Numbers, diet and feeding methods of Common Shelduck *Tadorna tadorna* wintering in the estuarine bays of Aiguillon and Marennes-Oléron, western France

ANOUCK VIAIN[1,5]*, FRÉDÉRIC CORRE[2], PHILIPPE DELAPORTE[3], EMMANUEL JOYEUX[4] & PIERRICK BOCHER[1]

[1]Laboratory of Coastal Environment and Societies UMR 6250 LIENSs CNRS-University of La Rochelle, 2 rue Olympe de Gouges, F-17000 La Rochelle, France.
[2]Réserve Naturelle de la Baie de l'Aiguillon, Ligue pour la Protection des Oiseaux, Ferme de la Prée Mizottiere, F-85450 Sainte Radegonde des Noyers, France.
[3]Réserve Naturelle de Moëze-Oléron, Ligue pour la Protection des Oiseaux, Plaisance, F-17180 Saint-Froult, France.
[4]Réserve Naturelle de la Baie de l'Aiguillon, Office National de la Chasse et de la Faune Sauvage, Ferme de la Prée Mizottiere, F-85450 Sainte Radegonde des Noyers, France.
[5]Current address: Département de Biologie, 300 allée des Ursulines, Université du Québec à Rimouski, Rimouski G5L 3A1, Québec, Canada.
*Correspondence author. E-mail: anouck.viain@uqar.qc.ca

Abstract

Common Shelduck *Tadorna tadorna* were studied in western France, at two wintering sites of international importance for this species. The numbers, densities, feeding activity, feeding methods and diet of Shelduck feeding in the soft sediments of Aiguillon Bay and Marennes-Oléron Bay, on the Charente-Maritime and South Vendée coast, were examined. The birds spent 60% of their time feeding. Prey were obtained mainly by Shelduck moving their bills in a scything action through the mud and sieving small organisms < 8.0 mm long from the upper two centimetres of the surface. Faecal analysis indicated that the diet was composed mainly of small invertebrates, primarily the mudsnail *Hydrobia ulvae*. However, the presence of plants and other invertebrates in the diet indicated that they also exploited food resources in adjacent saltmarshes.

Key words: feeding activity, food resources, *Hydrobia ulvae*, mudflats, wintering duck.

The population of Common Shelduck *Tadorna tadorna* (hereafter Shelduck) wintering in northwest European has been estimated at 270,000 individuals in recent years, with numbers remaining stable or increasing slightly over the past three decades (Burfield & van Bommel 2004; Delany & Scott 2006). Shelduck wintering on the Atlantic and Channel coasts of France represent approximately 18% of the population, with total mid-winter numbers varying between 49,125 individuals in January 2001 and 52,782 individuals in January 2008 (Wetland International counts, Deceuninck *et al.* 2008). Along with the Picardie coast, the most important areas for Shelduck in France are estuarine bays on the coast of Charente-Maritime and South Vendée (Deceuninck *et al.* 2008), which represent the most southern wintering sites of international importance for this species along western European shores (Snow & Perrins 1998). These sites support 7,500–19,000 birds in mid-winter, representing approximately 7% of the northwest European population. However, the sites do not constitute a major breeding area, with numbers estimated at only 900–1,300 breeding pairs (Boileau & Delaporte 2003; Corre & Joyeux, unpubl. data).

Shelduck arrive in western France from their summer moulting areas on north European coasts from early autumn, and numbers continue to increase until January. Numbers thereafter steadily decrease until early spring when most birds leave for their breeding sites, although some do remain to breed. During winter, birds aim to maximise their food intake rates in order to increase their survival (Vangilder *et al.* 1986); consequently, the choice of the wintering site is crucial and is directly related to food availability and site quality. Shelduck favour coastal habitats during this period, especially estuaries or brackish marshes (Thompson 1981; Patterson 1982). In intertidal habitats they feed on invertebrates by sieving the upper layers of the sediment (Thompson 1981; Campbell 1947). Goethe (1961) and Olney (1965) found a predominance of the mudsnail *Hydrobia ulvae* in the Shelduck diet, while other authors have reported a wider range of food items (Swennen & van der Baan 1959; Jenkins *et al.* 1975; Evans *et al.* 1979). Bryant & Leng (1975) and Buxton (1975) concluded that there was a strong association between the concentration of birds and the density and biomass of their main prey, *Hydrobia*, in estuaries of the United Kingdom.

The interpretation of diet selection by birds generally relies on comparisons between prey items taken and those available. But for Shelduck, the study of prey selection remains difficult because they usually sieve variable quantities of sediment containing parts of organisms that are sometimes too small to be identified. This paper examines for the first time the numbers, densities, feeding activity, feeding methods and diet of Shelduck on the central French Atlantic coast. We assess the diet by examination of faecal contents and highlight some of the factors determining the birds' distribution and abundance during the winter.

Methods

Study sites

The two study sites were Aiguillon Bay and Marennes-Oléron Bay, which belong to the "Pertuis Charentais" complex located on the Atlantic coast in the south of Vendée and the north of Charente-Maritime (Fig. 1). These bays support large numbers of

