

## FEEDING ECOLOGY OF DUNLIN *CALIDRIS ALPINA* IN A SOUTHERN EUROPEAN ESTUARY

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SUMMARY.—*Feeding ecology of Dunlin Calidris alpina in a southern European estuary.*

**Aims:** The feeding ecology of Dunlin *Calidris alpina* wintering in southern European wetlands is poorly known. The aim of this paper is to describe the diet, prey selection, foraging habitat selection, and feeding behaviour of wintering Dunlins, and interpret this information in the light of the current knowledge on the feeding ecology of this species.

**Location:** The study was carried out in the sediment flats of the Tagus estuary, Portugal, which is the largest estuary in Iberia, and harbours large numbers of wintering waders.

**Methods:** Diet of Dunlin was investigated using dropping analysis. Foraging habitat selection was studied using bird counts and behavioural observations, in sectors located on different types of sediment. The abundance of invertebrates in the sediment was sampled to evaluate prey availability and to interpret patterns of habitat selection by the birds.

**Results:** Scrobicularid bivalves and the gastropod *Hydrobia ulvae* were the most consumed prey items, followed by the isopod *Cyathura carinata* and insects. Prey species with higher biomass, such as *Hediste diversicolor* and Scrobicularid bivalves were preferred. The smallest and largest sizes of some important prey species were avoided. Dunlins showed a clear preference to forage in muddy, rather than sandy, sediments. Overall pecking rates were similar in all types of sediment, but deep probes were more frequent in softer mud.

**Conclusions:** Some of the staple preys of Dunlin in Tagus estuary are also abundantly consumed in northern latitudes. However, other prey species important in northern Europe are here replaced by similar and locally common species. In the Tagus estuary, Dunlins feed upon a broad spectrum of invertebrate species, but show clear patterns of selection of prey species and sizes. Dunlins prefer to forage on muddy substrates, probably because their main prey are more abundant and accessible here than in harder, sandier, substrates.

*Key words:* *Calidris alpina*; diet; feeding behaviour; invertebrates; prey selection; sediment type; Tagus estuary

RESUMEN.—*Ecología alimentaria del Correlimos Común Calidris alpina en un estuario del sur de Europa.*

**Objetivos:** La ecología alimentaria del Correlimos Común, *Calidris alpina*, durante el invierno está poco estudiada. El objetivo de este trabajo es describir la dieta, la selección de presa, la selección del hábitat de alimentación y el comportamiento de alimentación del Correlimos Común durante el invierno, e interpretar esta información a la luz del conocimiento actual de la ecología alimentaria de la especie.

**Área de estudio:** El estudio se llevó a cabo en el estuario del Tajo en Portugal, el cual es el más grande de Iberia y acoge un gran número de limícolas invernantes.

**Métodos:** La dieta se investigó a partir del análisis de heces. La selección de hábitat se estudió a partir de censos de aves y observaciones del comportamiento en sectores con tipos diferentes de sedimento. Se muestreó la abundancia de invertebrados en el sedimento para evaluar la disponibilidad de presas e interpretar los patrones de selección de hábitat.

**Resultados:** Las presas más consumidas fueron bivalvos escrobicularidos y el gasterópodo *Hydrobia ulvae* seguido del isópodo *Cyathura carinata* e insectos. Las presas con mayor biomasa tales como *Hedis-*

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*te diversicolor* y los bivalvos escrobicularidos fueron las presas preferidas. No fueron consumidas tanto las presas más pequeñas como las mayores de algunas de las presas más importantes. Los correlimos mostraron una clara preferencia por utilizar como lugares de alimentación los sedimentos fangosos en lugar de los sedimentos arenosos. Las tasas de picoteo fueron similares en todos los tipos de sedimentos, pero los sondeos profundos fueron más frecuentes en el fango.

**Conclusiones:** Algunas de las presas que el Correlimos Común ingiere en el estuario del Tajo las consume abundantemente en latitudes septentrionales. Sin embargo, otras presas que son importantes en el norte de Europa son reemplazadas en el estuario del Tajo por otras similares y que son más comunes aquí. En el estuario del Tajo el Correlimos Común se alimenta de un amplio espectro de especies de invertebrados aunque muestra un claro patrón de selección de especies y tamaños. El Correlimos Común prefiere como lugares de alimentación los substratos fangosos, probablemente debido a que su presa principal es más abundante y accesible en ellos que en los substratos más duros o arenosos.

*Palabras clave:* *Calidris alpina*, comportamiento de alimentación, dieta, estuario del Tajo, selección de presa, tipo de sedimento.

## INTRODUCTION

The Dunlin, *Calidris alpina*, is the most abundant wader within the East Atlantic Flyway, with an overall population of more than 2 million individuals (Smit & Piersma, 1989). During the non-breeding season this population is distributed along the coastline from West Africa to northwest Europe (Cramp & Simmons, 1983). Hockey *et al.*, 1992 demonstrated that density of waders during the non-breeding season increases from northern to southern latitudes. The reason for this phenomenon has been discussed but is still poorly understood (*e.g.* Zwarts *et al.*, 1990; Hockey *et al.*, 1992). Since waders are often limited by their food resources (*e.g.* Desholm, 2000), it might be expected invertebrates would to show similar gradients. However, latitudinal gradients on invertebrate assemblages are much less obvious. Existing evidence indicates enormous variation in the density, biomass, availability and annual production of invertebrates at different latitudes (*e.g.* Warwick & Ruswahyuni, 1987; Kalejta & Hockey, 1991; Piersma *et al.*, 1993). Nevertheless, the existent knowledge is unbalanced along the latitudinal gradient since most of tropical and sub-tropical areas are almost unknown. Also, the majority of the invertebrate studies are not focused on evaluat-

ing food supply for the birds, providing only rough measurements of invertebrate availability, such as overall biomass or density.

The feeding ecology of wader species is also not well studied along their non-breeding distributions. In the case of the Dunlin most studies on the feeding ecology have been conducted on the European north Atlantic coast (*e.g.* Worrall, 1984; Kelsey & Hassall, 1989; Le V. Dit Durell & Kelly, 1990; Mouritsen & Jensen, 1992; Nehls & Tiedemann, 1993; Mouritsen, 1994; Dierschke *et al.*, 1999). Conversely, there are only a few studies about this species in the southern European and African coasts. In fact, only two studies were found on the feeding ecology of Dunlin in this region (namely, Barbosa, 1996 and Lopes *et al.*, 1998). The lack of information on feeding ecology of waders and on their food resources in the southern region of their wintering distributions is still limiting the comprehension of the amazing migration of waders.

