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DIET AND FORAGING BEHAVIOUR OF OYSTERCATCHERS (*HAEMATOPUS OSTRALEGUS*) AND GREY PLOVERS (*PLUVIALIS SQUATAROLA*): THE IMPORTANCE OF INTERTIDAL FLATS

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ABSTRACT: Many shorebirds feed on macrobenthic fauna that become available at low tide in coastal intertidal flats. Waders differ in the method used to search for food. This paper presents results of a study on the feeding behaviour, diet and energetic needs of oystercatchers and grey plovers at the Bay of Heist, Belgium, using focal bird observations and macrobenthos sampling. The two bird species differed in their success rate and foraging rate but not in their foraging efficiency. Oystercatchers spent 70.2 % of time for handling mussels and 28.6 % for worms whereas grey plovers spent 93.3 % of the time for handling worms. During the whole period of observation, 75.5% and 42.5% of prey were identified for oystercatchers and grey plovers, respectively. Of these, polychaete worms comprised 51.3% and mussels 23.4% of oystercatchers prey, and worms 41.2% of grey plovers′ prey. For both species of birds, the overall size of prey estimated was significantly correlated with the corresponding biomass (worms R^2 = 0.97*;* mussels, R^2 = 0.99). Oystercatchers obtained a total of 158.8KJ daily energy intake from mussels, worms, and grey plovers 2.37 KJ from worms only. Mussels comprised an important contribution to the total energy intake of oystercatchers and worms for the grey plovers. Habitat partitioning between the two species of birds was not observed.

Key words/phrases: Daily energy intake, Diet, Foraging behaviour, Macroinvertebrates, Shorebirds, Tidal flat.

INTRODUCTION

Shorebirds (order Charadriiformes) occupy a wide range of environment. Habitats include coastal, saline, and freshwater wetlands, flooded agricultural fields, interior grasslands, and Arctic Tundra. Many of them use exposed shores for roosting or loafing, nesting, and chick rearing (Hubbarda and Dugan, 2003). Hence, they are ideal study species for a range of ecological and behavioural investigations (Sarah and dit Durell, 2000). The ability to predict the outcome of foraging decisions, such as where to feed, on what to feed, and for how long to feed, is a fundamental component in

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understanding life histories and population growth rates, as foraging plays a central role in ecology. The demands of food acquisition impose significant challenges to both the physiology and behaviour of birds (Granadeiro *et al*., 2006). Efficient foraging is a result of decisions regarding patch choice, patch exploitation strategy and selection of resources (Dias *et al.,* 2009). All food items have both a cost that is waste of energy and valuable time and a benefit of net energy intake (calories consumed) per unit of time (Moreira, 1996).

Shorebirds are important predators of invertebrates in intertidal soft-bottom communities (Bruschetti *et al*., 2009). They can exhibit various feeding strategies related to their social status, age, sex, individual skills and food availability (Kohler *et al.,* 2009). Foraging behaviour is known to vary within species between locations owing to differences in prey abundance, prey size, and substrate differences (Barbosa and Moreno, 1999). Waders differ in the method used to search for food. Visually foraging waders assess prey size and profitability prior to handling the prey. Although each species tends to prefer a particular searching technique, they can switch from one to another in response to environmental conditions (Dias *et al*., 2009). Many shorebirds detect their prey by touch via probing with their bills in soft ground, or by sweeping their bills through shallow water. Others detect their prey by sight, and some use a mixture of visual and tactile cues (Thomas *et al*., 2006). Shorebirds detect prey by visual and tactile sensory mechanisms, exhibiting a wide range of feeding styles such as pecking, probing, stabbing, sweeping, and ploughing. Pecking and probing are thought to be the main methods for visual and tactile foraging, respectively (Jing *et al*., 2007). Birds also search for their prey by moving over the ground steadily or intermittently.

In relation to their feeding behaviour, the diversity of shorebirds is reflected in their varied bill shapes and leg lengths. Most shorebirds have small bodies with long, thin legs for wading. Quantifying energy budgets of species, studying their diet preferences and identifying their core foraging areas are important premises for understanding ecosystem processes (Dierschke *et al.,* 1999). The nature of food supply varies in space or time, and individuals may specialize in a particular diet because it is the only one that they encounter (Sarah and dit Durell, 2000). They have a relatively high metabolic rate and the largest daily food requirement relative to body weight of any marine predator especially migrating ones. It is known that shorebirds should choose to feed in places where they can get the most food in the shortest time (Finn *et al.,* 2008). Although some studies have evaluated the effects of foraging strategies on the habitat use of shorebirds, the present study dealt with foraging behaviours in relation to the habitat use and prey profitability. The basic hypothesis of the study is that bird foraging behaviour is dependent upon the habitat in which it is feeding. The present study aimed to:

- See how these birds are capable of behaviourally responding for their prey availability.
- Examine diet and foraging behaviour of oystercatchers and grey plovers.
- Determine prey preferences of the two species of birds.
- Estimate the energy obtained by these birds through predation on their benthic prey.