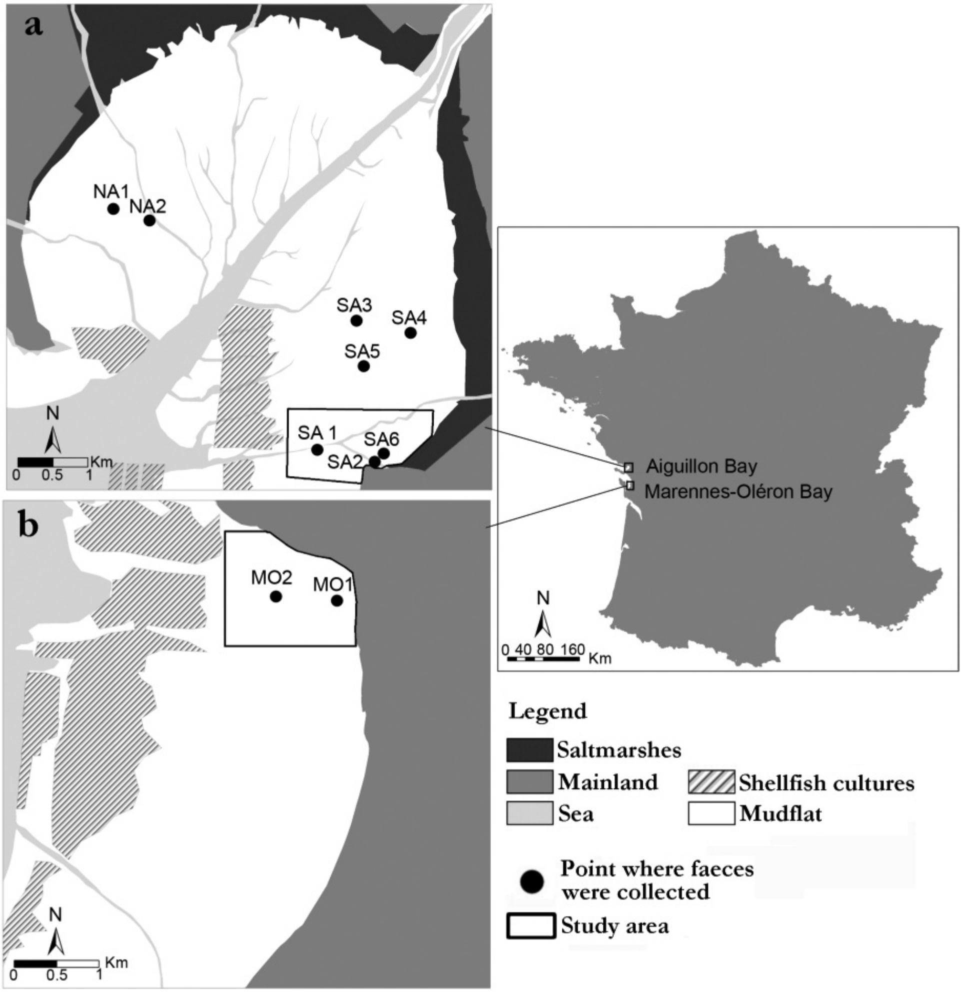

Figure 1. Map of France showing the study areas: Aiguillon Bay (a) and the northeastern part of Marennes-Oléron Bay (b), with the feeding activity survey area (boxed area) and points where faeces were collected (black dots).

shorebirds and waterfowl staging or wintering along the French coastline (Deceuninck & Mahéo 1998; Deceuninck *et al.* 2008). Both bays include some of the largest mudflat areas with macro-tidal systems in Europe and have high proportions of soft, silty sediments (Eisma 1998).

Aiguillon Bay. The bay (46°20'N, 01°18'W) is divided into two equal parts by the Sèvre River. It comprises 38 km² of intertidal mudflats surrounded by saltmarshes and is limited by dykes to the north and east, and by cliffs to the south (Fig. 1a). The upper and middle reaches of the intertidal zone are bare muddy flats (mean median grain size = 8 μm, and almost 90% silt; Bocher *et al.* 2007), but the lower reaches are intersected by a network of channels flowing into the Sèvre River. Faeces and macrofauna samples were collected in two distinct parts of the bay (Fig. 1a), one in the northwest called "North Aiguillon", which is the sandiest area near the "Pointe de l'Aiguillon" sand spit, and the other in the southeast called "South Aiguillon". Higher sampling and observation effort was carried out in "South Aiguillon" because this area supported a greater number of Shelduck than the rest of the bay during recent winters (Meunier & Joyeux 2003). The whole of the bay is protected through its designation as a National Nature Reserve.

Marennes-Oléron Bay. The bay (46°55'N, 01°18'W) is 40 km south of Aiguillon Bay (Fig. 1b). It covers 150 km^2 and is enclosed by Oléron Island to the west and by the mainland to the east. On the mainland side of the bay, an intertidal area extending over 4 km is bordered by cliffs to the north and by dykes around the rest of the bay. The upper and middle mudflats on the mainland side have a typical ridge and runnel structure (Gouleau *et al.* 2000), whereas the low-lying mudflats are occupied by mussel *Mytilus edulis*–oyster *Crassostrea gigas* cultures or abandoned oyster farms, as in Aiguillon Bay. We confined our study to the northeast part (Fig. 1b). In this area, the mudflats are slightly less muddy than in Aiguillon Bay (median grain size = 17 μm, 85% silt; Bocher *et al.* 2007). The intertidal mudflats on the Oléron side are mainly covered with Dwarf Eelgrass *Zostera noltii* and are rarely visited by Shelduck. The central part of the bay is included in the Moëze-Oléron National Nature Reserve.

Bird counts

From 1998–2008, Shelduck, as well as other waterbirds, were counted each month on both sites by staff of the Nature Reserves. At Aiguillon Bay, the bay was divided into sectors and Shelduck on the upper part of the intertidal area during the flood tide were counted simultaneously by observers using telescopes. At Marennes-Oléron Bay, birds were only counted while roosting at high tide.

Feeding activity and methods

Surveys were designed to determine the percentage of time that birds spent feeding and the proportion of the different feeding methods that were used, as well as how they changed during the tidal cycle. Feeding activity in both bays was observed in a delimited area in which it was possible to record behaviour during four consecutive hours on ebb or flood tides (Fig. 1). These areas covered the entire tidal range of the mudflats except for the banks of wild oysters lying on the lower part of the shore. In Aiguillon the survey area covered 186 ha while at Marennes-Oléron it covered 184 ha. Both areas had previously been noted as being regular feeding areas for large numbers of Shelduck (Deceuninck *et al.* 2008).

Between 19 January and 5 March 2008, counts were made over a 4-h period, either from Low Tide (LT) to LT plus 3 h (LT+3) or from LT minus 3 h (LT-3) to LT, depending on the time of low tide during daylight hours. Feeding activity and methods were recorded over nine periods of 4-h-long observations with one count made every hour (on six flood tides and three ebbs) at Aiguillon Bay, and for five observation periods at Marennes-Oléron Bay (made on three flood tides and two ebbs). For each count, birds are divided in several flocks (2–353 birds; mean = 45 ± 76 birds; two birds were considered in the same flock when less than *c.* 10 m apart) and the positions of flocks were recorded on a map. For each flock, individuals were categorised as using one of the six feeding methods commonly described for the species (Swennen & van der Baan 1959; Olney 1965; Bryant & Leng 1975): 1) surface digging on exposed mud (the bird is out of water and pushes its bill on the mud surface); 2) scything on exposed soft mud (the bird walks along and moves its bill from left to right through the mud and back again); 3) scything in shallow water (1–10 cm water depth); 4) dabbling on exposed mud; 5) up-ending in deep water (25–40 cm); 6) head-dipping in water (10–25 cm), the swimming bird feeding with head submerged; and 7) birds feeding but observer unable to define the feeding method. Non-feeding birds were denoted as: 8) at rest, or 9) preening (Walmsley & Moser 1981).