In this study the feeding ecology of Dunlin in the Tagus estuary (Portugal) during the winter was examined. The Tagus estuary is one of the largest European wetlands and harbours a regular winter population over 14,000 Dunlins. Diet, prey selection, habitat selection and feeding behaviour were analysed and this information was interpreted in light of the current knowledge on the feeding ecology of this species.

## MATERIAL AND METHODS

### *Study area*

Field-work was carried out in the southern margin of the Tagus estuary, Portugal (38°45'N, 8°59'W) in the winter of 2000/2001. The study site was a 2.3 km long stretch of tidal flats, gradually changing from sand at the western end, to mud at the east. During the spring tides (amplitude > 2.7 m), these tidal flats remain exposed for approximately three hours. Such areas are particularly important for foraging Dunlins, supporting some of the highest densities in the whole estuary (Moreira, 1995; Rosa *et al.*, 2003).

Three 1.5 ha (100x150m) plots were marked using stakes in each of the sediment types available: sand, mixed sediments and mud. The classification of sediments was based on the analysis of six sediment samples collected in each of the nine plots (laboratory procedures followed Buchanan, 1984). Mean ( $\pm$ SD) percentage of weight of silt (particles < 0.063 mm) was  $7.1 \pm 4.8$  ( $n = 18$ ),  $24.4 \pm 8.2$  ( $n = 18$ ), and  $79.1 \pm 24.7$  ( $n = 18$ ) for sand, mixed sediments and mud, respectively.

### *Invertebrate sampling*

The composition and abundance of the invertebrate fauna was determined from three to six sediment cores (86.6 cm<sup>2</sup>, 30 cm deep) taken randomly in each plot in January 2001. The upper 5 cm of the cores was separated and sieved through a 0.5 mm mesh, and the remaining fraction was sieved through a 1 mm mesh. All invertebrates were separated from the sediment and stored in 70% alcohol.

Specimens in good condition were measured using a calliper or a stereomicroscope with a reticular eyepiece. Small worm species, less than 10 mm long, were not measured. Regression analysis was used to relate size and ash free dry weight (AFDW). These relation-

ships were constructed for *Hydrobia ulvae* and small scrobicularids (*Scrobicularia plana* and *Abra* sp. were pooled) using individuals collected in the study plots. For the remaining species, relationships available in the literature were used (see Table 1). To measure AFDW for small scrobicularids and *H. ulvae*, the specimens were grouped into size classes, dried to constant weight (48 h at 60°C) and then incinerated in a muffle furnace (2 h at 500°C). The samples were weighed after drying and again after incineration, and the AFDW was calculated as the difference between dry weight and ash weight. The shells of the bivalves were removed before drying. *H. ulvae* was incinerated with shell, but 12.5% was subtracted from the AFDW, which were assumed to approximately represent the organic fraction of the shell (Dekker, 1979). The average AFDW was also determined for some abundant small worm species, namely for *Alkmaria ramniji*, *Tharyx* sp., *Streblospio shrubsolli*, Oligoqueta and Nematoda. A considerable number of individuals (over 40) of each species were grouped in 1 to 3 samples and processed as described above, to determine the individual AFDW.

The AFDW per m<sup>2</sup> was calculated by multiplying the mean density of each species by its mean AFDW, obtained directly (for small worms) or estimated from the size (for all other species).

### *Dropping analysis*

One hundred droppings (separated in individual vials) were collected monthly between January and March 2001 from the eastern side of the study area. The collection was carried out during the rising tide, when the birds were concentrated close to the coast. Bird flocks were observed for at least 30 min. prior to the collection of droppings, to reduce the possibility of collecting droppings with remains coming from outside of the study area. Flocks were then followed at a short distance, and only fresh

TABLE 1

Equations used to estimate the size and the ash free dry weight of invertebrate species. APL: antero-posterior length (mm); TL: total length (mm); TW: total width (mm); CL: cephalic length (mm); CTL: cardinal tooth length (mm); ML: mandible length (mm); AFDW: ash free dry weight (mg). <sup>1</sup> Equation used for both *Abra* sp. and small *S. plana*. <sup>2</sup> Equation used for large *S. plana*. [a] present study; [b] Masero *et al.* (1999); [c] Zwarts & Blomert (1992); [d] Zwarts & Wanink (1993); [e] Marques *et al.* (1994).

[Ecuaciones utilizadas para estimar el tamaño y el peso seco libre de cenizas de las especies de invertebrados. APL: longitud antero-posterior (mm); TL: longitud total (mm); TW: anchura total (mm); CL: longitud cefálica (mm); CTL: longitud del diente cardinal (mm); ML: longitud de la mandíbula (mm); AFDW: peso seco libre de cenizas (mg). <sup>1</sup>Ecuación utilizada para *Abra* sp. y *S. plana* pequeños. <sup>2</sup> Ecuación utilizada para *S. plana* grandes. [a] este estudio; [b] Masero *et al.* (1999); [c] Zwarts & Blomert (1992); [d] Zwarts & Wanink (1993); [e] Marques *et al.* (1994).

Species [Especie]	Equation [Ecuación]	Explained variance [Varianza Explicada]	Sample size [Tamaño de muestra]	Range [Rango]	Source [Fuente]
<i>Scrobicularia plana/Abra</i> sp.	APL=22.94CTL+0.40	0.98	60	1.9-19.3	[a]
<i>Hydrobia ulvae</i>	TL=2.35TW-0.34	0.96	134	0.5-2.6	[a]
<i>Hediste diversicolor</i>	TL=40.173ML-3.4225	0.98	41	25-95	[b]
<i>Scrobicularia plana/Abra</i> sp. <sup>1</sup>	AFDW=0.013APL <sup>2,23</sup>	0.97	17	0.5-13	[a]
<i>Scrobicularia plana</i> <sup>2</sup>	AFDW=0.008APL <sup>2,87</sup>	>0.995	158	12-45	[c]
<i>Cerastoderma edule</i>	AFDW=0.012APL <sup>2,97</sup>	>0.995	1351	1-42	[c]
<i>Hydrobia ulvae</i>	AFDW=0.0154TL <sup>2,61</sup>	0.92	28	1.75-5.25	[a]
<i>Corophium volutator</i>	LnAFDW=2.8lnTL-5.244	0.994	526	2-10	[d]
<i>Cyathura carinata</i>	AFDW=19.0549CL <sup>2,71815</sup>	0.964	800	1-12	[e]
<i>Hediste diversicolor</i>	LnAFDW=2.208lnTL/10-0.898	0.996	3586	10-130	[d]
<i>Nephtys hombergii</i>	LnAFDW=2.017lnTL/10-0.183	0.962	263	20-120	[d]

droppings were collected. The shape of the droppings and the footprints around them helped us to separate between the droppings produced by Dunlins and by other species. Only 2% of the birds present in the area were small waders that produce droppings that can be confused with those of Dunlins.

