ACTA ORNITHOLOGICA
Vol. 48 (2013) No. 2

Distribution, phenology and long-term population trends in Black-tailed Godwits *Limosa limosa* wintering in coastal France

Pierrick BOCHER[1], Frédéric ROBIN[1], Bernard DECEUNINCK[2] & Emmanuel CAILLOT[3,4]

[1]Laboratory Littoral Environnement et Sociétés, UMR 7266 LIENSs CNRS-University of La Rochelle, La Rochelle, FRANCE, e-mail: pierrick.bocher@univ-lr.fr
[2]Ligue pour la Protection des Oiseaux LPO, Rochefort, FRANCE
[3]Observatory of Coastal Shorebirds, Réserves Naturelle de France, Quétigny, FRANCE
[4]Réserve Naturelle Nationale du Domaine de Beauguillot, ACHB, Beauguillot, Sainte-Marie du Mont, FRANCE

Bocher P., Robin F., Deceuninck B., Caillot E. 2013. Distribution, phenology and long-term population trends in Black-tailed Godwits *Limosa limosa* wintering in coastal France. Acta Ornithol. 48: 141–150. DOI 10.3161/000164513X678793

Abstract. Species with known long-term changes in abundance and distribution enable exploring the role of newly accessible sites in population regulation. In Western Europe, the Black-tailed Godwit *Limosa limosa islandica* is one of the few wintering shorebirds with increasing populations. The French coasts comprise a major wintering site within its global wintering area, with several thousand individuals at some sites. Nevertheless, the role and importance of French sites in general distribution patterns of the species remain unclear, especially as its hunting was legal there until 2008. In contrast, recent increases in protected areas in France (from 4,000 ha in 1973 to 28,000 ha in 2005) offer new safe sites and suitable habitats for the species. In this study, we assessed the numbers and distribution of Black-tailed Godwits along the coasts of Western France. The main wintering sites in France are progressively occupied from August, reaching peak occupation in late autumn or early winter although few of the ten sites listed showed similar patterns of monthly variations in the distribution of Godwit numbers. France welcomes c. 28% of the total *L. l. islandica* population in mid-winter over the period 2003–2007. Numbers declined steadily from the base year (1977) until 1991, then progressively increased, reaching a maximum in 2010 (c. 27,000 individuals). The creation of Nature Reserves throughout the 1990s probably contributed to the increasing number of Godwits in France, with new accessible sites visited and occupied intensively during the period of population increase. The clearly contrasting phenologies between the British Isles and France suggest that most of the individuals first arrive in the United Kingdom after the breeding season, and then some of the birds move to southern sites in either France or Iberia, while very few birds fly directly to France from Iceland.

Key words: wintering distribution, migration, population trend, nature reserve, hunting, waders, shorebirds, waterbirds, coastal habitat

Received — Oct. 2012, accepted — Oct. 2013

INTRODUCTION

Bird populations can be regulated by density dependence within sites as a result of resource limitation, competition, territoriality or dominance rankings (Sutherland 1996, Ricklefs et al. 2000, Rodenhouse et al. 2003). At a larger-scale, long-term changes in distribution can lead to new sites being used. In a buffer effect system, for example, at lower population sizes, higher quality habitats are preferentially occupied (Kluyver & Tinbergen 1953, Brown 1969, Gill et al 2001a). At higher population sizes, an increasing number of individuals is forced to occupy habitats with lower quality in terms of e.g. availability or quality of food or limited access to roost. Nevertheless, good quality sites for migrating birds during stopover or wintering can be inaccessible in time or/and space due to intensive human disturbances such as, for example, hunting (Weller 1999). In this context, birds prioritize utilizing safe areas, and can frequently be restricted in their distribution according to the availability of suitable habitat enclosed in protected areas (Colwell 2010). Species with known changes in abundance and distribution provide an opportunity to explore for the role of newly accessible sites in population regulation.

The Black-tailed Godwit *Limosa limosa* is one of the rare shorebird species with an increasing population in Europe (Delany et al. 2009). This

growing population comprises individuals that breed in Iceland (*L. l. islandica*), estimated at 47,000 individuals — they winter in Western Europe (Gunnarsson et al. 2005a). On the other hand, the breeding population of Black-tailed Godwits in the Netherlands and Germany, which belongs to the subspecies *L. l. limosa*., is now in decline throughout much of its range (Gill et al. 2007) and does not winter in Europe except for some individuals in Iberia (Alves et al. 2010). The continental individuals can only be found in France in stopovers during their migration and few breeding couples in western regions (Robin et al. 2012).

Within the EU, France was one of the very few countries where the species was legally hunted, until it was classified as protected for a period of five years (2008–2013), because of the decline in the western European population (Jensen & Lutz 2006). Although the precise size of the French hunting bag was unknown, Black- and Bar-tailed Godwits *Limosa* spp. represented an estimated 16% to 25% of the 11 species of coastal waders bagged annually in France in the 1990s (Trolliet & Girard 2000), i.e. at the time when water bird hunting was allowed from early August to late February (Jensen & Lutz 2006). Moreover, since the start of the International Wetland Census in France in the mid 1970s, very few coastal areas that included appropriate habitats for the species benefited from the legislation that protected them (Caillot 2012). An extension of carrying capacity into an area with protection from human disturbances and predation could lead to the increase of some waterbird populations (Jackson et al. 2004). The increase in the number of reserves that have high level of protection for birds over the last 30 years within the national territory (Caillot 2012) could act as tool for the conservation of waterbirds, in particular Black-tailed Godwits which are highly specialized to a restricted number of feeding habitats (Robin et al. 2013).

Given the general distribution and migration patterns of the Black-tailed Godwit, France, with 6,460 km of shoreline and its many inland wetlands, has several potential wintering grounds for *L. l. islandica*. France has previously been estimated, to welcome up to c. 14,000 *L. l. islandica* individuals in January (see Triplet et al. 2007). However, very little is known about the importance and use of French sites and their role in the context of the distribution according to the buffer effect described for the British Isles.