Diet

Individual faeces were collected from the two sub-sites on Aiguillon and the single site at Marennes-Oléron, then stored in a plastic jar before being frozen and preserved at –20°C. At least 10 faeces were collected from areas where tens to hundreds of birds were feeding, except for one area where only five faeces were found. A total of 75 faeces were collected at Aiguillon Bay and 20 at Marennes-Oléron Bay. In the laboratory, each faecal sample was thawed then washed over a 0.3 mm sieve to separate food items from mud particles and simultaneously over a 0.064 mm mesh sieve to collect jaws and paragnaths of worms. After drying at 55°C for three days, faeces were weighed to obtain dry mass (DM_{faeces}). Three sub-samples of 5% of DM_{faeces} were sorted to determine their prey composition, using the method described by Dekinga & Piersma (1993), to reconstruct the diet of mollusc-eating shorebirds. Fragments of bivalves, mudsnails and other items were separated into species categories and then weighed. As Anders *et al.* (2008) noticed, not all *Hydrobia* found in the faeces were dead and digested by Shelduck; some survived passage through the gut. Consequently, if the entire *Hydrobia* shell (with operculum) was found, it was considered to be alive and excluded from sample before the diet reconstruction, because the *Hydrobia* had not been assimilated during the digestive process. Allometric equations obtained from measurements of entire individual bivalves and gastropods found in core samples collected at the same time as the faeces (Appendix 1), or from other studies, were used to extrapolate from the measured bivalve hinges and complete gastropod whorls found in faeces to entire individuals. Jaws or paragnaths of worms found in faeces were measured from the tip to the inner end of the toothed section and from the apex to the posterior edge of the larger mouth lamella of the jaw and used to determine the size of entire prey based on equations from Abrantes *et al.* (1999) and Olive *et al.* (1985). For diet reconstruction, dry mass (DM) was calculated by drying retrieved food items for three days at 55°C, and ash free dry mass (AFDM) by drying for 5 h at 550°C. The DM and AFDM values for bivalves were determined for flesh only, on being separated from the shell.

Macrofauna

The distribution and densities of molluscs were determined by taking cores at predetermined stations, located by GPS on a grid with points 250 m apart, in January 2008 at Aiguillon and during February 2008 at Marennes-Oléron. The 64 sampling stations (8 × 8) at each sub-site covered the main part of the intertidal range. A 150 mm diameter sediment core covering 0.018 m^2 was taken to a depth of 20–25 cm at each sample site (Bocher *et al.* 2007; Kraan *et al.* 2009). Molluscs that were collected were stored in a plastic bag in a freezer (–20°C). Only molluscs were identified to the species level and counted.

Statistical Analysis

Data were analysed using Xlstat (Addinsoft) software. We used Mann-Whitney tests (U) to evaluate changes in the mean number of Shelduck counted in the two bays each winter and to compare DM_{faeces} values across sites. The Student's unpaired t-test (t) was used to test for differences in the density of birds recorded. The occurrence of copepods and gastropod *Retusa obtusa* at the different sites was compared using a Chi-squared test. Tests were considered significant at $P \leq 0.05$ and means are given ± s.d. values throughout.

Results

Phenology and numbers of Shelduck

Shelduck were present on the Charente-Maritime and south Vendée coastline throughout the year. The seasonal patterns of presence were similar at the two study sites, with the highest number of individuals in winter from November–March and very few individuals during the breeding and moulting periods from May–September (Fig. 2). Peaks were recorded for both bays during January in most years (mean = 8,091 ± 3,587, n = 10 and mean = 3,694 ± 1,540, n = 11 for Aiguillon and Marennes-Oléron, respectively). In some years, peaks were recorded in December or February. Numbers started to decrease from January or February and continued until May.

The number of wintering Shelduck increased at both Aiguillon and Marennes-Oléron between 1998 and 2008 (Fig. 3). Mean numbers recorded at Aiguillon Bay were significantly lower in winters 1998/99–2001/02 than in winters 2002/03–2007/08 (U = 19, P < 0.0001). From winters 1998/99–2001/02, the mean number of wintering Shelduck remained stable at around 3,617 ± 435 individuals. Since 2002, the mean number has increased by 218%. At Marennes-Oléron, the mean numbers of Shelduck recorded each year in winters 2004/05–2007/08 have increased significantly in comparison with the mean numbers counted in winters 1998/99–2003/04 (U = 92, P = 0.003). Numbers

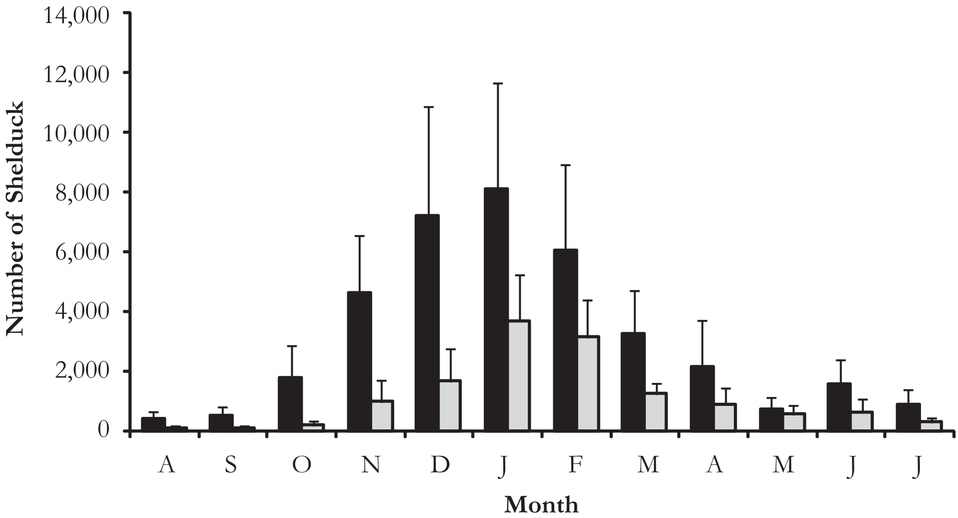

Figure 2. Mean monthly numbers ± s.d. of Common Shelduck at Aiguillon Bay (in black) and at Marennes-Oléron Bay (in grey) between 1998 and 2008.

were relatively stable at around 1,822 ± 91 individuals from 1998/99–2003/04, but have increased by 120% since 2004.