MATERIALS AND METHODS

Study area and habitats

This study was carried out in the Bay of Heist, Belgium (51° 20′ N, 3°13′ E). Prior to the actual field observation, metal sticks were placed at regular distances on the intertidal flat forming 151 grid cells. A GPS receiver was used to locate the delimitations of each grid cell (20 m x 20 m) with accuracy of 4 m. The grid cells were merged and defined into five habitats based on the zonation patterns of Mussels, *Lanice conchilega* tubes, and nature of the sediment, hereafter referred to as Tidal flat high (TFH), Tidal flat low (TFL), *Lanice conchilega* area (L), Mussel bed (MB) and Muddy area (MUD). The grid data were pooled per habitat type.

Bird selection

The most abundant birds were selected based on five days consecutive count that gave an average abundance of 365 and 92 individuals in the total study area for oystercatchers and grey plovers, respectively.

Observation period and tools

During ebb tides, observations started when the sea receded from high water mark exposing the study area. For flood tides, observations began at low water and ended when all the habitats were covered. Bird observations were conducted only on calm days. The data on all activities of the two species of birds were collected for 12 days from February 8, 2010 until March 31, 2010. Observations were made with the use of SWAROVSKI HABRICHT AT80 zoom telescope (magnification X 20 - X 60) and binocular

MINOLTA Classic 8 x 20W during daylight from a vantage point of 40-120 m away from the bird. This distance from the grids was used not to scare birds during observation.

Focal observations began after the observer was in a position and relatively still for at least 5 min in the grid cells. Each grid cell received almost an equal number of visits during the observation that resulted in 200 focal bird observations. The activity patterns of birds were recorded using PHILIPS 7620 voice tracer. After each successful recording, a different individual bird was selected randomly in the centre of the field of view (Ntiamoa-Baidu *et al.,* 1998) to resume a new recording. While feeding, identification of prey type was only possible for larger items, or if the feeding bird was sufficiently close to the observer. Behavioural data collected on focal birds with an average length of observation period: 300.1 s, range: 265 - 326 s, N = 100; average 224.5 s, range 122 - 302 s, N = 100 for oystercatchers and grey plovers, respectively. The target bird was followed for 5 min or less until it moved out of range of the grid cells (Kvitek and Bretz, 2005). Time was standardized by dividing the total number of prey caught per total seconds used in each observation.

Feeding behaviour

Focal bird observations were used to quantify the feeding behaviour of the two species (Barbosa and Moreno, 1999; Nebel and Thompson, 2005; Granadeiro *et al.,* 2006; Finn *et al*., 2008). Sizes of prey taken were estimated visually by comparing prey total length with bill length (Finn *et al.,* 2008). Bill length was approximately 75 mm in oystercatchers and 30 mm in grey plovers. In order to avoid probable length overestimation in stretched worms while pulled out of the sediment, worm size estimates were not made until the prey was totally pulled out and hanging from the bill (Moreira, 1996, 1997). For a very small prey, their intake was generally detected from the typical swallowing movements of the bird's head (Moreira, 1996). Prey items were identified using a guide (Degraer *et al.,* 2006).

Diet and estimation of biomass

During field observation, prey captured by oystercatchers were identified and classified into the following groups: mussels, *Ensis* spp., polychaete worms, crabs, and surface items and for grey plovers polychaete worms, crabs and surface materials. Surface items were prey that were picked off the surface, could not be identified because they were too small to see, and were considered as unidentified items. Cockle (0.31%) and *Ensis* spp. (0.51%) from oystercatcher's food items observed; other bivalves (0.83%) and crabs (0.55%) from grey plovers that represented below 1% of the total prey were rejected from the energy budget analysis. The size of each prey and the corresponding biomass, Ash Free Dry Weight (mg AFDW) varying among the two bird species were derived using a standard AFDW–Length relationship equation 1 Goss-Custard *et al.* (2001) for mussels and equation 2 (J. Mees, unpublished data) for worms, respectively.

$$\mathrm{Log_e A} = -32{\cdot}85 + 18{\cdot}0743\,\mathrm{Log_e L} - 2{\cdot}0427((\mathrm{Log_e L})^2) \qquad \text{Eq. 1}$$

$$\ln \mathrm{AFDW} = -5.882 + 1.674 \ln L \qquad \text{Eq. 2}$$

Where AFDW, Ash Free Dry Weight in mg, L = prey length in mm, ln = $\mathrm{Log_e}$ = natural logarithm. The net energy intake was calculated using the following equation:

$$\mathrm{NEI} = 2.4\text{-}4.9 * \mathrm{BMR} * 1/Q \qquad \text{Eq. 3}$$

Where, NEI = net energy intake, Q = assimilation efficiency = 85%

Using these formulae, the total biomass ingested during each observation period was estimated by summing the estimated weights of each prey. The intake rate (Energy value per second), success rate (number of preys consumed per second), foraging efficiency (prey per peck in percentage) and foraging rate (number of foraging events per second) were calculated in each habitat and compared between habitats. In the case of grey plovers, the feeding action for worms was often very quick and they did not always place their bills deep into the sediment. As grey plovers do not probe and oystercatchers behaved both in probing and pecking, determination of foraging efficiency and foraging rate was done by considering both pecks and probes together as a foraging event (Moreira, 1996; Jing *et al.,* 2007).