In this study, we assessed long-term trends and as well as changes in distribution of wintering Black-tailed Godwits along the coasts of France. We analysed International Wetland Count data collected since 1977 and the synchronized monthly counts on the main wintering sites (2000–2010). We have updated and discussed the importance of the French coasts as one of the main wintering regions of *L. l. islandica* in Western Europe. We have examined the long-term trend of a medium-migrating species in just one part of the whole area of its distribution area, taking into account the creation of protected areas over the past thirty years.

MATERIAL AND METHODS

The International Wetland Counts data

Collection of the International Wetland Counts (IWC) data for waterbirds in winter began in France in 1976 (Deceuninck & Mahéo 2000). This scheme covers every estuary and major non-estuarine area holding large numbers of waders in mid-January (Deceuninck & Mahéo 2000). Those shorebird counts have been summarized by Mahéo (1977–2010). The locations of the major coastal survey sites are presented in Fig. 1A according to Deceuninck et al. (2008). The coast of the Channel is defined as extending from the Belgian border to Brest (Brittany), while the Atlantic coast extends from Brest to the Spanish border, and the French Mediterranean coast includes also the coast of Corsica (Fig. 1A).

Monthly counts

Exhaustive counts were made on around the 15th day of each month from the year 2000 onwards using a standardized method within a network of 16 National Nature Reserves along the Channel and Atlantic coasts (Fig. 1B, Appendix 1). This long-term survey was initiated by the Observatory of Coastal Shorebirds under the auspices of the "Reserves Naturelles de France" (network of National Nature Reserves). This scheme divides every site into functional units, including feeding area, and the pre-roost and roost areas. Depending on the site, the counts are made during roosting or at low tide in the intertidal zone using a telescope. The results of these counts are summarized annually by Caillot & Elder (2000–2010). The so-called Pertuis Charentais area includes the bays of Aiguillon, Yves, Marennes-Oléron and Ré Island; the South Brittany area

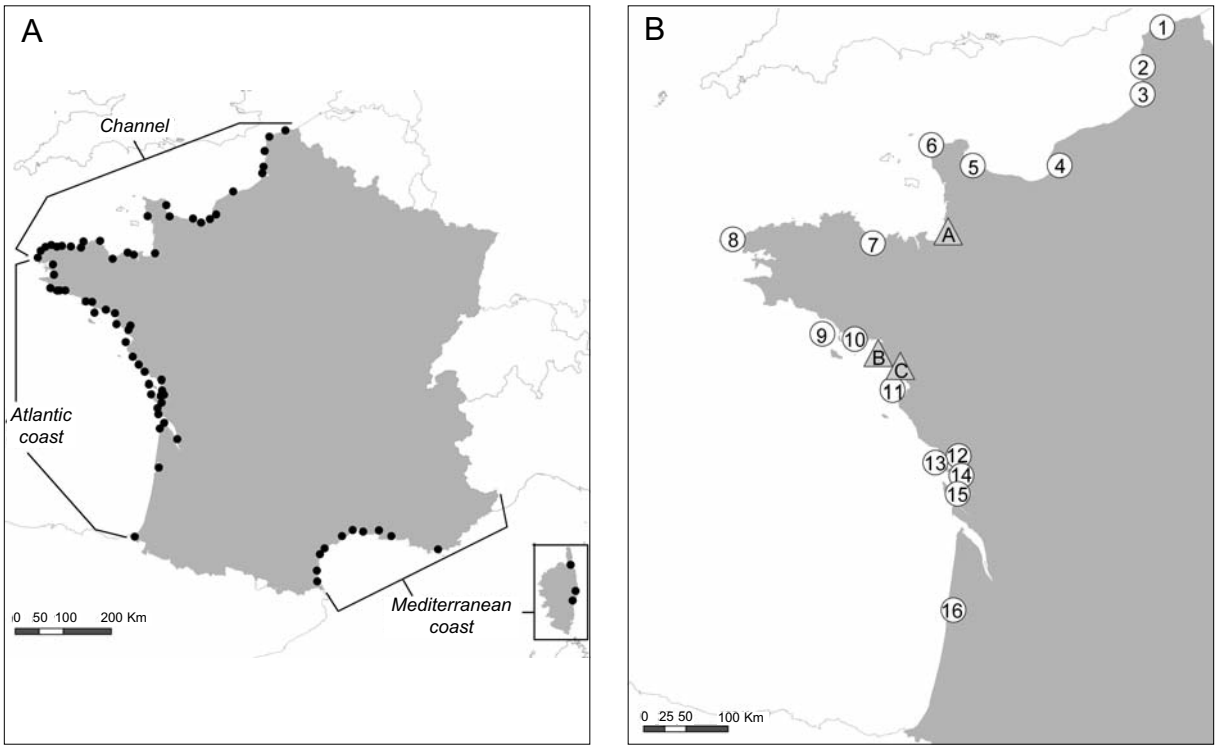

Fig. 1. Locations of major coastal survey sites (black dots) of the annual International Waterbird Census in mid-January (A) and of the National Nature Reserves (numbered circles, see Appendix 1) belonging to the Observatory of Coastal Shorebirds (B). Triangles indicate sites of national or international importance for Black-tailed Godwits that were not surveyed monthly.

includes the sites in the Morbihan Gulf, Guérande Peninsula, Loire Estuary and Bourgneuf Bay. The data presented for Mont Saint-Michel Bay were extracted from a previous study reported by Le Dréan Quenech'du et al. (1995) but which only covers two years. The numbers of Black-tailed Godwits on the Guérande Peninsula were provided by the "Ligue pour la Protection des Oiseaux" of the Loire-Atlantique. Counts were made from October to April between in the winters of 2000–2001 and 2008–2009.

The size of the functional unit for waders and the surface area, the dates of creation of the sites, including the protected areas participating in the Observatory of Coastal Shorebirds and other main wintering sites for the species were established from report of "Reserve Naturelle de France" (Caillot 2012).