During our study of Shelduck feeding activity in winter 2007/08, peak numbers at Aiguillon and Marennes-Oléron were 12,820 and 6,129 individuals respectively.

Feeding activity and methods

The mean density of birds was 1.6 ± 0.3 individuals ha^{-1} at Aiguillon during the period from LT-3 to LT+3 (overall count), and 3.0 ± 0.2 individuals ha^{-1} at Marennes-Oléron (Table 1). The higher density of birds recorded at Marennes-Oléron was statistically significant ($t_{45} = -3.86$, $P < 0.001$).

Shelduck fed throughout the tidal cycle with the highest percentage of birds recorded feeding at LT-3, both at Aiguillon (66.0%) and at Marennes-Oléron (71.1%) (Table 2). Feeding activity decreased steadily (–1.7%) from LT-3 until LT+1, then sharply (–34.7%) when approaching LT+3 (42.4%) at Aiguillon. At Marennes-Oléron, the decrease in the number of feeding birds was slow at first (–1%) between LT-3 and LT-1, but this was followed by a greater decrease (–28%) at LT, reaching a minimum of 50.0% of birds feeding at this time. Thereafter, feeding activity at Marennes-Oléron returned to its previous level of around 70% Shelduck feeding until LT+3.

As long as the mudflats were free from inundation, feeding activity remained close to 60% at Aiguillon and 70% at Marennes-Oléron. Non-feeding birds either rested (28.9–57.1%) or preened (0.0–1.5%) (Table 2). The proportion of individuals at rest in both study areas represented roughly a third of birds whatever the state of the tide, except during LT at Marennes-Oléron (48.5%) and LT+3 at Aiguillon (57.1%). Of

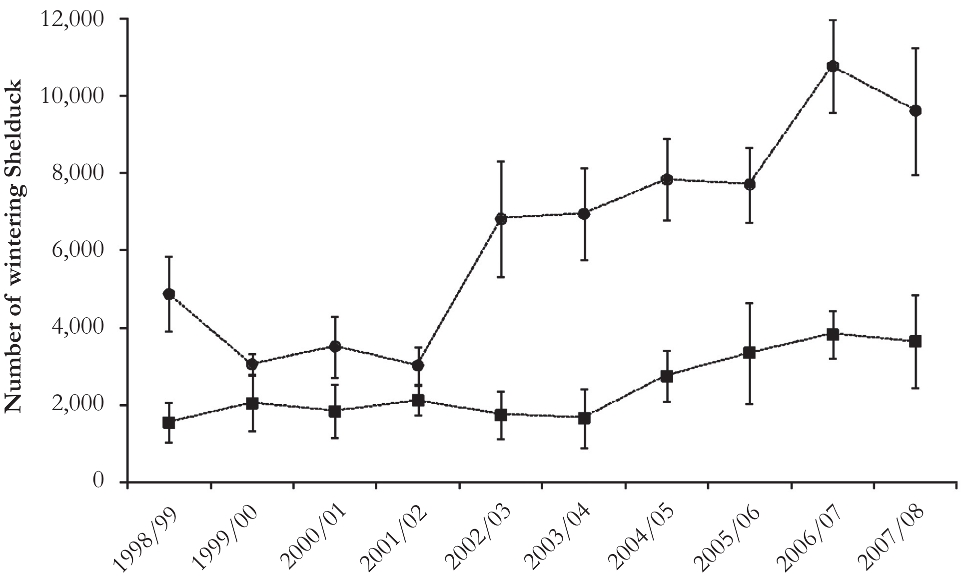

Figure 3. Mean numbers of Common Shelduck ± s.e. counted during winter (mean of November–December–January–February) at Aiguillon Bay (black dot) and Marennes-Oléron Bay (black square) during 10 consecutive wintering periods.

the six categories used to define feeding methods (Table 2), "scything on mud" was the most common, ranging from 30.7–53.7% of all individuals at any time at Aiguillon, and was especially common during the ebb tide. At Marennes-Oléron, scything was particularly common between LT-1 (49.2%) and LT+2 (56.4%) but reduced in favour of "head dipping" the rest of the time, falling to 47.2% at LT-3. Digging was the second most common feeding method used by birds on exposed flats (3.4–24.3% at Aiguillon; and 5.6–11.6% at Marennes-Oléron). There was more "head-dipping" during the flood tide compared to the ebb tide, even though feeding activity on water was rare (Table 2).

Diet

A total of 95 faeces samples were collected at two locations at North Aiguillon (NA1 and NA2; 2 × 10 faeces), six at South Aiguillon (SA1 to SA6; 5 × 10 and 1 × 5 faeces) and two at Marennes-Oléron (MO1 and MO2; 2 × 10 faeces) (Table 3). DM_{faeces} was highly variable between faeces from the same location, between locations and between sites. The minimum DM_{faeces} was 0.02 g (SA3) and the maximum 4.20 g (SA6). Nevertheless, the DM_{faeces} difference between Marennes-Oléron (1.64 g) and North Aiguillon (1.98 g) was not significant (U = 239, n.s.), but there was a significant difference between DM_{faeces} at South

Table 1. Mean number and densities (individuals per ha) of Common Shelduck feeding per hour in relation to low tide, during the period 19 January–5 March 2008. n = number of daily counts for each stage of the tide.