Macrobenthos sampling

By merging four grids into one, we reorganized the 151 grid cells for macroinvertebrates sampling. The sampling was carried out two times. Eight and 49 macrobenthic samples were taken in March 3 and 31, 2010, respectively. The first eight samples were not uniformly distributed throughout the study area. Hence, analyses on the macrobenthic community were based only on the 49 samples taken on March 31.The median sediment grain size among the five habitat types was analyzed using samples from the macrocorer. This was used to confirm the habitat types classified based on visual observation. The density of all macroinvertebrates obtained from the core sample was estimated and extrapolated into all habitat types. The density of *Lanice conchilega* reefs in each grid cell was estimated using 10 X 10 cm^2 randomly placed quadrats. This provided an estimate of *Lanice conchilega* in the study area. The samples were taken using a metal macrocorer (18 cm diameter, 30 cm depth) and sieved in the field over a 1 mm mesh. After fixation (8% formalin) and staining with Bengal rose, macro benthic animals were picked out in the laboratory. Animals were preserved in a 4% neutralised formalin solution. After sorting, to determine the ash free dry weight (AFDW), animals were first dried for 48h at 60°C, weighed and then burned for 3h at 500°C.

Data analyses

Prior to data analyses, Exploratory Data Analysis (EDA) was carried out. Whenever this analysis showed the normality of data, ANOVA tests were carried out. In order to improve normality of the raw data, square root transformation was done. Once ANOVA *F* test was checked and significance was observed, *post hoc* tests were performed to determine which means differed. One-Factor ANOVA was used to check the energy intake rate in mg AFDW s^{-1}, foraging rate in peck events s^{-1}, foraging efficiency and success rate (prey s^{-1}) of the birds. The mean bird's behavioural activity was made by pooling the records based on separate observations on each grid cell by habitat types. Statistical software SPSS 17.0 was used to perform all the analyses.

RESULTS

Sediment characteristics

Fine sand (125–250 µm) was an important sediment fraction in most samples, with a mean contribution (± SE) of 45 ± 2 %. Silt (4 – 38 µm) was the major contributor with (mean ± SE) 34 ± 11 %. There was a statistically significant difference in mud content of sediment samples $F_{4,\ 153} = 9.252$, $P < 0.01$ (highest at the muddy area); median sediment grain size $F_{4,\ 153} = 12.770$, $P < 0.01$ (highest at mussel bed) among the five habitat types. This result was used to confirm the habitats classified based on visual observation.

Diet, foraging activity and behaviour

Oystercatchers showed a statistically significant difference in foraging efficiency ($F_{4,\ 95} = 7.752$, $P < 0{\cdot}001$; success rate $F_{4,\ 95} = 6.773$, $P < 0{\cdot}001$ and foraging rate $F_{4,\ 95} = 6.794$, $P < 0{\cdot}001$) for all habitats tested. The post hoc test showed that *Lanice conchilega* area for all the three behavioural parameters and *Lanice conchilega* and Mussel bed for success rate produced high contribution for the mean differences (Table 1). For grey plovers, there was a significant difference on their foraging efficiency ($F_{4, 95} = 2.831$, $P = 0{\cdot}029$) among the habitat types of which *Lanice conchilega* area showed the maximum contribution for the difference. Nevertheless, there was no significant difference in their success rate ($F_{4, 95} = 2.020$, $P = 0{\cdot}098$ and foraging rate $F_{4, 95} = 1.790$, $P = 0{\cdot}137$). Levene's Test of Equality of Error Variances which >0.05 showed the error variances of all the three dependent variables (foraging efficiency, foraging rate and success rate) were equal across the habitat types (Table 1).

Concerning time spent by the two species of birds in each habitat, MANOVA indicated that, the proportion of time spent by oystercatchers showed a statistically significant difference among habitats for pecking behaviour ($F_{4, 95} = 6.877$, $P < 0.001$). Relatively high time was spent on the tidal flat high walking ($F_{4, 95} = 2.593$, $P < 0.05$) and large proportion of time was spent in the *Lanice conchilega* area running ($F_{4, 95} = 3.493$, $P < 0.05$). Comparatively extra time was used at the tidal flat high and time to stop ($F_{4,95} = 2.722$, $P < 0.05$) with much time spent to pause at the *Lanice conchilega* area (Fig. 1). Nevertheless, time spent by oystercatchers for swallowing prey ($F_{4, 95} = 1.398$, $P > 0.05$) and turning ($F_{4, 95} = 1.389$, $P > 0.05$) did not show a significant difference among habitats.