Data analysis

Trend analysis was carried out on the basis of population indices computed using the TRIM software, which generates missing values (Trends and Indices for Monitoring Data, version 3.0; Pannekoek & van Strien 2005).

RESULTS

Winter distribution and long-term trends

Between 1977 and 2010, the total number of Black-tailed Godwits counted in France in January ranged between a minimum of c. 3,600 individuals in 1991 (1990 was not taken into consideration because no count was made at the main site in Aiguillon Bay) and a maximum of c. 27,000 individuals in 2010 (Fig. 2). In the late 1970s and early 1980s, the winter population was c. 10,000 individuals and subsequently declined until 1990–1991 (Fig. 2; $y = 0.0054x^2 - 21.6400x + 21519$, $r^2 = 0.89$). During the early 1990s, the population began to increase regularly, reaching a maximum in 2010 (Fig. 2). The number of individuals increased steadily from the mid-1990s, from very low number in South Brittany ($y = 0.0019x^2 - 7.5164x + 7487$, $r^2 = 0.91$) to more than 6,000 individuals in recent years. The pattern of the long-term trend for Pertuis Charentais area was closer to that for the whole of France, given that most of the individuals are located in this area. The Godwits were distributed across a very limited number of sites before the mid-1990s (Fig. 3). The general increase

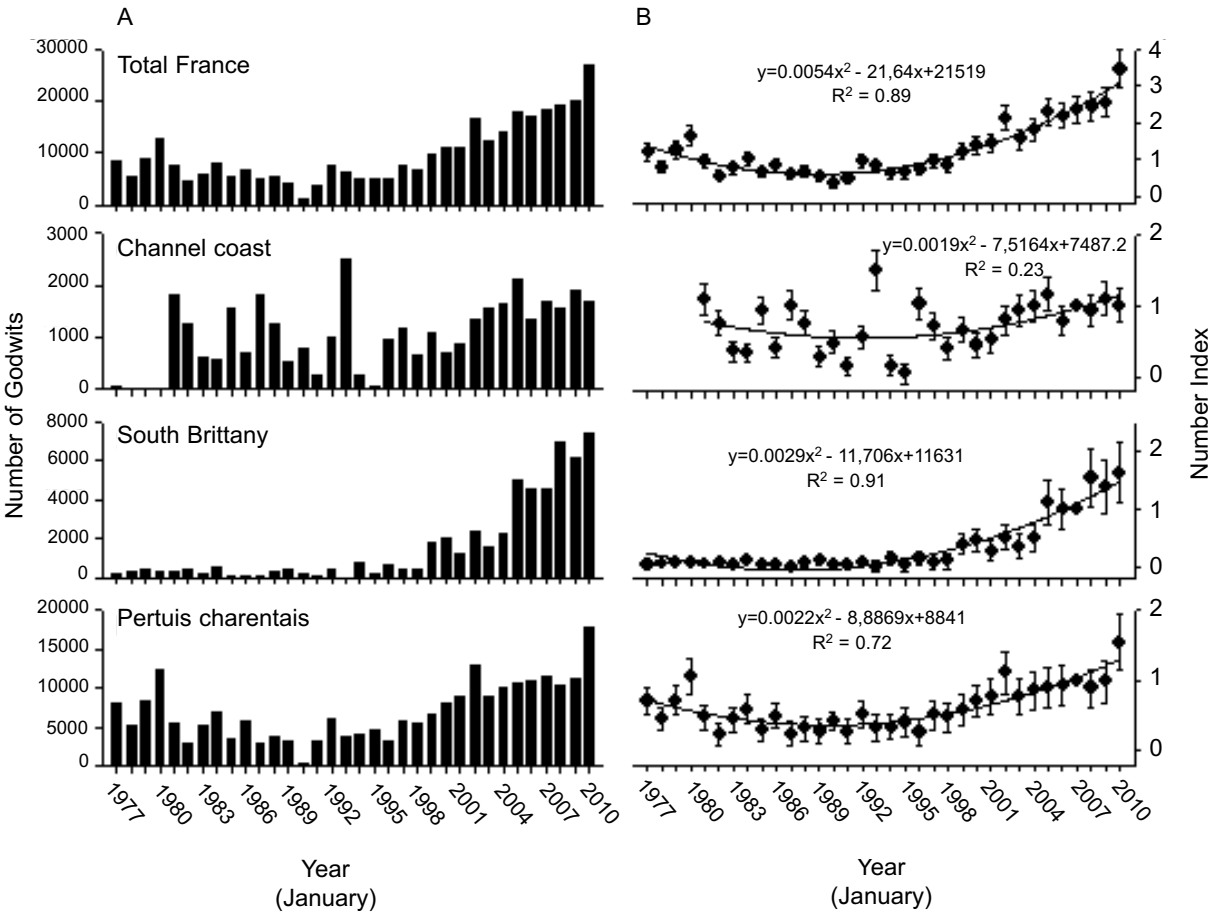

Fig. 2. Variations in numbers (A) and TRIM index (B) of Black-tailed Godwits in January in France between 1977 and 2010 (IWC counts) with distinctions between the Channel coast, South Brittany and Pertuis Charentais.

in this species corresponds to the use of new sites over the last two decades. The Mediterranean coast was excluded from the analysis since less than 0.5% of total number of individuals were counted there in the winter. During the 1980s, between 82% and 97% of the wintering population was concentrated at only two sites: Mont Saint-Michel Bay on the Channel coast and Aiguillon Bay in the Pertuis Charentais area (Figs 2, 3). In the 1990s, new sites were used more frequently by an increasing number of birds (from north to south: Somme Bay, Morbihan Gulf, Guérande Peninsula, Loire Estuary, Bourgneuf Bay, Ré Island, Yves Bay and Marennes-Oléron Bay) (Fig. 3). Mont Saint-Michel Bay was visited irregularly during this period (Coefficient of Variation = 92.3%) but Aiguillon Bay carried a regular number of Godwits (C.V. = 26.8%) and remained the major site. During the 2000s, these new sites continued to be exploited by ever increasing numbers of Godwits.