Study sites		**South Aiguillon**			**Marennes-Oléron**	
	n	**Mean number/ day/sector (± s.d.)**	**Number of individuals/ ha (± s.d.)**	***n***	**Mean number/ day/sector (± s.d.)**	**Number of individuals/ ha (± s.d.)**
LT-3	4	310 ± 47	1.7 ± 0.3	2	593 ± 161	3.2 ± 0.9
LT-2	3	307 ± 64	1.7 ± 0.3	2	527 ± 211	2.9 ± 1.1
LT-1	4	196 ± 130	1.1 ± 0.7	3	598 ± 232	3.3 ± 1.3
LT	7	303 ± 281	1.6 ± 1.5	5	394 ± 202	2.1 ± 1.1
LT+1	6	251 ± 101	1.3 ± 0.5	3	539 ± 221	2.9 ± 1.2
LT+2	6	357 ± 364	1.9 ± 2.0	3	552 ± 274	3.0 ± 1.5
LT+3	6	372 ± 243	2.0 ± 1.3	3	517 ± 185	2.8 ± 1.0

Aiguillon and the two other areas, with an average of only 0.45 g (U = 1014 and U = 999 for North Aiguillon and Marennes-Oléron respectively, both $P < 0.0001$). Most of the DM_{faeces} was due to the presence of mollusc shell fragments, indicating a high amount of molluscs in the birds' diet.

The gastropod *Hydrobia ulvae* was found in all faeces analysed and was also the most abundant prey both in terms of dry mass of shell fragments (DM_{shell}) (Table 3) and of reconstructed AFDM. Bivalves occurred in 95%, 69% and 90% of faeces from North Aiguillon, South Aiguillon and Marennes-Oléron respectively. Identified individuals measured < 8.0 mm in length and were mainly *Abra tenuis*, *Cerastoderma edule* and *Macoma balthica*, with a few *Scrobicularia plana* and *Tapes* sp. Bivalve fragments represented ≤ 5% of DM_{faeces} in the three areas (Fig. 4) while more than half of the faecal samples contained foraminifera (main species identified was *Ammonia tepida*). Undetermined Ostracods were found in 40% of faeces (Fig. 5). Harpacticoïd copepods appeared in approximately a quarter of samples (average = 23%) and the gastropod *Retusa obtusa* in some of them, but none were found alive. These were more frequent at Marennes-Oléron (up to 30%) (Fig. 5). The occurrences of copepods and the gastropod *Retusa obtusa* were significantly different between North and South Aiguillon (χ^2_8 = 15.58, $P < 0.05$) and

Table 2. Mean percentage of Common Shelduck (± s.d.) performing different behaviours in relation to low tide in Aiguillon Bay and Marennes-Oléron Bay. LT corresponds to a period that starts at low tide and ends at low tide + 1 hour maximum. *n* = number of daily counts for each stage of the tide.

Behaviour	**Time/low tide**						
Aiguillon	**LT-3**	**LT-2**	**LT-1**	**LT**	**LT+1**	**LT+2**	**LT+3**
n	4	3	4	7	6	6	6
Feeding (% activity)	**66.0 %**	**61.1 %**	**62.7 %**	**60.6 %**	**64.9 %**	**57.3 %**	**42.4 %**
Digging	3.4 ± 3.3 %	11.8 ± 13.9 %	8.5 ± 8.4 %	13.6 ± 16.4 %	24.3 ± 29.0 %	14.9 ± 23.3 %	8.0 ± 13.2 %
Scything mud	39.9 ± 18.4 %	42.5 ± 15.5 %	53.7 ± 34.1 %	44.6 ± 19.7 %	35.2 ± 18.4 %	30.7 ± 20.1 %	30.4 ± 26.5 %
Scything water	2.2 ± 3.1 %	0.8 ± 1.5 %	0.0 %	0.3 ± 0.6 %	0.4 ± 0.6 %	0.0 %	1.4 ± 1.4 %
Dabbling	0.0 %	0.0 %	0.0 %	1.6 ± 4.0 %	1.5 ± 3.6 %	0.7 ± 1.3 %	0.2 ± 0.5 %
Upending	0.0 %	0.0 %	0.0 %	0.0 %	0.0 %	0.2 ± 0.4 %	0.1 ± 0.3 %
Head dipping	20.5 ± 9.2 %	6.0 ± 5.1 %	0.5 ± 0.9 %	0.0 %	2.3 ± 5.6 %	10.8 ± 17.4 %	2.3 ± 4.1 %
Indeterminate feeding	0.0 %	0.0 %	0.0 %	0.5 ± 1.3 %	1.2 ± 2.9 %	0.0 %	0.0 %
Other activities (%)	**34.0 %**	**38.9 %**	**37.3 %**	**39.4 %**	**35.1 %**	**42.7 %**	**57.6 %**
Preen	1.2 ± 1.4 %	0.7 ± 1.2 %	0.0 %	0.2 ± 0.4 %	0.0 %	0.6 ± 1.1 %	0.5 ± 0.9 %
Rest	32.8 ± 17.5 %	38.2 ± 15.3 %	37.3 ± 33.3 %	39.2 ± 22.2 %	35.1 ± 12.4 %	42.1 ± 10.8 %	57.1 ± 22.4 %

Table 2 *(continued)*.

Behaviour	Time/low tide						
Marennes-Oléron	**LT-3**	**LT-2**	**LT-1**	**LT**	**LT+1**	**LT+2**	**LT+3**
n	2	2	3	5	3	3	3
Feeding (% activity)	**71.1 %**	**70.7 %**	**70.4 %**	**50.0 %**	**69.9 %**	**70.0 %**	**66.2 %**
Digging	6.3 ± 7.3 %	9.6 ± 9.2 %	8.3 ± 8.2 %	5.6 ± 6.2 %	6.8 ± 7.1 %	11.6 ± 10.7 %	5.6 ± 3.8 %
Scything mud	4.0 ± 4.5 %	22.9 ± 15.8 %	49.2 ± 31.1 %	31.5 ± 18.8 %	49.9 ± 39.2 %	56.4 ± 16.3 %	22.1 ± 13.3 %
Scything water	13.3 ± 14.6 %	0.7 ± 1.1 %	3.3 ± 6.5 %	2.3 ± 2.3 %	0.2 ± 0.4 %	1.5 ± 1.5 %	1.0 ± 0.6 %
Dabbling	0.3 ± 0.4 %	0.1 ± 0.1 %	0.0 %	0.2 ± 0.5 %	0.0 %	0.1 ± 0.2 %	0.1 ± 0.2 %
Upending	0.0 %	0.0 %	0.0 %	0.0 %	0.0 %	0.3 ± 0.6 %	15.0 ± 25.4 %
Head dipping	47.2 ± 5.0 %	37.4 ± 25.7 %	5.5 ± 13.9 %	1.2 ± 2.7 %	0.0 %	0.0 %	22.4 ± 29.6 %
Indeterminate feeding	0.0 %	0.0 %	4.1 ± 7.7 %	9.2 ± 13.2 %	13.0 ± 22.6 %	0.1 ± 0.2 %	0.0 %
Other activities (%)	**28.9 %**	**29.3 %**	**29.6 %**	**50.0 %**	**30.1 %**	**30.0 %**	**33.8 %**
Preen	0.0 %	0.0 %	0.0 %	1.5 ± 3.3 %	0.0 %	0.0 %	0.0 %
Rest	28.9 ± 22.8 %	29.3 ± 17.9 %	29.6 ± 27.0 %	48.5 ± 15.1 %	30.1 ± 16.8 %	30.0 ± 10.4 %	33.8 ± 15.2 %