For grey plovers, no statistically significant difference for time spent was obtained within habitats for pecking ($F_{4,95} = 1.409$, $P = 0.237$); walking ($F_{4,95} = 0.836$, $P = 0.506$); running ($F_{4, 95} = 0.801$, $P = 0.528$); stop ($F_{4, 95} = 2.046$, $P = 0.094$); swallowing ($F_{4, 95} = 1.267$, $P = 0.288$) and turning ($F_{4, 95} = 0.523$, $P = 0.719$). The percentage of time spent by both species was relatively high in the *Lanice conchilega* area (Fig. 1). Concerning time for handling prey, oystercatchers spent 70.2 % of time for mussels and 28.6 % for worms, whereas grey plovers spent 93.3 % of the time for handling worms, 5.3 % for crabs and 1.4 % for other bivalves. The time spent by oystercatchers for worms and mussels ($F_{3,458} = 35.863$, $P < 0.001$, $N = 462$) was different. They spent extra time for handling mussels than worms. Overall time spent by grey plovers for handling worms was higher than other bivalves and crabs ($F_{2,151} = 11.095$, $P < 0.001$ $N = 154$).

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Table1. Mean (SE) of foraging rate (FR), foraging efficiency (FE) and success rate (SR) of oystercatchers (OC) and grey plovers (GP).

		TFH		L		TFL		MB		MUD		Total	
		Mean (SE)	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	N
OC	FR	0.13 (0.02)	23	0.16 (0.01)	39	0.09 (0.02)	15	0.10 (0.01)	11	0.10 (0.02)	12	0.13 (0.01)	100
	FE	1.01 (0.12)	23	1.30 (0.10)	39	0.57 (0.10)	15	1.10 (0.06)	11	0.60 (0.10)	12	1.00 (0.06)	100
	SR	0.021 (0.0)	23	0.026 (0.0)	39	0.012 (0.0)	15	0.02 (0.00)	11	0.014 (0.0)	12	0.021 (0.0)	100
GP	FR	0.06 (0.01)	16	0.07 (0.01)	50	0.06 (0.01)	24	0.06 (0.01)	6	0.03 (0.01)	4	0.06 (0.00)	100
	FE	0.66 (0.08)	16	1.12 (0.07)	50	1.04 (0.09)	24	0.79 (0.20)	6	0.98 (0.14)	4	1.00 (0.05)	100
	SR	0.01 (0.00)	16	0.02 (0.00)	50	0.02 (0.00)	24	0.01 (0.00)	6	0.02 (0.00)	4	0.02 (0.00)	100

TFH = Tidal flat high, L = Lanice conchilega area, TFL = Tidal flat low, MB = Mussel bed, MUD = Muddy area.

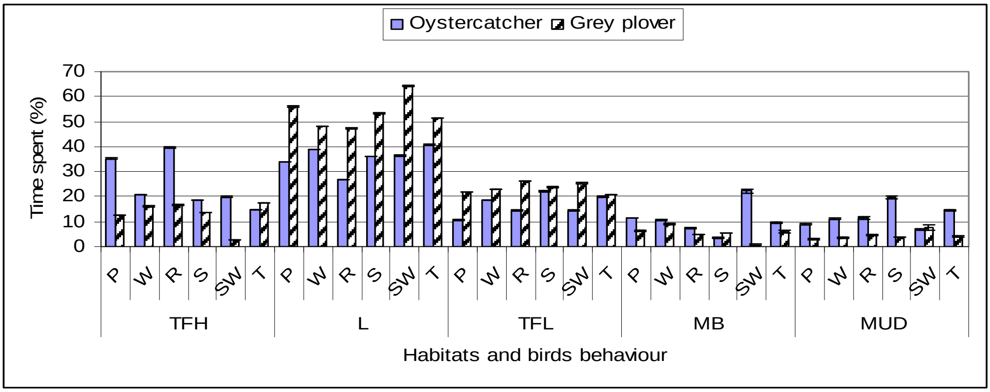

Fig. 1. Percentage of time (± SE*)* spent by oystercatchers and grey plovers in various activities on the intertidal flat. P = Pecking, W = walking, R = running, S = Stop/ searching, SW = Swallowing, T = Turning. TFH = Tidal flat high, L = *Lanice conchilega* area, TFL = Tidal flat low, MB = Mussel bed, MUD = Muddy area.

Prey availability

A total of 636 and 362 successful foraging events were observed. Of these, it was possible to identify 480 (75.5%) and 154 (42.5%) preys of oystercatchers and grey plovers, respectively. Unidentified preys were 156 (24.5 %) and 208 (57.5%) for oystercatchers and grey plovers, respectively (Table 2). From all identified preys, polychaete worms comprised 51.3% followed by mussels 23.4% for oystercatchers and worms 41.2% for grey plovers. The total number of preys caught by birds was significantly different among habitat types, oystercatchers ($F_{4, 95} = 6,581$, $P < 0.001$) and for grey plovers ($F_{4, 95} = 2,761$, $P < 0.05$).