Phenology at major wintering sites

The mean numbers of Godwits per month (in 2000–2010) at all the main wintering sites (except Mont Saint-Michel) confirmed the presence of the species in France from July to April (Fig. 4). The highest mean number of Godwits was recorded in January (13,809 ± 2,011) but the mean number did not differ significantly between November, December, January and February (one way ANOVA, $F = 0.303$, $df = 3$, $p = 0.741$) (Fig. 4). At every site, Godwits were either rare or absent during the breeding season (May and June), and those individuals that were present were assumed to be second-year birds that were over-summering. We distinguished the Lay Estuary from the adjacent Bay of Aiguillon in the northern area of the Pertuis Charentais. None of the ten sites listed (north to south in Fig. 4) showed significantly different patterns of monthly variations in the distribution of Godwit numbers (Two-way ANOVA, $F = 55.87$, $df = 8$,

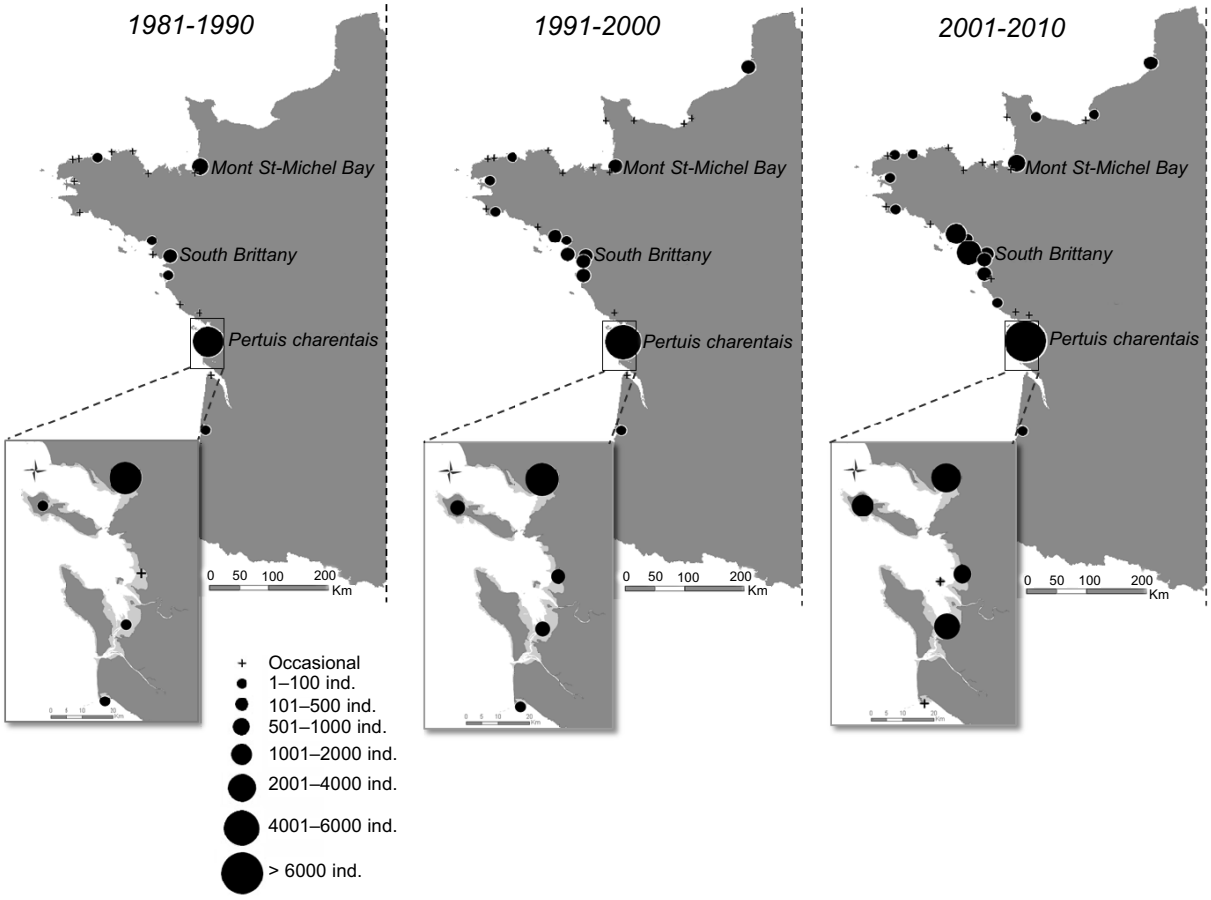

Fig. 3. Mean numbers of Black-tailed Godwits and their distribution in January along the coast of France for the decades 1981–1990, 1991–2000 and 2001–2010 (IWC counts).

$p < 0.001$, Mont Saint-Michel was excluded of the analysis) except between Ré Island and Guérande Peninsula (Student-Newman-Keuls all Pairwise Multiple Comparison, $p = 0.094$) between Lay Estuary and Yves Bay ($p = 0.054$) and between Bourgneuf Bay and Somme Bay ($p = 0.082$).

Godwits in protected areas

Between 1973 and 2005, the total protected coastal area that contained suitable habitats for Godwits increased from c. 4,000 ha to c. 28,000 ha (Fig. 5). In 1980, 97% of the c. 12,600 individuals were restricted to Aiguillon Bay, within the protected area of 2,300 ha, while in 2009, 95% of the c. 19,000 individuals were located at ten sites within the total protected area of 16,300 ha (Fig. 5). Hunting activities are totally prohibited within the limits of the protected area, but pressure by hunters could be high in the periphery (P. Delaporte – pers. comm.).