Pellets were never found in the study area, so the diet analysis was based on the frequency of occurrence of prey in droppings. Although this procedure may result in an underestimation of prey types that leave few identifiable remains in the faeces, it is the most widely used technique for dietary analysis in waders. In any case, most of the invertebrates available in the study area are known to leave detectable

remains in the droppings (see Le V. Dit Durell & Kelly, 1990: Table 1).

Droppings were examined with a stereomicroscope, and prey species were identified using all possible diagnostic remains such as shell fragments, mandibles, exoskeletons, and acicules. A sub-sample of each dropping was examined under a microscope (at 400x magnification) to search for polychaete setae, which were subsequently identified using a reference collection and published literature (*e.g.* Fauvel, 1977; Ramberg & Schram, 1982; Chambers & Garwood, 1992).

The setae and acicules of annelids and hairs of insects found in microscopic analysis were used to record the presence of the item in the

diet, but were not used in calculations of the frequency of occurrence. As these structures are particularly numerous, it is likely that remains of one prey will be released in the faeces for a long period, resulting in an overestimation of its occurrence.

Invertebrate size and AFDW were estimated from the size of some remains found in the droppings (cardinal tooth of scrobicularids, shells of *H. ulvae* and mandibles of *Hediste diversicolor*) by using the relationships shown in Table 1. The sizes of ingested *H. ulvae* were measured directly, in the case of intact shells, or estimated from the width of partially broken shells.

Due to the difficulties in distinguishing the remains of *S. plana* from *Abra* sp., these species were grouped in a single diet item, referred hereafter as *S. plana/Abra* sp.

### Prey selection

Prey type and size selection were determined by comparing results of the analysis of droppings with the abundance and size of invertebrates found in sediment cores.

Densities of feeding Dunlins differed among the study plots. Therefore, the invertebrate sampling were stratified according to bird density, to ensure that invertebrate abundances used for comparison were representative of what was used by birds within the study area. A subset of cores was randomly selected such that the total number of cores *per* sediment type was proportional to bird abundance. This procedure assumes that droppings collected from the eastern side of the study area result from feeding activity over the entire study area. Observations of flock movements during the study confirm that this assumption was valid.

Prey type selection was determined using the Manly-Chesson preference index (Chesson, 1983), described as,

$$\alpha_i = \frac{r_i/p_i}{\sum_{j=1}^m r_j/p_j}, \quad i = 1, \dots, m,$$

where  $\alpha_i$  is the preference for prey *i* when *m* prey are available,  $r_i$  is the relative abundance of prey *i* in diet, and  $p_i$  is the relative abundance of prey *i* in sediment. This preference index varies between 1, if the diet consists entirely of one food item, and 0, if the food item is absent from the diet. Values of  $\alpha > 1/m$  indicate positive selection and  $\alpha < 1/m$  indicate negative selection. This index considers only relative abundances of prey species, so it is possible to compare the abundance of invertebrates in the sediment assessed by sediment samples with the prey abundance in diet obtained from dropping analysis. Differences from null selection ( $\alpha = 1/m$ ) were tested following Manly (1974). This procedure involves the estimation of the variance and the calculation of the statistic (*G*) (defined as the difference between the obtained value of  $\alpha$  and the hypothesized  $\alpha$  for null selection, divided by the standard deviation). This statistic is then tested against a standard normal distribution. The frequency of occurrence was used as a descriptor of the abundance of invertebrate species, both in the sediment and in the diet. Droppings collected between January and March were grouped, to perform the analysis of prey type selection, in order to increase the statistical power of the comparisons. This analysis did not cover species that do not leave detectable remains in droppings or that could only be detected by the presence of setae or acicules. Nematodes, nemertini, oligochaetes, large bivalves (> 13 mm), and several polychaete species were therefore excluded. The presence of insects in the diet, together with the absence of insects in intertidal sediments, may indicate that insect remains were probably retained for a long time in the digestive tract of the birds, so these prey were also excluded from the analysis. Size selection was performed only for the two main prey types, *S. plana/Abra* sp. and *H. ulvae*, because there was no sufficient data for the other prey species. Only droppings collected in January were used in this analysis.

TABLE 2

Density (individuals *per* m<sup>2</sup>± SE), size (± SE, in mm), and ash free dry weight (AFDW - g *per* m<sup>2</sup>) of invertebrates found in the study plots (sample size in parentheses). Densities in the three sediment types were compared with a Kruskal-Wallis test (ns: non-significant; \**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001), followed by a Dunn test (superscript with identical letters indicates non-significant difference at *P* > 0.05). # Individuals with broken shells were excluded.

[Densidad (individuos *por* m<sup>2</sup>± SE), tamaño (± SE, en mm), y peso seco libre de cenizas (AFDW - g *por* m<sup>2</sup>) de los invertebrados encontrados en los puntos de muestreo (tamaño de muestra entre paréntesis). Densidades en los tres tipos de sedimento comparados con un test de Kruskal-Wallis (ns: no significativo, \**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001), seguido por un test de Dunn (letras iguales en el superíndice indica que no hay diferencias significativas, *P* > 0.05). # Los individuos con las conchas rotas fueron excluidos].