The data of prey densities from field observations (prey m^{-2}) of oystercatcher worms ($F_{4, 95} = 21.56$, $P < 0.001$) mussel ($F_{4, 95} = 10.11$, $P < 0.001$) were significantly different among the habitats types. However, no significant difference was found in density of *Ensis* ($F_{4, 95} = 2.42$, $P > 0.05$) and cockle ($F_{4, 95} = 0.88$, $P > 0.05$) among the habitat types. For grey plovers, prey density (worms m^{-2}) at tidal flat high showed significant difference from Lanice and tidal flat low ($F_{4, 95} = 4.35$, $P < 0.01$) (Fig. 2A). On the other hand, prey from benthos sample worms ($F_{4,153} = 27.997$, $P < 0.001$) and mussels ($F_{4,153} = 35.818$, $P < 0.001$), showed a significant difference among the habitat types with high density of worms obtained at the mussel bed and Lanice and high density of mussels at mussel bed (Fig. 2B).

Table 2. Prey taken by oystercatchers (A) and grey plovers (B) in all habitats.

A. Oystercatchers

Habitats	Worms	Mussel	*Ensis* spp.	Cockle	Unidentified
TFH	6.29	6.45	0	0.16	9.75
L	39.78	2.20	0.16	0	6.29
TFL	2.04	3.14	0	0.16	3.45
MB	2.20	8.49	0	0	1.42
MUD	0.94	3.14	0.31	0	3.62
Total (%)	51.25	23.42	0.47	0.32	24.53

B. Grey plovers

Habitats	Worms	Bivalve	Crab	Unidentified
TFH	0.83	0.28	0	9.39
L	23.47	0.55	0.28	31.77
TFL	12.71	0	0.28	11.88
MB	2.49	0	0	2.21
MUD	1.66	0	0	2.21
Total (%)	41.16	0.83	0.56	57.46

TFH = Tidal flat high, L = *Lanice conchilega* area, TFL = Tidal flat low, MB = Mussel bed, MUD = Muddy area.

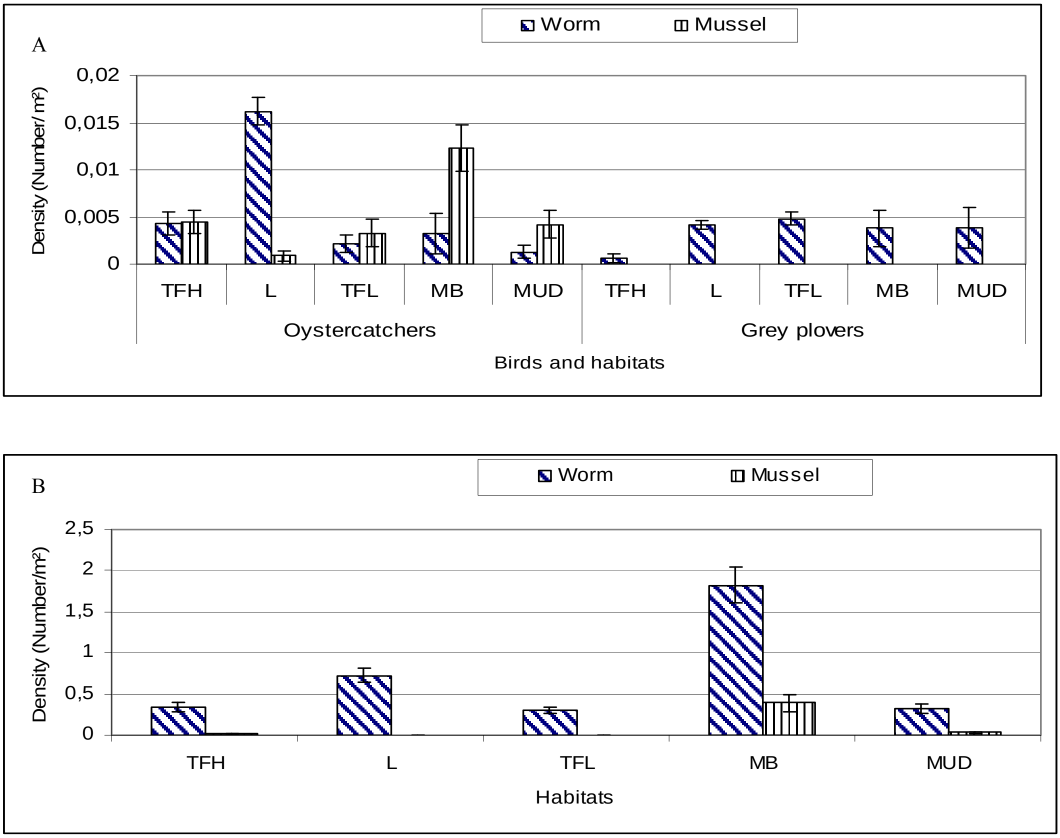

Fig. 2. Average density (± SE) of prey caught by oystercatchers and grey plovers from field observation (A), Average density (± SE) of prey obtained from benthos sample (B). TFH = Tidal flat high, L = *Lanice conchilega* area, TFL = Tidal flat low, MB = Mussel bed, MUD = Muddy area.