Table 3. Summary of faeces collected with their mean dry mass ± s.d. (minimum–maximum) and their percentage of dry mass made of mudsnails *Hydrobia ulvae* per collection area at the study sites.

Study site	Collection point	Faeces (*n*)	Dry mass of faeces (g)	% of dry mass *Hydrobia ulvae*
North Aiguillon				
07/01/2008	NA1	10	2.42 ± 0.95 (0.43–3.59)	93.1 ± 6.9 (74.1–97.2)
07/01/2008	NA2	10	1.55 ± 0.70 (0.50–3.04)	94.4 ± 2.3 (92.1–98.7)
South Aiguillon				
06/01/2008	SA1	5	0.91 ± 0.57 (0.18–1.63)	85.1 ± 26.4 (38.1–98.4)
12/02/2008	SA2	10	0.29 ± 0.30 (0.06–0.18)	55.5 ± 24.2 (14.2–85.3)
25/01/2008	SA3	10	0.04 ± 0.02 (0.02–0.07)	48.2 ± 20.2 (22.1–82.1)
25/01/2008	SA4	10	0.06 ± 0.05 (0.03–0.16)	58.0 ± 24.9 (18.6–93.0)
07/02/2008	SA5	10	0.11 ± 0.05 (0.05–0.18)	15.3 ± 10.8 (2.7–34.2)
25/02/2008	SA6	10	1.52 ± 1.55 (0.19–4.20)	67.6 ± 20.6 (41.7–94.1)
Marennes-Oléron				
21/01/2008	MO1	10	1.78 ± 0.81 (0.39–3.04)	92.3 ± 5.1 (78.9–96.8)
22/02/2008	MO2	10	1.51 ± 0.62 (0.54–2.17)	91.0 ± 5.3 (80.6–98.3)

between South Aiguillon and Marennes-Oléron ($\chi^2_8 = 21.37$, $P < 0.01$). Jaws of the polychaete *Hediste diversicolor* and paragnaths of *Nephtys hombergii* were only recorded at South Aiguillon and occurred in 22% of faeces. The main prey species was *H. diversicolor* with a mean reconstructed length of 21 ± 8 mm (5–50 mm, $n = 104$). The other worm species *N. hombergii* ingested had a mean size of 30 ± 3 mm (27–34 mm, $n = 6$). In addition to these items, some fragments of insects were also found but only at South Aiguillon. Some seeds of *Salicornia* sp. were identified in a few samples.

There was a clear difference in prey composition between sampling locations at South Aiguillon and the two other sites (Fig. 4). The frequency of DM_{faeces} of *Hydrobia* at North Aiguillon and Marennes-Oléron ranged from 90–95%, whereas DM_{faeces} was significantly lower at South Aiguillon ($U = 1008$ in comparison with North Aiguillon; $U = 977$ in comparison with Marennes-Oléron; $P < 0.0001$ in each case), at around 50% except for location SA1 where *Hydrobia* accounted for 85% of DM_{faeces}. For bivalves, the numbers found in faeces in both Aiguillon areas were lower than those in Marennes-Oléron, but in this area, individuals were

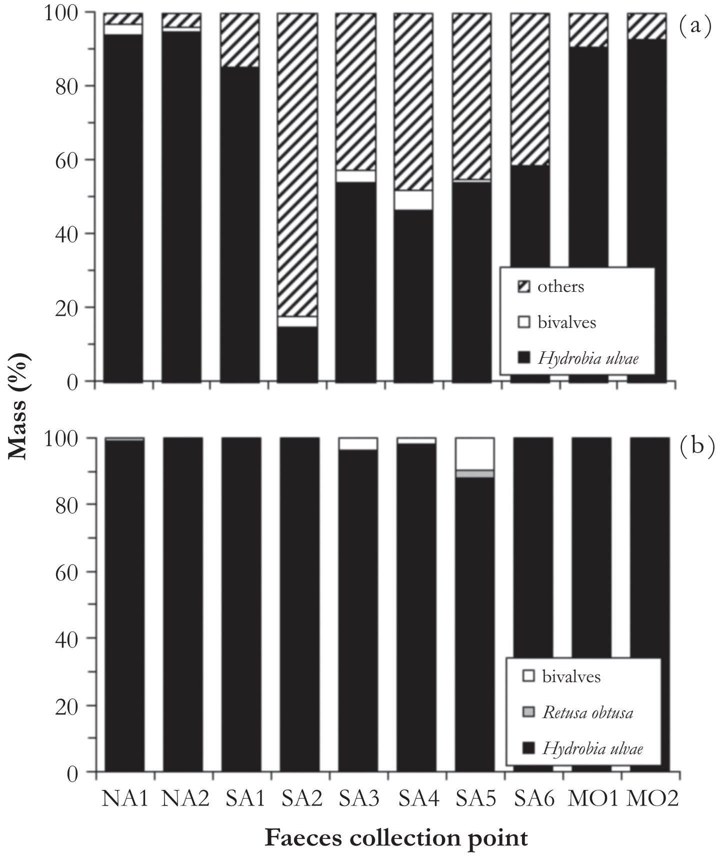

Figure 4. Common Shelduck diet expressed as: (a) the dry mass of shell fragments or plant fragments. and (b) calculated ash-free dry mass of the tissue of the prey.

too small (< 3 mm) to appear significantly in DM and in AFDM. The category defined as "others" was essentially made up of undetermined plant fragments and sometimes of unidentified green seaweed. These appeared mainly and regularly in faeces collected in South Aiguillon.