Species [Especie]	Density [Densidad]					Size [Tamaño] AFDW	
	Sand [Arena] (n = 16)	Mixed [Mezcla] (n = 13)	Mud [Fango] (n = 17)	H	Total (n = 46)		
<b>Mollusca</b>							
<i>Abra</i> sp.	150±65	231±88	72±23	1.0 ns	146±35	2.1±0.2(26)	0.01
<i>Cerastoderma edule</i>	41±18	9±9	7±7	4.3 ns	20±7	19.4±4.9(6)	3.08
<i>Scrobicularia plana</i>	102±25 <sup>a</sup>	195±30 <sup>ab</sup>	332±58 <sup>b</sup>	13.6**	208±28	27.1±2.3(53)	-
<i>S. plana</i> <13 mm <sup>#</sup>	61±18	62±21	144±45	2.2 ns	90±19	8.9±0.6(24)	0.17
<i>S. plana</i> >13 mm <sup>#</sup>	20±15	98±22 <sup>a</sup>	144±26 <sup>a</sup>	14.5***	85±15	42.2±0.5(29)	31.94
<i>Hydrobia ulvae</i>	9633±3750	1688±454	1516±272	2.1 ns	4564±1449	1.5±0.04(333)	0.35
<b>Crustacea</b>							
<i>Corophium volutator</i>	14±10	44±21	14±10	2.4 ns	23±8	4.0±0.8(4)	0.01
<i>Cyathura carinata</i>	313±57 <sup>a</sup>	249±60 <sup>a</sup>	72±31	14.3***	211±32	8.5±0.6(34)	1.65
<b>Polychaeta</b>							
<i>Alkmaria ramniji</i>	7±7 <sup>a</sup>	418±158 <sup>b</sup>	188±110 <sup>ab</sup>	14.5***	186±63	-	0.003
<i>Capitela capitata</i>	231±100 <sup>a</sup>	62±38 <sup>ab</sup>	0 <sup>b</sup>	11.7**	103±40	-	-
<i>Glycera tridactyla</i>	27±13 <sup>a</sup>	0 <sup>a</sup>	0 <sup>a</sup>	7.3*	10±5	-	-
<i>Hediste diversicolor</i>	34±17	9±9	0	4.9 ns	15±7	32.9±21.2(4)	0.24
<i>Nephtys hombergii</i>	14±10	9±9	14±10	0.2 ns	13±5	49.3±12.2(4)	0.31
<i>Polydora ciliata</i>	7±7	44±16	36±20	4.4 ns	28±9	-	-
<i>Pygospio elegans</i>	618±248 <sup>a</sup>	98±39 <sup>ab</sup>	29±22 <sup>b</sup>	11.3**	266±97	-	0.003
<i>Streblospio shrubsolli</i>	8825±2316 <sup>a</sup>	9701±2147 <sup>a</sup>	3183±830	13.6**	7110±1132	-	0.08
<i>Tharyx</i> sp.	414±209 <sup>a</sup>	3749±707	917±379 <sup>a</sup>	19.3***	1532±324	-	0.07
Nemertini	0	0	36±22	5.9 ns	13±8	-	-
Nematoda	679±189	18±18 <sup>a</sup>	7±7 <sup>a</sup>	27.4***	259±82	-	0.0003
Oligoqueta	245±112	1954±578 <sup>a</sup>	729±159 <sup>a</sup>	14.6***	896±201	-	0.01

### *Bird counts and feeding behaviour*

Dunlins feeding in the plots were counted twice a month (during the spring tides) between November 2000 and April 2001. To control for potential tidal variation in the number of birds present within the plots (see Burger *et al.*, 1977; Nehls & Tiedemann, 1993), the counting period ( $\pm 1$  h from the low tide) was divided into three equal sub-intervals. Each plot was counted preferentially only once within one of different sub-intervals, in each counting day. In each month all plots were counted at least twice in each sub-interval.

The pecking rate of feeding Dunlins was recorded during 1 minute intervals in all types of sediment, using a 20-60x telescope. Pecks were assigned to three classes according to the penetration of the bill in the sediment: superficial pecks (bill inserted *ca.* 0-1 cm into the sediment), median probes (half bill inserted; *ca.* 1-2 cm) and deep probes (whole bill inserted; *ca.* 2-3 cm). Stitching behaviour was rarely observed and so it was not considered in the analysis. To minimize the possibility of sampling the same individuals more than once, each plot was only visited once in the same day and no more than 8 individuals were observed in each plot, each day. All birds observed within the same plot were chosen ensuring a minimal distance of 20 m from the previously observed bird, or moving the field of vision of the telescope in the opposite direction of the flock movement.

Means are presented  $\pm$  SE and statistical procedures followed Sokal & Rolf (1995)

## RESULTS

### *Invertebrate abundance*

The invertebrate fauna was numerically dominated by three species: the gastropod *H. ulvae*, and the polychaetes *S. shrubsolli* and *Tharyx* sp. However, these species only con-

tributed 1% to the overall invertebrate biomass (AFDW, Table 2). There were also a few other species that were very scarce in the study area (occurring in densities  $< 100$  individuals *per m*<sup>2</sup>) that contributed virtually nothing in terms of biomass. Large individuals of *S. plana*, ranging 35-50 mm, clearly dominated the assemblage in terms of biomass, representing *ca.* 85% of the overall AFDW.

Different assemblages were found in the three studied types of sediment. *S. plana* and oligochaetes tended to be more abundant in muddy sediments, whereas nematods, *Capitela capitata*, *Pygospio elegans*, *Cyathura carinata* and *S. shrubsolli* were more abundant in sandy sediments (Table 2).

### *Diet composition*

Nine different preys were found in droppings during the winter (Table 3). The bivalves *S. plana/Abra* sp., and the gastropod *H. ulvae* were the most frequently consumed prey, but the isopod *C. carinata* and insects were also regularly found in droppings. Five species of annelids were detected, but were not quantified in importance (in terms of frequency of occurrence) of some of those, because only setae were found (see methods).

The sizes of ingested prey were determined only for *S. plana/Abra* sp., *H. ulvae*, and *H. diversicolor* due to the absence of measurable structures for the other prey (Table 3). Studies with Knot *Calidris canutus* demonstrated that small shells of *H. ulvae* remain undamaged after digestion more often than larger ones, thus creating a bias on the size estimated from droppings (Zwarts & Blomert, 1992; Dekinga & Piersma, 1993). However, in this study, no significant difference was found between the size of intact shells and the size estimated from partially broken shells (Mann-Whitney test,  $U = 5183$ ,  $P = 0.61$ , 137 broken shells and 79 intact shells), which indicates that in this case the digestion was not size selective.