Prey size and biomass

The estimated length of the mussels that oystercatchers were observed consuming from the mussel bed ranged from 20 to 60 mm, with a mean of 38.9 ± 0.7 mm (n = 149). The modal length was 30 mm, which included 18% of the mussels. In total, 97.3% was between 30 and 50 mm in length and 0.7% of the mussels was 20 mm long and 2% was 60 mm long. The size distribution of the observed mussels consumed, differed significantly among the habitats ($F_{4,\ 144} = 10.215$, n = 149, $P < 0.001$). The post hoc test of size distribution among the habitats revealed the presence of a significant difference of prey sizes between habitat tidal flat high and tidal flat low, mussel bed and mud area, and *Lanice* area and tidal flat low area ($P < 0.05$).

The estimated length of worms that oystercatchers were observed eating from the area ranged from 30 to 150 mm, with a mean of 56.6 ± 1.6 mm (n = 322). The modal length was 30 mm, which included 33.9% of the worms. In total, 2.1% was between 130 and 150 mm in length. The size distribution of the observed worms consumed did not differ significantly among the habitats ($F_{4,\ 317} = 0.431$, n = 322, P = 0.786), corresponding biomass in mg ash free dry weight ($F_{4,\ 317} = 0.504$, n = 322, P = 0.733). The estimated length of worms that grey plovers were observed eating ranged from 30 to 150 mm, with a mean of 66.9 ± 2.54 mm (n = 148). The modal length class was 50 mm, which included 29.1% of the worms and 0.7% of worms estimated to be 90 mm long. In total, 8.1% was between 120 and 150 mm in length. For grey plovers, the size distribution of the observed worms consumed did not differ significantly among the habitats ($F_{4,\ 143} = 2.14$, n = 148, P = 0.078) and corresponding biomass ($F_{4,\ 143} = 0.597$, n = 148, P = 0.665).

A total of 149 mussels and 475 worms were successfully observed. For both species, the overall size of estimated prey (worms $R^2 = 0.97$, $F_{1,\ 468} = 18556.41$, $P < 0.001$and mussels, $R^2 = 0.99$, $F_{1,\ 147} = 27540.67$, $P < 0.001$) was significantly correlated with the corresponding biomass. The basal metabolic rate (BMR) of oystercatchers was 251.52 KJday^{-1}.

The daily energy intake of oystercatchers was 710 -1450 KJ. Taking a range of 22-26 KJ/g and mean 23.7KJ/g ash free dry weight calorific content of benthic animals, oystercatcher's daily energy intake corresponds to 32.3 - 65.9g ash free dry weight of benthic prey per day. Oystercatchers consumed an average biomass of 98.1mg ash free dry weight day^{-1} and 6598.6 mg ash free dry weight day^{-1} from worms and mussels, respectively. From the mean calorific content of benthic animals, oystercatchers could get a total of 158.8KJ daily energy from mussels and worms. However, for grey plovers, daily energy intake was 434-887KJ that corresponded to 16.7g - 40.3g ash free dry weight of benthic prey per day. Biomass obtained from worms was estimated to be 0.1 g AFDWday^{-1}; hence, grey plovers could get a daily average NEI of 2.37 KJ from worms. Biomass (mg AFDW) obtained by oystercatchers from mussels showed a significant difference among habitats ($F_{4,\ 144} = 10.137$, $P < 0.001$). The test revealed that *Lanice* area was different from tidal flat low and tidal flat low was different from mussel bed. However, the biomass of worms did not show a significant difference among habitat types ($F_{4,\ 317} = 0.338$, P = 0.85). Regarding grey plovers, the amount of biomass they obtained did not show a significant difference among habitats.

Regarding the mean worms' biomass in mg AFDW m^{-2} obtained by the two species from field observation and sampled spots; for grey plovers, the biomass from core sample showed a significant difference among habitat types ($F_{4, 155} = 12.498$, $P < 0.001$). Similarly, the biomass obtained from field observation was ($F_{4, 155} = 19.520$, $P < 0.001$) with a small amount of biomass from tidal flat high (Fig. 3). Nevertheless, the correlation between the two values did not show difference ($r = -0.031$, $P > 0.05$). However, the biomass of oystercatchers from field observation showed no significant difference among the habitat types ($F_{4, 321} = 1.564$, $P < 0.184$). Biomass from core sample was significantly different among habitat types $F_{4, 321} = 7.473$, $P < 0.001$ with the maximum amount obtained at mussel bed (Fig. 3) and the correlation between the two values did not show difference ($r = - 0.097$, $P > 0.05$).