DISCUSSION

In this study, we mainly refer to *L. l. islandica* present in France from July to March (P. Bocher, unpublished data). Individuals of Icelandic and Continental populations can only be observed simultaneously at a few sites in France during the northward migration in February and March (Alves et al. 2010). The population size of the subspecies *L. l. islandica* has been estimated at about 47,000 individuals between 1999 and 2002 (Gunnarsson et al. 2005a) and at 75,000 individuals including juveniles in 2002 (Gudmundsson in Kirby & Scott 2009).

In the British Isles, the maximum number counted was c. 37,000 individuals in September 2004 in the United Kingdom (Cranswick et al. 1999, Baker et al. 2006, Banks et al. 2006, Musgrove et al. 2007) and at c. 11,000 individuals in January 2006 in the Republic of Ireland (Boland & Crowe 2004–2006). In the UK, after the arrival of

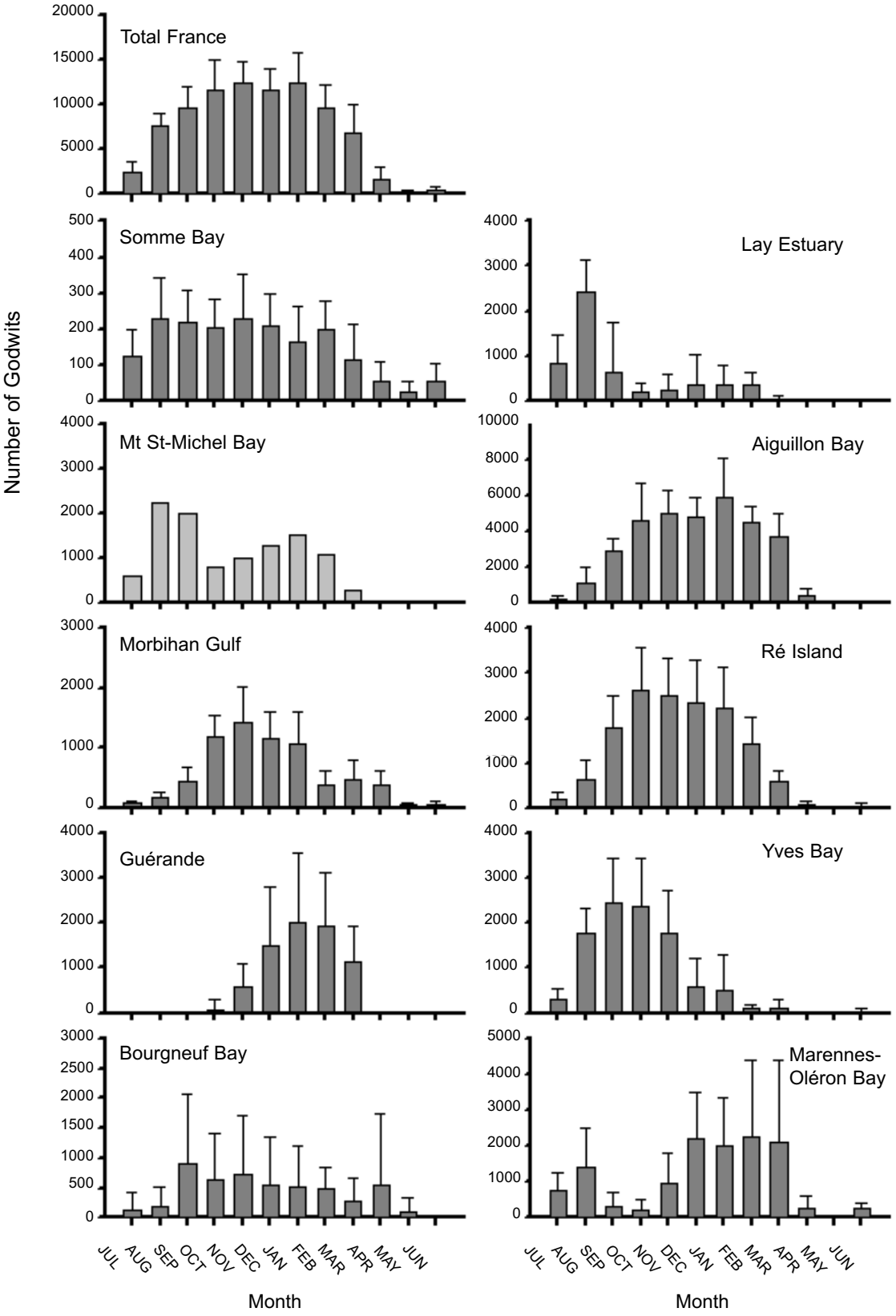

Fig. 4. Mean numbers of Black-tailed Godwits per month (2000–2010) in France and per main wintering sites cited in Appendix 1. The data presented for Mont Saint-Michel Bay were extracted from Le Dréan Quenech'du et al. (1995).

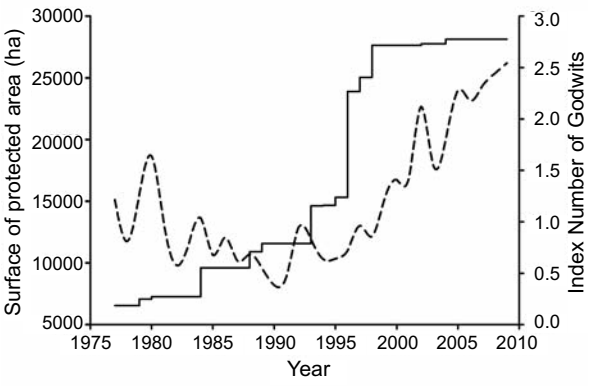

Fig 5. Variations in TRIM number index of Black-tailed Godwits in January in France between 1977 and 2009 (dashed line) and surface of protected area in suitable habitats for Godwits per year.

large numbers in the autumn, the number of individuals decreases until January to approximately 50–60% of the autumn number, reaching c. 20,000 individuals during the period 2004–2008 (Banks et al. 2006). Alves et al. (2010) estimated that Iberia supports c. 15,000 individuals. Over the period 2003–2007, 17,000 individuals were on average present on the coasts of France in January. Thus, the *L. l. islandica* population in Western Europe in winter (January) was divided between Ireland (c. 9,000 individuals, 15%), the United Kingdom (c. 20,000 individuals, 33%), Iberia (c. 15,000 individuals, 24%) and France (28%).