TABLE 3

Winter diet of Dunlins. Frequency of occurrence was calculated as the % of droppings with prey present ( $n = 244$  droppings). Mean size ( $\pm$  SE, range in parentheses, in mm), and the corresponding ash free dry weight (AFDW) (in mg) are indicated for species that could be measured. Droppings without any identifiable prey (ca. 19%) were excluded.

[Dieta del Correlimos Común durante el invierno. La frecuencia de aparición se calculó como el porcentaje de heces con presas ( $n = 244$  heces). El tamaño medio ( $\pm$  SE, rango en paréntesis en mm), y el peso seco libre de cenizas correspondiente (AFDW) (en mg) se indican en las especies en las que se pudo medir. Se excluyeron las heces sin ninguna presa identificable (ca. 19%).]

Prey [Presas]	Frequency occurrence [Frecuencia de aparición]	Size [Tamaño]	AFDW
Mollusca			
<i>Hydrobia ulvae</i>	39.3	1.8 $\pm$ 0.03 (0.8-3.4); $n = 216$	0.07
<i>Scrobicularia plana</i> /Abra sp.	49.6	7.1 $\pm$ 0.1 (2.3-12.4); $n = 169$	1.03
Crustacea			
<i>Cyathura carinata</i>	26.2	-	-
Polychaeta			
<i>Hediste diversicolor</i>	5.3	37.8 $\pm$ 3.2 (9.1-66.4); $n = 34$	7.68
<i>Nephtys hombergii</i>	0.8	-	-
<i>Polydora ciliata</i>	Present	-	-
<i>Streblospio shrubsolii</i>	Present	-	-
Oligoqueta	Present	-	-
Insects	23.4	-	-
Non-identified.	2.9	-	-

### Prey selection

Among the invertebrates taken by Dunlins, *S. plana*/Abra sp. and *H. diversicolor* are the preferred prey while *H. ulvae*, and *C. carinata* show lower values of selectivity (Table 4).

Only a narrow range of the available sizes of *S. plana*/Abra sp. were consumed by Dunlins. In fact, the size of the shells found in the sediment and in the diet was significantly different (Mann-Whitney test,  $U = 1140$ ,  $P < 0.05$ ,  $n = 74$  for sediment and 40 for droppings). Dunlins preferred specimens ranging 4-10 mm and avoided both smaller and larger individuals (Fig. 1). Roughly the same pattern of selection was observed

in *H. ulvae* (Mann-Whitney test,  $U = 15685$ ,  $P < 0.001$ ,  $n = 333$  for sediment and 163 for droppings). Nevertheless, *H. ulvae* larger than 3 mm were not abundant in the sediment.

### Dunlin distribution and feeding behaviour

The densities of feeding Dunlins were higher in muddy sediments ( $16.0 \pm 1.6$  birds/ha,  $n = 101$ ), followed by mixed sediments ( $9.8 \pm 0.8$  birds/ha,  $n = 119$ ), and sandy sediments ( $2.3 \pm 0.3$  birds/ha,  $n = 106$ ). Densities of birds on muddy and sandy sediments showed roughly the same temporal pattern (Fig. 2), but there

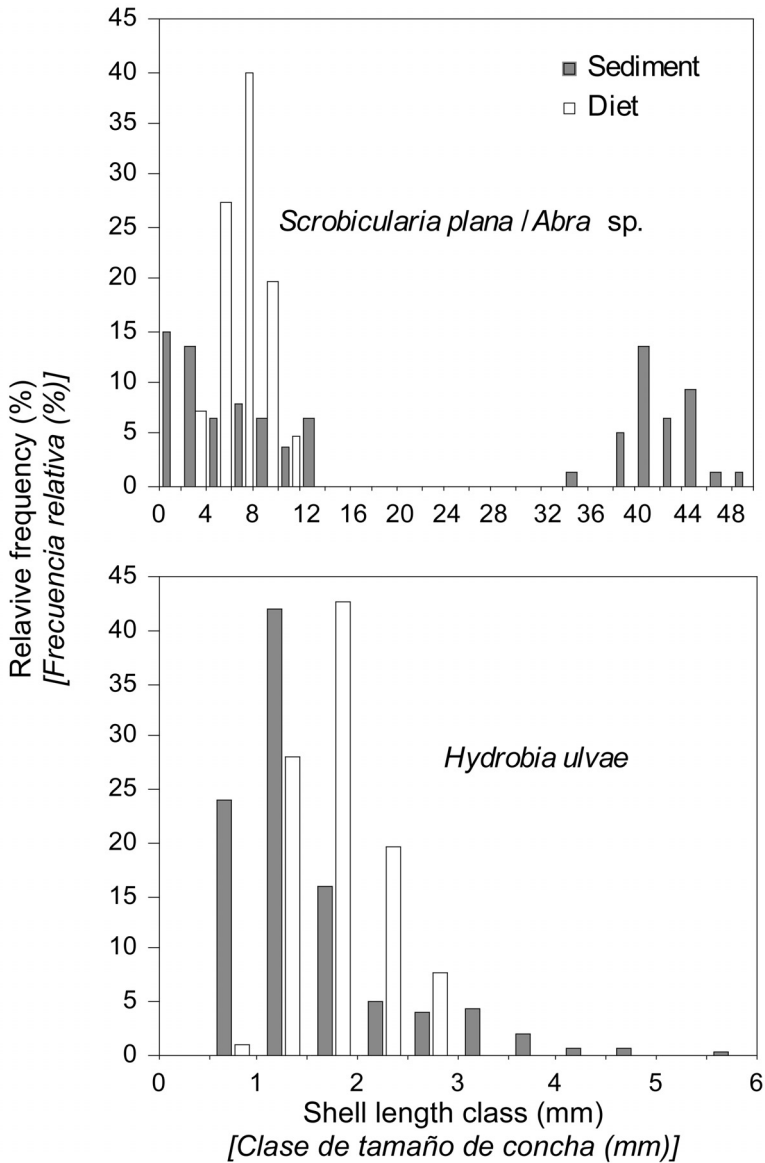


FIG. 1.—Size frequency distribution of *Scrobicularia plana/Abra sp.* and *Hydrobia ulvae* found in the sediment and in the droppings of Dunlin. Only the droppings collected in January were used. Sample size: *S. plana/Abra sp.*,  $n = 74$  in sediment,  $n = 40$  in droppings; *H. ulvae*  $n = 333$  in sediment,  $n = 163$  in droppings.