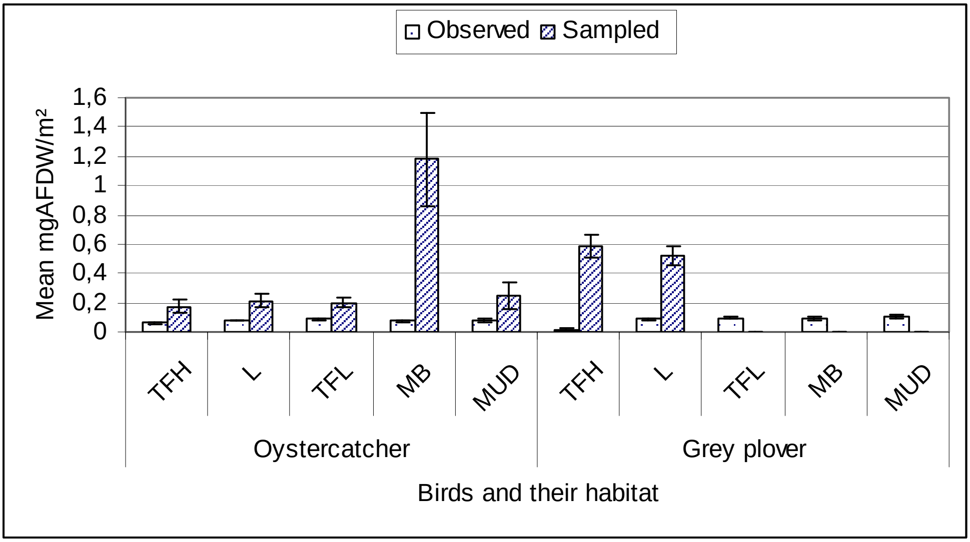

Fig. 3. Biomass (mean ± SE) of worms eaten by oystercatchers and grey plovers observed in the grids and collected at lumped grids. The data are Sqrt transformed. TFH = Tidal flat high, L = *Lanice conchilega* area, TFL = Tidal flat low, MB = Mussel bed, MUD = Muddy area.

DISCUSSION

Most waders eat a variety of prey available in the intertidal foraging areas. Both oystercatchers and grey plovers consumed different prey species in the habitats studied. Grey plovers were collecting worms from all of the habitats but oystercatchers fed on both worms and mussels. Many studies have shown that diet of oystercatchers and grey plovers consist of mussels and polychaete worms (Moreira, 1996). These results indicated that a nature reserve that is small in size could support relatively high number of a diverse array of actively foraging shorebird species. In contrary to the study of Jing *et al.* (2007), shorebirds used pause travel strategy of feeding consumed a higher proportion of crustaceans. However, in the present study, grey plovers consumed proportionally smaller number of crabs. This might be due to their short bill that could not penetrate the sediment to the depth where crustaceans are located, whereas oystercatchers using their tactile cues could consume more worms and mussel.

The feeding rate of the two species of birds was very high at the *Lanice conchilega* area (Table 1), probably to compensate for lower exposure time of the area and get enough prey. The results suggest that, although the two species of birds were similar in their foraging efficiency, they differed in their success and foraging rate. The *Lanice conchilega* area and mussel bed had contributed high on success rate of oystercatchers. This is related to the higher density of prey in the two habitats of the study area. This holds the same for grey plovers. At the *Lanice conchilega* area, they were more efficient than other habitats. Finn *et al.* (2008) suggested that shorebirds choose to feed in places where they can get the most food within the shortest time. Different foraging methods may indicate that different prey species are being taken, and the birds may feed in specific areas where preferred prey species are more abundant. Grey plovers were observed walking limited distance to capture prey instead of walking to new search areas. Successful pecks were followed by shorter walks than were unsuccessful pecks. This is because prey can be captured only within the search radius. Besides, both species changed their foraging site in response to the relative availability and detectability of different prey types. The quality of feeding habitats sites showing high abundance and availability and quality of prey species might play an important role in habitat usage (Schwemmer and Garthe, 2008).

Observations of avian behavioural activity in the intertidal zone exhibited different patterns among species corresponding to differences in their time budget. In this study, birds spent most of their time in the intertidal zone foraging and performing other activities, but spent relatively small proportion of time in the muddy area. This is because the area was not convenient to walk and run (Dare and Mercer, 1973). Both species spend a large proportion of time in other habitats other than the muddy area, because other habitats on the flat offer high opportunity for foraging, walking and searching. Oystercatchers restrict themselves utilizing the mussel bed area available at low tide. In contrast, grey plovers do not frequently visit the mussel bed area, but they use *Lanice* area. This might be related to the exposure of prey when the tide retreats.