The *L. l. islandica* population is one of the rare shorebird populations to have been increasing in numbers since the 1920s (Gunnarsson et al. 2005b, 2006). Consequently, the wintering numbers, at least in the UK, have been gradually increasing, with the 1996–1997 population index for Britain (Waters et al. 1998) being more than three times that of the base year (1972–1973). Based on the count in winter 2007–2008, this number has continued to increase locally (Musgrove et al. 2007). In France, the pattern of long-term changes differ — numbers have not increased steadily from the base year (1977), but declined between 1977 and 1991 and then increased progressively to reach a maximum in 2009 (c. 20,000 individuals). It thus appears that France could be welcoming some of the new individuals produced each year (i.e. juveniles), although it is not possible to determine the exact proportion. The exceptional recording of c. 27,000 individuals in January 2010 probably reflects the severe climatic conditions in northern Europe, as it did in 2002.

Along the French coast, the gradual increase in the number of wintering Godwits since the early 1990s has led to the spread of the species to new sites (a maximum of over 3,000 individuals at Guérande, Yves and Ré), while the two traditional sites at Mont Saint-Michel and Aiguillon have retained approximately the same numbers of birds. In 2008, eight sites in France could be classified as being of international importance (> 470 individuals, Ramsar criteria n°6) for the species. The expansion of their range in the UK has followed the pattern of buffer effect theory, with traditional sites being occupied first and new sites of lower quality being filled up later (Gill et al. 2001a,b, Norris et al. 2004). The eight main wintering sites in France are progressively occupied from August, reaching peak occupation in late autumn or early winter. The contrasting phenologies between the British isles (Banks et al. 2006, Musgrove et al. 2007) and France seems to indicate that, after the breeding season, most of the *L. l. islandica* individuals first arrive in the United Kingdom, after which some of the birds move to southern sites in either France or Iberia. Given the high number of Godwits recorded in September in the UK (> 30,000 birds), it is likely that very few birds fly directly to France from Iceland.

The distributions and peak numbers differed between sites in France; we thus suspected there to be substantial movements between sites. These differences could even be due to the continuing movements of Godwits either arriving from or leaving for the British Isles and Iberia. During the pre-breeding period (February to April), only the Marennes-Oléron Bay site displays a noteworthy increase in Godwits, which may correspond to a stopover by continental and/or Icelandic Godwits arriving from Iberia (Lourenço et al. 2010), or it may be the next stopover site for the Icelandic birds (Kirby & Scott 2009). Other coastal sites are deserted in favour of proximate inland marshes or meadows, as observed in the Marais Poitevin in the north of the Pertuis Charentais and in the Marais Breton, West of Bourgneuf Bay (F. Robin pers. obs.).

The distribution of the increasing number of Godwits needs to be investigated on a larger scale in order to identify whether *L. l. islandica* individuals wintering in France disperse overtime, dependent on accessibility, to higher quality sites, i.e., depending on their food resources, roost availability, etc. (Gill et al. 2001a,b). In addition to differences in the intrinsic quality of sites (Goss-Custard et al. 2002, van Gils et al. 2004), another

explanation for the recent distribution of Godwits could be the creation of protected areas with suitable habitats that are exempt from hunting or other major human disturbances. Between 1973 and 2005, the total area of protected coastal region with suitable habitats for Godwits increased considerably in France from c. 4,000 ha to c. 28,000 ha (Fig. 5). The creation of Nature Reserves throughout the 1990s could have contributed to the increase in the number of Godwits in France in the context of the general increase in the size of the population, absorbing individuals exceeding the carrying capacities of sites in the British Isles. On the other hand, the increase in the carrying capacity of the French coast could have contributed to an increase in the survival of individuals and could consequently have led to a higher number of breeding birds in Iceland as a result of chick production. Nevertheless, the number of Godwits decreased in France between 1977 and 1991. Moreover, some sites such as Ré, Yves and Moëze were not used until several years had elapsed after their classification as protected areas. Consequently, the increased protection of suitable areas does not appear to be the only explanation for the increasing residence of Godwits in France.

Recent legislative changes in France have led to less hunting in August and an earlier closing of the season, by the end of January. Given that 95% of Icelandic Godwits were concentrated in the winter within eight sites classified totally or partially as protected areas, the annual bag of Godwits could have consisted mainly of continental Godwits shot during the autumn and spring migrations (Trolliet & Girard 2000). The recently established closing dates for hunting in late January will protect the continental subspecies during the spring migration. However, locally, hunting activities could remain the main factor influencing the distribution of Black-tailed Godwits at sites such as the Arçay Estuary, where birds leave the site as soon as the hunting season begins, moving to the adjacent Nature Reserve of Aiguillon Bay (E. Joyeux pers. comm).

The increase in the number of suitable habitats classified as Nature or Hunting Reserves may have favoured the continued increase in the number of *L. l. islandica* individuals in France during the last 20 years. However, we were unable to prove a direct relationship between these two events. The decline in the number of hunters in France in recent years may also have contributed to reducing the pressure on the species over the last few decades. The western coast of France appears consequently to be a crucial area for the wintering survival of almost a third of the *L. l. islandica* population. During migration phases, the area of the Pertuis Charentais and especially the coastal marshes, which are located on the migratory route of *L. l. limosa* between The Netherlands and Iberia–Africa, could provide an essential stopover area for some individuals and, therefore, should benefit their conservation. Subsequently, the maintenance of habitat quality in wintering and migration sites in France appears to be a key issue at the European level in the preservation of both populations.