[Distribución de frecuencias del tamaño de *Scrobicularia plana/Abra sp.* y *Hydrobia ulvae* encontrados en el sedimento y en las heces del Correlimos Común. Sólo se utilizaron las heces recolectadas en enero. Tamaño de muestra *S. plana/Abra sp.*,  $n = 74$  en el sedimento,  $n = 40$  en las heces; *H. ulvae*  $n = 333$  en el sedimento,  $n = 163$  en las heces.]

TABLE 4

Prey selection by Dunlins. Abundance of prey in sediment and in diet is represented by frequencies of occurrence (% of samples with the prey present). Selection is represented as  $\alpha - 1/m$ , such that 0 represents null selection, negative values indicate negative selection, and positive values indicate positive selection (see methods). The values of  $\alpha$  were compared with the expected value for null selection using the G statistic (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ). Large *Scrobicularia plana* (> 13 mm) present in sediment samples were excluded.

[Selección de presas por el Correlimos Común. La abundancia de presas en el sedimento y en la dieta se representa por la frecuencia de aparición (% de muestras con presas presentes). La selección se representa como  $\alpha - 1/m$ , de forma que 0 representa una selección nula, valores negativos indican selección negativa y valores positivos indican selección positiva (ver métodos). Los valores de  $\alpha$  se compararon con el valor esperado para la selección nula utilizando el estadístico G (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ). Las *Scrobicularia plana* grandes (> 13 mm) presentes en el sedimento fueron excluidas].

Prey [Presas]	Sediment [Sedimento] (n = 29)	Diet [Dieta] (n = 244)	Selection [Selección]	G
Mollusca				
<i>Scrobicularia plana</i> /Abra sp.	75.9	49.6	0.170	5.3***
<i>Hydrobia ulvae</i>	100	39.3	0.045	2.1*
Crustacea				
<i>Corophium volutator</i>	17.2	0	-0.143	-
<i>Cyathura carinata</i>	58.6	26.2	0.071	2.6**
Polychaeta				
<i>Glycera tridactyla</i>	3.4	0	-0.143	-
<i>Hediste diversicolor</i>	10.3	5.3	0.104	2.0*
<i>Nephtys hombergii</i>	10.3	0.8	-0.105	-

was an increase on the relative importance of mixed sediments during March and April (Fig. 2). In fact, there were significant differences among months in the densities of birds, sediment types and their interaction (Repeated measures ANOVA with sediment type as independent factor; month effects,  $F_{5,20} = 6.9$ ,  $P < 0.001$ ; sediment effects,  $F_{2,4} = 58.5$ ,  $P < 0.01$ ; interaction effects,  $F_{10,20} = 2.5$ ,  $P = 0.04$ ; counts made on the same month were pooled).

The pecking rate was similar in all sediment types (Kruskal-Wallis test,  $H = 0.33$ ,  $P = 0.85$ ;  $n = 119, 140, 111$  for sand, mixed sediments and mud, respectively; overall mean,  $37.0 \pm 26.3$  pecks.min<sup>-1</sup>). However, there were significant differences among sediment types in the rate of superficial pecks, median probes

and deep probes (Kruskal-Wallis test; superficial pecks  $H = 29.9$ ,  $P < 0.0001$ ; median probes  $H = 82.1$ ,  $P < 0.0001$ ; deep probes  $H = 180.7$ ,  $P < 0.0001$ ). In sandy substrate, almost all pecks were superficial, while in mixed and muddy sediments a substantial part of the pecks were median or deep probes (Fig. 3).

## DISCUSSION

### Diet composition

The species *H. ulvae* and *H. diversicolor* have been reported as the main prey of Dunlin along the east Atlantic coast (Davidson, 1971; Fuchs, 1975; Goss-Custard *et al.*, 1977; Wor-

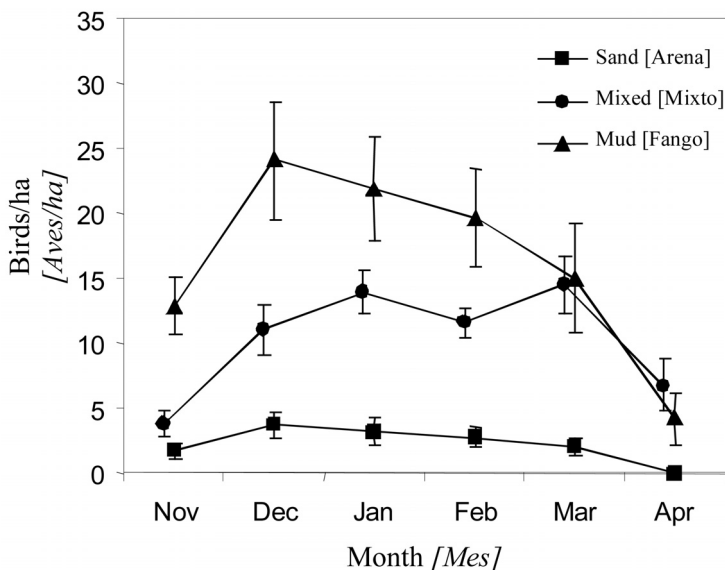


FIG. 2.—Phenology of Dunlin in the three sediment types. Symbols represent mean densities and vertical lines their SE.  $n = 18$  except for a few samples of November (mud = 16, mixed = 26) and December (mud = 13, mixed = 21, sand = 16).