Grey plovers exhibited a range of behaviour from short, slow foraging moves at the muddy area and mussel bed where worms were scarce (Table 2), to long rapid moves at the *Lanice* area where prey density was high. Longest search times were recorded at the *Lanice conchilega* area where more polychaete worms were available. This agrees with the findings of Kraan *et al.* (2009) that clear spatial patterning of prey enables foragers to distinguish among different prey densities more accurately and optimize their movements. At the mussel bed, oystercatchers used relatively short peck, walk, run time and they spent much time for swallowing prey. This is because they took extra time to handle mussels at this site where their density was high. This coincides with the results of Kohler *et al.* (2009) that prey occurring at high densities allow birds to minimize foraging times. Oystercatchers spent relatively less proportion of time for pecking at the muddy area as probing is difficult in such areas (Bruschetti *et al.,* 2009). Grey plovers never foraged in the shallow water, whereas oystercatchers frequently made use of it. This was because oystercatchers have long bill and use tactile means to get hidden prey, but in the case of grey plovers, their relatively insensitive, short bill prevents them from using tactile foraging. Oystercatchers fed in the habitats by moving continuously shifting from one habitat to the other. Besides, they were sweeping in the shallow water continuously by inserting their bill into the water. However, grey plovers fed by running and taking a pause whenever they get a prey. In the *Lanice conchilega* area where worm reef formation was observed, both species exploited this area using their respective cues. This agreed with the work of Thomas *et al.* (2006) that probing is associated with use of visual cues mainly used by visually feeding birds and to some extent by tactile cue users like oystercatchers. This shows that oystercatchers use both their tactile and visual cues to locate their prey.

During neap tides, some upper intertidal areas may remain exposed at high tide, and birds can choose to roost there. As Dias *et al.* (2006) indicated, shorebirds feed on the exposed intertidal flats, but as the tide rises, they were forced to leave their foraging grounds and concentrate at high water roosting sites. At the tidal flat high area, the density of worms obtained by grey plovers was the least. This might be due to the relative hardness of this habitat because of higher proportion of large grain size sediment. This shows that sediment characteristics influence prey densities and availability (Lourenço *et al*., 2005). Shorebirds at sandy beach did not probe beneath the surface and fed only on prey available on wrack lying on the beach. An increased sand content may result in a decrease of the time waders spent foraging. Sediment type also correlates with the moisture content of the substrate, which in turn is of great importance to prey availability. In the case of oystercatchers, the density of worms obtained at the mussel bed was small compared to mussels. This is because mussels dominate the mussel bed, hence oystercatchers concentrate feeding on mussels. Besides, they could not probe at this site due to the relative toughness of this habitat. Granadeiro *et al.* (2006) have suggested that although the main factor seems to be prey density, sediment characteristics, such as water content, can also be important for the behavior of feeding. The less resistant the substrates, the deeper the birds' bill can penetrate in search of prey and the lower the foraging costs (Finn *et al.,* 2008). However, from the benthos sampling, the density of worms at mussel bed area was the highest compared to other habitats. The benthos sample confirmed that mussel bed is the richest habitat of all.

Our results indicated that, oystercatchers via their probing behaviour could access large number of prey from the *Lanice conchilega* area. This might be because of the attractiveness of this area with tube aggregations that helped to host rich macrofauna (Crooks, 2002; Rabaut *et al.*, 2007, 2009). However, the benthos sampling result showed the highest density of worms at the mussel bed. The density of worms consumed by oystercatchers could have been high during field observation if they could probe at the mussel bed. The same holds true for grey plovers that foraged with high rate at the tidal flat low area and *Lanice* area, where the density of worms was high compared to other habitats. This shows that shorebirds may feed at higher rates in areas of greater prey densities. Clear spatial patterning of prey enables foragers to distinguish among different prey densities more accurately and to optimize their movements by spending most time in rich areas (Kraan *et al.,* 2009).

Harvestable prey often comprises only a small portion of the total benthic biomass present and oystercatchers are extreme specialists in their feeding behaviour and prey selection (Dierschke *et al.,* 1999). In this study, oystercatchers ate 97.3% of mussels within a size range of 30-50 mm, which was comparable to the findings of Meire and Ervynck (1986). This was supported by the idea that oystercatchers can identify very small differences in the prey environment, even within prey species. This result suggested that birds are really size-selective. The rejection of small prey is because of their low profitability, and large prey may be avoided due to an unprofitable increase in handling time. For grey plovers, even though, the biomass obtained from ranges of size classes did not show a difference among all the habitats, they were observed feeding on worms with an average size of 66.9 ± 2.54 mm but the proportion of very small and big size classes were relatively small. Prey of suitable size becomes inaccessible when the burying depth of the prey exceeds the probing depth of the bird (Dierschke *et al.,* 1999).

In this study, it was difficult to identify small-sized prey. There are two main problems in addressing energy-based questions using purely observational techniques, extrapolation from inaccurate data and incomplete data. Bearing these shortcomings in mind, it was reasoned out why energy intake rates differed between the two species and identify instances in which there was evidence that the birds' daily intake rates differed substantially from measurements of intake rates. The levels of daily energy intake of oystercatchers and grey plovers were in a range of 710-1450 KJ and 434-887KJ, respectively. Mussels made an important contribution to the total energy intake of oystercatchers. This was because mussels were available in clusters at the mussel bed and oystercatchers were exploiting this habitat more intensively to fulfill their daily energy requirements. Area restricted search maximizes the intake rate when prey items are clustered in continuous patchy environments (Dias *et al*., 2009) and thus waders need to maximize their immediate intake rate to fulfill their energetic demands. Our benthos samples confirmed that mussel bed was the richest habitat of all. Mussels made an important contribution to the total energy intake of oystercatchers, and worms for the grey plovers.

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