ACKNOWLEDGEMENTS

We are grateful to all the anonymous volunteers participating in the International Wetland counts. We thank the managers and data recorders of the Nature Reserves and other site members of the Observatory of Coastal Waders: Alexandre Driencourt (RNN Platier d'Oye), David Lavogiez (RNN Baie de Canche), Patrick Triplet and François Sueur (RNN Baie de Somme), Christophe Aulert (RNN Estuaire de Seine), Jean-François Elder (RNN Domaine de Beauguillot), Thierry Demarest (RNN Mare de Vauville), Alain Ponsero (RNN Baie de Saint-Brieuc), Jean-Yves Legal (RNN Iroise), Catherine Robert (RNN François Le Bail), Guillaume Gélinaud (RNN Marais de Séné), Franck Latraube (RCFS Le Massereau), Didier Desmots (RNN Marais de Müllembourg), Emmanuel Joyeux and Frédéric Corre (RNN Baie de l'Aiguillon), Marie Laure Cayatte and Cyril Goulevant (RNN Marais d'Yves), Jean-Christophe Lemesle (RNN Lilleau des Niges), Régis Marty (RNR Polder de Sébastopol), Philippe Delaporte (RNN Marais de Moëze-Oléron), and Jean-Christophe Le Noc (RNN Banc d'Arguin).

REFERENCES

Alves J. A., Lourenço P. M., Piersma T., Sutherland J., Gill J. A. 2010. Population overlap and habitat segregation in wintering Black-tailed Godwits. Bird Study 57: 381–391.

Baker H., Stroud D. A., Aebischer N. J., Cranswick P. A., Gregory R. D., McSorley C. A., Noble D. G., Rehfisch M. M. 2006. Population estimates of birds in Great Britain and the United Kingdom. Brit. Birds 99: 25–44.

Banks A. N., Collier M. P., Austin G. E., Hearn R. D., Musgrove A. J. 2006. Waterbirds in the UK 2004/2005: the wetland bird survey. BTO/WWT/RSPB/JNCC, Thetford, UK.

Boland H., Crowe O. 2004–2006. Irish wetland bird survey: results of waterbird monitoring in the Republic of Ireland. BirdWatch Ireland, Newcastle, Co. Wicklow.

Brown J. L. 1969. The buffer effect and productivity in tit populations. Am. Nat. 103: 347–354.
Caillot E. 2012. Section F. Généralisation de l'Observatoire „Littoral, limicoles et macrofaune benthique" RNF aux aires marines protégées. Bilan de l'existant et perspectives d'extension. RNF-AAMP-ACHB.
Caillot E., Elder J. F. 2000–2010. Synthèses annuelles, dénombrements mensuels des limicoles côtiers. Observatoire des limicoles côtiers, RNF.
Colwell M. A. 2010. Shorebird ecology, conservation, and management. University of California Press, Berkeley, USA.
Cranswick P. A., Pollitt M. S., Musgrove A. J., Hughes R. C. 1999. The wetland bird survey 1997–98: wildfowl and wader counts. BTO/WWT/RSPB/JNCC, Slimbridge, UK.
Deceuninck B., Mahéo R. 2000. Synthèse des dénombrements et analyse des tendances des limicoles hivernant en France 1978–1999. Ligue pour la Protection des Oiseaux/Wetlands International.
Deceuninck B., Mahéo R., Gabillard F. 2008. Wader population estimates in France resulting from the 1997/1998 non-estuarine coastal waterbird survey. In: Burton N. H. K., Rehfish M. M., Stroud D. A., Spray C. J. (eds). The European non-estuarine coastal waterbird survey. International Wader Studies 18. International Wader Study Group, Thetford, UK, pp. 20–30.
Delany S., Scott D., Dodman T., Stroud D. A. 2009. An atlas of wader populations in Africa and Western Eurasia. Wetlands International, Wageningen, The Netherlands.
Gill J. A., Langston R. H. W., Alves J. A., Atkinson P. W. et al. 2007. Contrasting trends in two Black-tailed Godwit populations: a review of causes and recommendations. Wader Study Group Bull. 114: 43–50.
Gill J. A., Norris K., Potts P., Gunnarsson T. G., Atkinson P. W., Sutherland W. J. 2001a. The buffer effect and large-scale population regulation in migratory birds. Nature 412: 436–438.
Gill J. A., Sutherland J., Norris K. 2001b. Depletion models can predict shorebird distribution at different spatial scales. P. Roy. Soc. Lond. B 268: 369–376.
Goss-Custard J. D., Stillman R. A., West A. D., Caldow R. W. G., McGrorty S. 2002. Carrying capacity in overwintering migratory birds. Biol. Conserv. 105: 27–41.
Gunnarsson T. G., Gill J. A., Appleton G. F., Gislason H., Gardarsson A., Watkinson A. R., Sutherland W. J. 2006. Large-scale habitat associations of birds in lowland Iceland: implications for conservation. Biol. Conserv. 128: 265–275.
Gunnarsson T. G., Gill J. A., Petersen A., Appleton G. F., Sutherland W. J. 2005a. A double buffer effect in a migratory shorebird population. J. Anim. Ecol. 74: 965–971.
Gunnarsson T. G., Gill J. A., Potts P. M., Atkinson P. W., Croger R. E., Gélinaud G., Gardarsson A., Sutherland W. J. 2005b. Estimating population size in Black-tailed Godwits *Limosa limosa islandica* by colour-marking. Bird Study 52: 153–158.
Jackson S. F., Kershaw M., Gaston K. J. 2004. The buffer effect and the selection of protected areas for waterbirds in Britain. Biol. Conserv. 120: 137–143.
Jensen F. P., Lutz M. 2006. European Union action plan for Black-tailed Godwit *Limosa limosa* 2006–2008. DDH Consulting, Roskilde, Danmark & Station Biologique de la Tour du Valet Le Sambuc, France.
Kirby J., Scott D. 2009. The Black-tailed Godwit *Limosa limosa*. In: Delany S., Scott D., Dodman T., Stroud D. (eds). An atlas of wader populations in Africa and Western Eurasia. Wetlands International, Waningen, The Netherlands.
Kluyver H. N., Tinbergen L. 1953. Territory and the regulation of density in titmice. Archives of Néerland De Zoology 10: 265–289.
Le Dréan Quenech'du S., Mahéo R., Boret P. 1995. The Mont Saint-Michel Bay: a site of international importance for wintering and migrating palearctic waders. Wader Study Group Bull. 77: 50–54.
Lourenço P. M., Kentie R., Schroeder J., Alves J. A., Groen N., Hooijmeijer J., Piersma T. 2010. Phenology, stop-over dynamics and population size of migrating Black-tailed Godwits *Limosa limosa limosa* at a key staging area, the Tejo and Sado rice plantations. Ardea 98: 35–42.
Mahéo R. 1977–2010. Limicoles séjournant en France (littoral); contribution française aux dénombrements internationaux des oiseaux d'eau organisés par wetlands international. Reports Office National de la Chasse et de la Faune Sauvage.
Musgrove A. J., Collier M. P., Banks A. N., Calbrade N. A., Austin G. E. 2007. Waterbirds in the UK 2005/06: the wetland bird survey. BTO/WWT/RSPB/JNCC, Thetford, UK.
Norris K., Atkinson P. W., Gill J. A. 2004. Climate change and coastal waterbird populations — past declines and futures impacts. Ibis 146: 82–89.
Pannekoek J., van Strien A. 2005. Trim 3.0 for Windows (trends and indices for monitoring data, 2005. Statistics Netherlands, Voorburg.
Robin F., Piersma T., Meunier F., Bocher P. 2013. Expansion into an herbivorous niche by a customary carnivore: black-tailed god wits feeding on rhizomes of *Zostera* at a newly established wintering site. Condor 115: 1–8.
Robin F., Robin J-G., Dulac P., Guéret J-P., Piersma T. 2012. Current state of Black-tailed Godwits *Limosa limosa limosa* breeding in France. Wader Study Group Bull. 119: 133–136.
Rodenhouse N. L., Sillett T. S., Doran P. J., Holmes R. T. 2003. Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. P. Roy. Soc. Lond. B. 270: 2105–2110.
Ricklefs R. E. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. Condor 102: 9–22.
Sutherland W. J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford, UK.
Triplet P., Mahéo R., Le Dréan Quenech'du S. 2007. La barge à queue noire *limosa limosa islandica* hivernant en france-littoral manche atlantique, 1977–2006. Alauda 75: 389–398.
Trolliet B., Girard O. 2000. Le vanneau huppé, le pluvier doré et autres limicoles. In: Landry P., Migot P. (eds). Enquête nationale sur les tableaux de chasse à tir, saison 1998–1999. Cahiers techniques. pp. 168–183.
van Gils J. A., Edelaar P., Escudero G., Piersma T. 2004. Carrying capacity models should not use fixed prey density thresholds: a plea for full application of the tools of behavioural ecology. Oikos 104: 197–204.
Waters R. J., Cranswick P. A., Musgrove A. J., Politt M. S. 1998. The wetland bird survey 1996–97: wildfowl and wader counts. BTO/WWT/RSPB/JNCC, Slimbridge, UK.
Weller M. W. 1999. Wetland birds: habitat resources and conservation implications. Cambridge University Press, Cambridge.