Food resources

Given the apparent scarcity of worms and crustaceans in the diet of the birds, the definition of prey stock was limited to bivalves and gastropods (Table 4). The gastropod *Hydrobia* was numerically the most abundant species within each of the three faeces collection areas. They occurred in 87.5%, 94.3% and 50.0% of the macrofauna sampling stations, with mean densities of 2,409 individuals/m^2, 1,714 individuals/m^2 and 1,014 individuals/m^2 in North Aiguillon, South Aiguillon and Marennes-Oléron, respectively. Other gastropods, namely *Akera bullata*, *Cyclope neritea* and *R. obtusa,* were rare or only

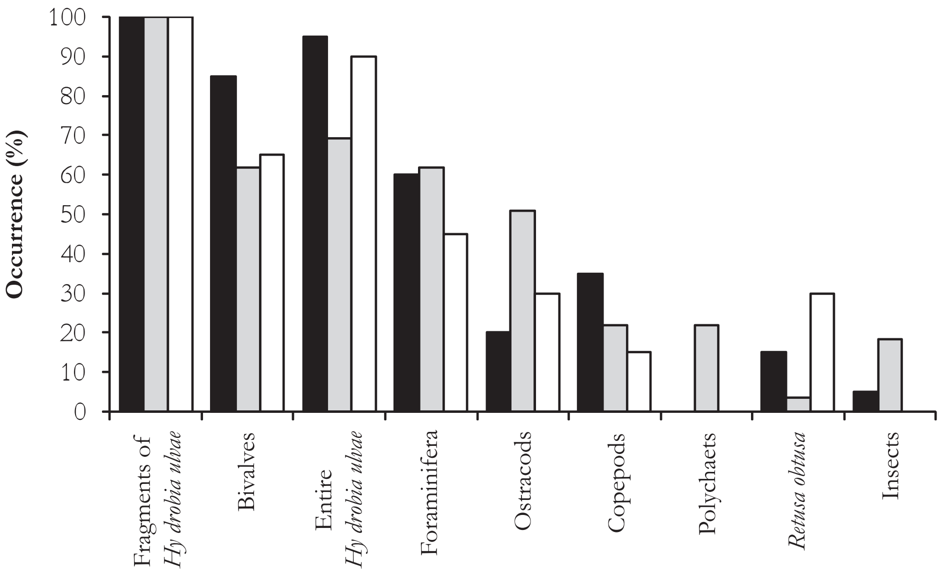

Figure 5. Frequency of occurrence of items found in Common Shelduck faeces at North Aiguillon (in black), South Aiguillon (in grey) and Marennes-Oléron (in white).

occasionally found. The bivalves, *A. tenuis*, *C. edule*, *M. balthica* and *S. plana* were common at the three sites. *Tapes* sp. was frequently found in the core samples taken on Marennes-Oléron and less frequently at both Aiguillon sub-sites (Table 4).

Discussion

Following a substantial increase in the number of Shelduck wintering in France from the late 1980s to the end of the 20th century, the total number nationally is now stable at around 50,000 individuals present in January, except in very cold winters such as January 1997 when 73,000 individuals were recorded (Deceuninck *et al.* 2008). Waterbird census data show a marked and continuing increase in the number of Shelduck occurring in the central region of the French Atlantic coast over the past 10 years, however, and the area is now the primary wintering site for this species in France. This increase could be the result of a decline in numbers at other sites in Europe (Rendón *et al.* 2008). Within this complex of inter-connected sites, Marennes-Oléron was the main wintering area locally before 1998, though numbers have varied greatly between years. The most impressive increase occurred in Aiguillon, however, where the 3,200 birds counted in January 2000, rising to more than 13,000 individuals in winter 2007/08, making this site the most important for the species in France, with about a quarter of the national wintering population.

The Shelduck is the only species of wildfowl feeding directly on the mudflats of

Table 4. Mean density (individuals/m^2) of molluscs available as prey at each of the study sites and percentages of occurrence in core samples. n = number of core samples per study site.

Species	Study site					
	North Aiguillon (n = 64)		**South Aiguillon (n = 123)**		**Marennes-Oléron (n = 64)**	
	Mean density (individuals/m^2)	**Occurrence in core samples (%)**	**Mean density (individuals/m^2)**	**Occurrence in core samples (%)**	**Mean density (individuals/m^2)**	**Occurrence in core samples (%)**
Gastropod						
Akera bullata	–	–	–	–	0.9	1.6%
Cyclope neritea	–	–	–	–	0.9	1.6%
Hydrobia ulvae	2,409.2	87.5%	1,714.1	94.3%	1,014.4	50.0%
Retusa obtusa	–	–	2.3	4.1%	13.9	18.8%
Bivalve						
Abra tenuis	64.9	26.6%	97.0	43.1%	47.6	21.9%
Cerastoderma edule	138.0	53.1%	7.5	12.2%	11.0	10.9%
Macoma balthica	60.1	51.6%	101.9	63.4%	18.9	17.2%
Scrobicularia plana	314.8	31.3%	327.7	38.2%	115.1	21.9%
Tapes sp.	9.9	15.6%	4.2	6.5%	21.6	18.8%

Aiguillon and Marennes-Oléron Bays except for some small flocks of Northern Pintails *Anas acuta* at Aiguillon. The high densities of birds recorded during this study confirm that this habitat is largely used for feeding during the non-breeding period. Sediment characteristics as well as the tidal regime are the key factors influencing the distribution, densities and behaviour of shorebird prey (Ravenscroft & Beardal 2003; Granadeiro *et al.* 2006). Sutherland (1982) and Goss-Custard *et al.* (1991) showed that areas with higher prey density and quality tend to attract and to concentrate waders. Bryant & Leng (1975) thought that the distribution of *Hydrobia ulvae* available at Skinflats in the upper Firth of Forth, Scotland, was the main factor that explained the high concentrations of Shelduck at the site. However, Buxton (1975) found no correlation between foraging periods and prey abundance. In the present study, the continuous freshwater flow from a partially-opened lock across the survey area at Marennes-Oléron could explain the concentration of Shelduck in this part of the bay compared to the rest of the mudflat. Freshwater may bring higher inputs of organic matter while keeping the mud surface sufficiently soft and wet to enable scythe-feeding during the low tide (Thompson *et al.* 1986; Montagna & Kalke 1992; Ravenscroft & Beardall 2003). At Aiguillon, Shelduck were not concentrated in a particular part of the bay but did seem to favour areas with a very soft-muddy surface.