[Fenología del Correlimos Común en los tres tipos de sedimentos. Los símbolos representan las densidades medias y las líneas verticales su SE.  $N = 18$  excepto para algunas muestras de noviembre (fango = 16, mezcla = 26) y diciembre (fango = 13, mezcla = 21, arena = 16).]

rall, 1984; Le V. Dit Durell & Kelly, 1990; Mouritsen, 1994; Lopes *et al.*, 1998; Luís, 1998; Dierschke *et al.*, 1999) and were also frequently taken by Dunlins in the Tagus estuary. The consumption of these preys across this latitudinal range is probably related with their wide distribution and not with a selective feeding behaviour of the birds. Other invertebrate species frequently consumed by Dunlins in northern Europe, like *Macoma balthica* and *Corophium volutator* (Davidson, 1971; Goss-Custard *et al.*, 1977; Worrall, 1984; Le V. Dit Durell & Kelly, 1990; Mouritsen, 1994; Dierschke *et al.*, 1999), are almost absent in south Europe, so they are replaced in the diet by species more common in southern latitudes such as *S. plana/Abra* sp. and *C. carinata* (Moreira, 1995; Lopes *et al.*, 1998; present study). Spionids, oligochaetes, *Nephtys* spp. and insects have also been reported in the Dunlin diet elsewhere (Fuchs, 1975;

Goss-Custard *et al.*, 1977; Lifjeld, 1983; Worrall, 1984; Le V. Dit Durell & Kelly, 1990; Mouritsen, 1994; Lopes *et al.*, 1998; Luís, 1998; Dierschke *et al.*, 1999).

The individuals of *S. plana/Abra* sp. consumed by Dunlins in the Tagus estuary were much larger than the *M. balthica* consumed in the Severn estuary (Worrall, 1984). In fact, the maximum size of *M. balthica* consumed by Dunlins in the Severn estuary was 7-8 mm (Worrall, 1984), whereas in Tagus estuary it was observed the consumption of 12 mm *S. plana/Abra* sp. The shells of juvenile *S. plana* are very fragile, and thus it is believed that these large individuals were probably *S. plana* that were smashed prior to ingestion. The consumption of *H. diversicolor* about 1.5 times larger than those preyed upon in northern Europe was also seen (Goss-Custard *et al.*, 1977; Worrall, 1984; Dierschke *et al.*, 1999). In contrast, the

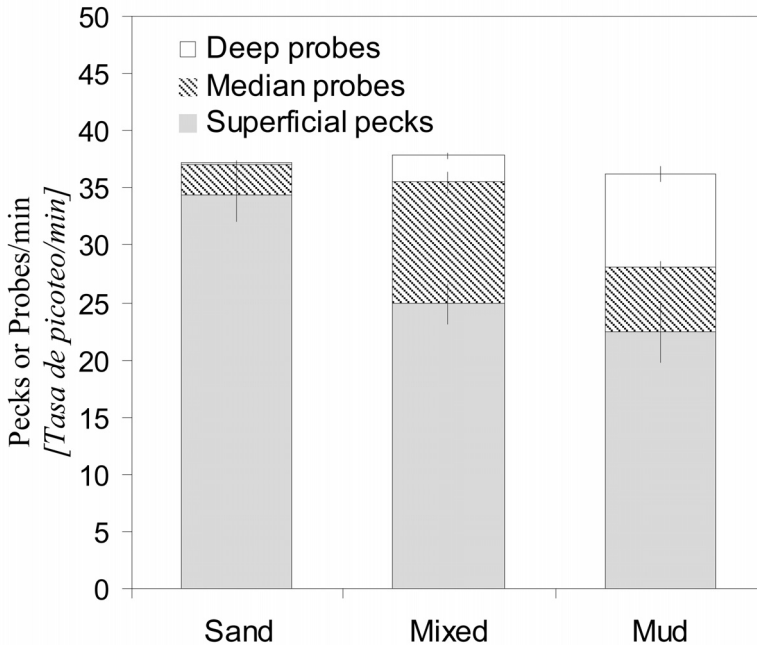


FIG. 3.—Pecking rate of Dunlin, separated by classes of peck depth, in the three sediment types. Values represent mean  $\pm$  SE of 119 observations for sand, 140 for mixed and 111 for mud.

[Tasa de picoteo del Correlimos Común separada por la profundidad del picoteo en cada uno de los tres tipos de sedimentos. Los valores muestran la media  $\pm$  SE de 119 observaciones en arena, 140 en mezcla y 111 en fango.]

individuals of *H. ulvae* consumed by Dunlins in the Tagus estuary were about 1.5 times smaller than those consumed in northern Europe (Goss-Custard *et al.*, 1977; Worrall, 1984). The consumption of relatively small *H. ulvae* has also been reported from Mondego estuary, Portugal (Lopes *et al.*, 1998). However, these north-south differences could be related with different availabilities on the invertebrate sizes between the places compared, and not with different feeding behaviour.

#### Prey selection

In the Tagus estuary, Dunlins feed upon a broad spectrum of invertebrate species, but following clear patterns of selection of prey

species and of prey size. The most preferred preys were those with higher biomass, such as *H. diversicolor* and *S. plana/Abra* sp. Small-sized invertebrate species and the smallest individuals of some important prey species were avoided. Previous studies demonstrated that the smallest sizes of *H. diversicolor* (Worrall, 1984; Dierschke *et al.*, 1999), *M. balthica* and *H. ulvae* (Worrall, 1984) were rarely taken by Dunlins, despite their abundance in foraging areas.

These results indicate that the lower limit of the prey size differs between preys and is probably established by their profitability. In fact, Dunlins seem to ignore small *S. plana/Abra* sp. that has the size of preyed *H. ulvae* (Fig. 1). It is believed that *H. ulvae* is more profitable than *S. plana/Abra* sp. of the same size because their

availability on the surface of the sediment allows birds to take them at a high rate.

The absence of *S. plana* larger than 13 mm in the diet of Dunlins is explained by an inability to swallow such large specimens. However, Dunlins are likely to consume siphons of large *S. plana*. These invertebrates are very abundant in the study area and siphon cropping seems to be a common feeding behaviour in other waders (Zwarts, 1986; Moreira, 1995). However, siphons do not leave identifiable remains in droppings, so the importance of *S. plana* is probably underestimated by this analysis.

#### *Habitat use*

In this study it was observed that Dunlins prefer muddy sediments as feeding areas during the winter, which agrees with observations made by other authors for the Tagus estuary (e.g. Granadeiro *et al.*, 2004) and for several locations in eastern north Atlantic coast (e.g. Wadden Sea, in the Netherlands, and The Wash, in England; Kelsey & Hassall, 1989; Nehls & Tiedemann, 1993). Nevertheless, there are some geographical and seasonal variations on the habitat preference of Dunlins. The winter densities of Dunlins in Banc d'Arguin (Mauritania) were similar on both sandflats and mudflats (Zwarts *et al.*, 1990). In the Wadden Sea, Dunlins prefer muddy substrates in winter and spring but appear to have no clear preference in summer and autumn (Nehls & Tiedemann, 1993). Moreira (1995) also observed seasonal variation in habitat selection of Dunlins in the Tagus estuary. Given that Dunlins are generalist, it is likely that they change their feeding habitat in response to different conditions of accessibility, availability, and profitability of invertebrates.

