation is mainly attributed to the presence of a bivalve species *Potamocorbula laevis*. Such domination by *P. laevis* within local benthos community with high spatial variation is also found in a critically important staging location for shorebird in Bohai Bay, 500 km west of our study area (H.-Y. Yang et al. in preparation). In contrast, the macrobenthic biomass in Saemangeum, which was another important staging location along the flyway, was dominated by an Inarticulata species while the Polychaeta and Bivalvia species had comparable biomass as the present study (Ryu *et al.* 2011b).

The total benthic biomass in the reserve showed an increasing trend between March and May in 2011 but a decreasing trend in 2012. Such trends were related to the change of *Potamocorbula laevis*, which constituted 80% of the average benthic biomass in this study (Table A1.4Table ). A closer investigation on the size distribution of *P. laevis* revealed a very different size structure between years, with young (<10 mm) dominated in 2011 while adults ( $\geq$ 10 mm) dominated in 2012. Therefore, the trends of biomass change

during the two boreal springs could be explained by the increase in young recruitments and growth in adults in April and May 2011, then a marked decrease in adults in April and May 2012.

In terms of the total macrobenthic biomass, the average of 15.4 g AFDM m<sup>-2</sup> (after taking eastern site 2 into account) is within the range  $(10-30g \text{ AFDM m}^{-2})$  of comparable studies conducted in intertidal flat in similar timeframe worldwide (Piersma et al. 1993a). A major contrast to the biomass composition found in Roebuck Bay, Australia, where many of the staging shorebirds in Yalu Jiang Estuary come from, is the high biomass contribution of Bivalvia and the relatively low contribution by Polychaeta in Yalu Jiang Estuary (Piersma et al. 1993a). The 10.7 g AFDM m<sup>-2</sup> of Potamocorbula laevis available in the top 5 cm in our study area is almost twice as much as the Bivalvia biomass found in Roebuck Bay of Australia (c. 6 g AFDM m<sup>-2</sup>), Banc d' Arguin of Mauritania (c. 6 g AFDM m<sup>-2</sup>) and the Wadden Sea in Europe (c. 4 g AFDM m<sup>-2</sup>; Tulp & de Goeij 1994). However, the overall average biomass in our study area would drop down to 3.6 g AFDM m<sup>-2</sup> if the dominant *P. laevis* is excluded. This indicates the vulnerability of the benthic community and raises a potentially very important issue that may affect the survival of shorebirds, if the population of *P. laevis* were to collapse. Therefore, there is an urgent need to investigate the life history of *P. laevis* and factors that may affect their growth and reproductive success. Future study should also investigate the factors affecting the distribution of shorebirds in the reserve; site 2 remained the area with the most number of shorebirds counted despite the low biomass available compare to site 5 (Chapter 2; Riegen *et al.* 2014). Factors such as distance to high tide roost and tidal flat elevation may play an important role in determining the distribution of shorebirds.

The Yalu Jiang Estuary National Nature Reserve is the critical staging site for many migratory shorebirds along the East-Asian Australasian Flyway during migration periods (Chapter 2; Ma *et al.* 2013b; Riegen *et al.* 2014). This study is the first to quantify the benthos resource available to staging shorebirds and shows that the macrobenthic biomass composition was dominated by a bivalve species *Potamocorbula laevis*. There is also evidence for large spatial variation and reasonable annual variation in the macrobenthic biomass composition. Given that there is often annual fluctuation in benthic production (Baird *et al.* 1985; Beukema 1979; Zwarts & Wanink 1993), long-term monitoring effort of the macrobenthic community in this site is recommended.