With regard to feeding activity, the immediate proximity of saltmarshes to the mudflats in the feeding area at Aiguillon could explain the decrease in numbers of birds at LT+3 as the birds could move onto the saltmarshes and continue to feed there as they do in the Morbihan Gulf in Brittany (Gelinaud 1997). Similarly at Marennes-Oléron, they can fly over the dyke and join the marshes in the Nature Reserve of Moëze-Oléron (P. Delaporte, unpubl. data).

The proportions of different feeding methods used by the birds were linked to the tidal cycle but not exclusively. Birds fed on mudflats throughout the tidal cycle with 60–70% of birds feeding at any one time. Scything was the primary method used at Aiguillon and Marennes-Oléron, particularly on the ebb tide, and presumably was made possible because of the very soft first few centimetres of the mud. This method allows birds to filter large amounts of very soft sediment while minimising movement, and consequently to ingest a higher amount of small prey. Later in the tide when the mud dries, digging became more frequent, particularly on the runnels that were common in the lower part of the mudflats at Marennes-Oléron. While the widespread and very accessible mudsnail *Hydrobia ulvae* was the main food source, as in other saline sites in Europe, the presence of plants and other invertebrates in their diet indicates they foraged in other habitats, such as saltmarshes during high tide. In the Camargue, where there is no tidal flow, prey type was the main factor influencing the choice of feeding method (Walmsley & Moser 1981). There, scything was used to capture *Artemia* cysts, head dipping for adult *Artemia*, and dabbling was used for feeding on a thick biofilm of *Cyanophyceae*.

In this study, the diet of the Shelduck was similar at both sites. Indeed, the major and recurrent prey found in faeces was *Hydrobia,* as was the case in numerous other wintering studies from sites in the British Isles (Olney 1965; Bryant & Leng 1975; Cramp & Simmons 1977) and in the Morbihan Gulf in France (Gelinaud 1997). Young (1970) reported that the feeding behaviour of Shelduck was linked to the movement, density and biomass of *Hydrobia* but that plants and some insects were also preyed upon when the birds fed on adjacent saltmarshes. Feeding on plant material was also demonstrated by Gelinaud (1997) during winter, with higher plant ingestion than in spring, while Meininger & Snoek (1992) noted the presence of plant material in Shelduck diet comprising mainly green algae from the surface biofilm.

In this study, as reported elsewhere in Europe (Cadée 2011; Anders *et al.* 2008), a few *Hydrobia* with intact operculum were found to have passed through the Shelducks' digestive tract. Cadée (2011) demonstrated that some of the *Hydrobia* with operculum, even those with only a damaged outer rim of the mouth opening, were still alive in faeces. The methods used in this study did not permit an assessment of whether entire *Hydrobia* were all still alive. However, *Hydrobia* with intact operculum were found in 4% and 25% of faeces at Aiguillon and Marennes-Oléron, respectively. They were mainly small individuals (< 3 mm height). Entire *Hydrobia* were more numerous in samples collected at Aiguillon than at Marennes-Oléron, but individuals were smaller in size. This suggests that Shelduck could be considered a vector for localised invertebrate dispersal within or between the bays of the Pertuis Charentais area, as demonstrated for Shelduck in the Wadden Sea (Cadée 2011), and for other waterfowl species dispersing other aquatic invertebrates in the Camargue (Brochet *et al.* 2010) and the Doñana wetlands (Frisch *et al.* 2007).

The estuarine bays on Central French Atlantic coast provide valuable wintering sites for Shelduck. Nevertheless, these areas support other wintering bird species such as Dunlin *Calidris alpina* and Red Knot *C. canutus,* which are also "tide followers" (Granadeiro *et al.* 2006) that forage for small invertebrates and particularly *Hydrobia* (Mendonça *et al.* 2007; Quaintenne *et al.* 2010). Future studies therefore should assess whether a continued expansion of wintering Shelduck may lead to inter-specific competition for food resources, to the detriment of other species using the same sites, especially at Aiguillon Bay.

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Appendix 1. Summary of equations used to reconstruct the diet of Common Shelduck from prey parts found during faecal analysis. $AFDM_{meat}$ = ash-free dry mass of meat of bivalves or *Hydrobia;* DM_{shell} = dry mass of shell; BL = total length of the worm; JL = length of the jaw; SL = length of the bivalve shell; HH = length of the hinge; and HTH = distance between the hinge and the top of the shell.

	Sites	Species	Equation	*n*	R^2	Reference
AFDM						
	Aiguillon					
		bivalves	$AFDM_{meat} = 0.0518 * DM_{shell}$	937	0.84	This study
		Hydrobia ulvae	$AFDM_{meat} = 0.2081 * DM_{shell}$	281	0.93	This study
	Marennes-Oléron					
		bivalves	$AFDM_{meat} = 0.0533 * DM_{shell}$	346	0.76	This study
		Hydrobia ulvae	$AFDM_{meat} = 0.2124 * DM_{shell}$	127	0.94	This study
	Aiguillon/ Marennes					
		Retusa obtusa	$AFDM_{meat} = 0.1113 * DM_{shell}$	13	0.74	This study
Size						
		Hediste diversicolor	BL cm = 3.932 * JL mm – 1.776		0.61	Abrantes *et al.* 1999
		Nephtys hombergii	BL cm = 2.4 * JL mm + 0.786		0.88	Olive *et al.* 1985
		Cerastoderma edule	SL mm = $15.458 * HH^{0.7403}$	125	0.71	Bocher *et al.* unpubl. data
		Macoma balthica	SL mm = $14.293 * HTH^{0.7169}$	260	0.81	Bocher *et al.* unpubl. data
		Scrobicularia plana	SL mm = $15.222 * HTH^{0.935}$	100	0.96	Bocher *et al.* unpubl. data