The observed preference for muddy substrates in the study area is probably related to two factors: prey abundance and prey detectability. In fact, *S. plana* is not only more abundant in muddy substrates but is probably also more

easily detected there than in harder, sandier, substrates. Mouritsen & Jensen (1992) demonstrated that sediment penetrability improves the probability of detecting buried prey by Dunlins. These focal observations of feeding Dunlins revealed that most bivalves and large worms were located by probing, and that probing was more frequently used on muddy areas. Therefore, these observations indicate that detection efficiency may play an important role in the selection of habitat by Dunlins.

#### *Latitudinal gradients of birds and invertebrates*

Densities of Dunlins clearly increase from northern to southern latitudes along their non-breeding distribution within the East Atlantic Flyway (Table 5). This pattern is also observed at a global scale pooling the density of all wader species (Hockey *et al.*, 1992). Several studies discuss this phenomenon but their conclusions are still limited by the insufficient information on the food availability for birds (e.g. Zwarts *et al.*, 1990; Hockey *et al.*, 1992).

Information was compiled on the invertebrate biomass along the wintering distribution of Dunlins within the East Atlantic Flyway, and did not detect any clear latitudinal trend (Table 5). Moreover, the two sites with the highest densities of birds (Merja Zerga, Morocco and Banc d'Arguin, Mauritania) presented much lower biomass of invertebrates than the Dutch Wadden Sea, which has the lowest densities of birds. However, the lack of clear patterns in this compilation of data has to be interpreted with care because of data insufficiencies.

A major problem with the available data is that food availability is not necessarily correlated to the overall biomass of invertebrates. This study demonstrated that only part of the invertebrates present in the sediment are actually exploited by the Dunlins, not only because their selective behaviour but also because sed-

TABLE 5

Densities of Dunlins during the winter and biomass of invertebrates in some of the most important sites for wintering Dunlins in the East Atlantic Flyway, based on published literature. [a] Meltotte *et al.* (1994); [b] Zwarts & Wanink (1993); [c] Eybert *et al.* (2003); [d] Deceuninck & Mahéo (2000), only counts 1993-1999; [e] Estimated from Landsat images, freely available at <http://glcfapp.umiacs.umd.edu>; [f] Rufino & Costa (1993), Costa & Rufino (1994, 1996a, 1996b, 1997); [g] Present study; [h] Sprung (1994), biomass from all habitats was pooled; [i] Pérez-Hurtado & Hortas (1992); [j] Masero *et al.* (1999), biomass from February and March samples was pooled; [k] Hockey *et al.* (1992); [l] Dakki *et al.* (2001); [m] Piersma *et al.* (1993); [n] Wolff *et al.* (1993), intertidal area excluded Sebkhass; [o] Zwarts *et al.* (1998a, 1998b). [Densidad de Correlimos Común durante el invierno y biomasa de invertebrados en algunos de los más importantes lugares de invernada en la vía de vuelo del Atlántico este según datos de la bibliografía. [a] Meltotte *et al.* (1994); [b] Zwarts & Wanink (1993); [c] Eybert *et al.* (2003); [d] Deceuninck & Mahéo (2000), solo censos 1993-1999; [e] Estimado a partir de imágenes del Landsat, disponibles libremente en <http://glcfapp.umiacs.umd.edu>; [f] Rufino & Costa (1993), Costa & Rufino (1994, 1996a, 1996b, 1997); [g] Este estudio; [h] Sprung (1994), la biomasa de todos los hábitats se trató en conjunto; [i] Pérez-Hurtado & Hortas (1992); [j] Masero *et al.* (1999), la biomasa de las muestras de febrero a marzo fue tratada conjuntamente; [k] Hockey *et al.* (1992); [l] Dakki *et al.* (2001); [m] Piersma *et al.* (1993); [n] Wolff *et al.* (1993), se excluyó la zona intermareal Sebkhass; [o] Zwarts *et al.* (1998a, 1998b)].

Site [Localidad]	Latitude [Latitud] (°N)	Intertidal area (ha) [Zona intermareal]	Numbers of Dunlins [Número de correlimos]	Density (Dunlins/ha) [Densidad correlimos/ha]	Invertebrate biomass (AFDW/m <sup>2</sup> ) [Biomasa de invertebrados]
Dutch Wadden sea, Netherlands	53	114,100 [a]	56,013 [a]	0.5	94.1 [b]
Mont Saint Michel Bay, France	49	24,000 [c]	29,394 [d]	1.2	13.3 [c]
Tagus estuary, Portugal	39	9,719 [e]	14,449 [f]	1.5	37.9 [g]
Ria de Faro, Portugal	37	5,183 [e]	18,397 [f]	4.7	18.1 [h]
Cadiz Bay, Spain	36	3,915 [e]	12,176 [i]	2.3	44.7 [j]
Merja Zerga, Morocco	35	2,200 [k]	25,704 [l]	11.7	22.6 [m]
Banc d'Arguin, Mauritania	19	49,250 [n]	947,743 [o]	19.2	17.0 [n]

iment characteristics seems to limit the exploitation of their prey.

The evaluation of food availability is further complicated by the fact that in most studies sampling schemes are very limited in terms of space and time covered. Additionally, size and burying depth of invertebrate species are rarely presented. Long-term studies on the invertebrate availability for waders reveal large seasonal and annual variation in abundance, size and burying depth of invertebrates (*e.g.* Zwarts & Wanink, 1993). Also, several studies have shown that invertebrates present

patchy distributions (*e.g.* Thrush, 1991), which are rarely taken into account in the sampling schemes.

The global populations of many wader species are currently decreasing (*e.g.* BirdLife International and European Bird Census Council, 2000; Stroud *et al.*, 2004). Although most of the important wintering areas have been identified, the evaluation of their food resources for waders is still missing, particularly for tropical and sub-tropical areas. It is generally recognized that, because most waders are migratory, conservation plans at a flyway scale are

necessary for the preservation of these birds. In this context, baseline knowledge (as diet and availability of food resources) in the least studied wintering areas is of major importance for the conservation of wader populations.

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