STRESZCZENIE

[Rozmieszczenie, fenologia i długoterminowe trendy liczebności populacji rycyka zimującej na wybrzeżu Francji]

Tereny odpowiednie dla wędrujących lub zimujących ptaków mogą nie być przez nie wykorzystywane w związku z różnymi zakłóceniami

antropogenicznymi, w szczególności w związku z aktywnością łowiecką. Zanik takiej presji na poszczególnych obszarach, a także wieloletnie dane o rozmieszczeniu i liczebności poszczególnych gatunków pozwalają na określenie roli nowo dostępnych odpowiednich terenów w regulacji liczebności populacji.

W zachodniej Europie jednym z niewielu gatunków ptaków siewkowych o wzrostowym trendzie liczebności jest podgatunek rycyka *Limosa limosa islandica*. Podgatunek ten gniazduje na Islandii, a jego głównymi terenami zimowiskowymi są wybrzeża Francji Na terenie tego kraju odnotowano wzrost powierzchni terenów podlegających ochronie, co mogło mieć wpływ na liczebność i rozmieszczenie ptaków, a także wprowadzono pięcioletni zakaz polowań na rycyki. Celem pracy było opisanie długoterminowych zmian liczebności oraz rozmieszczenia zimujących rycyków na wybrzeżu Francji.

Dane o liczebności i rozmieszczeniu rycyka zebrano w ramach międzynarodowego programu liczenia ptaków wodno-błotnych, prowadzonego od 1976 r., na kilkudziesięciu stanowiskach wzdłuż wybrzeża Francji, oraz w ramach comiesięcznych liczeń ptaków na terenie 16 rezerwatów przyrody (Fig. 1, apendyks 1). Liczebność zimujących we Francji rycyków spadała do początku lat 90. XX wieku, a następnie zaczęła rosnąć, osiągając maksimum — 27 tys. ptaków — zimą 2010 r. (Fig. 2). Autorzy szacują, że we Francji zimuje ok. 28% światowej populacji rycyka podgatunku *L. l. islandica*. W latach 80. XX wieku, 82–97% zimującej populacji obserwowane było tylko na dwóch stanowiskach — Zatoce Wzgórza Świętego Michała (Normandia) oraz w okolicy ujścia rzeki Charente (Fig. 3). W kolejnych latach rosło znaczenie innych miejsc zimowania, szczególnie w południowej Bretanii (Fig. 3). Główne tereny zimowisk są wykorzystywane przez rycyki od sierpnia, a najwięcej ptaków obserwowanych jest późną jesienią i wczesną zimą (Fig. 4).

Wzrost powierzchni terenów chronionych najprawdopodobniej przyczynił się do do wzrostu liczebności (Fig. 5), a także zmian w rozmieszczeniu zimujących rycyków. Autorzy, porównując występowanie rycyków w kolejnych miesiącach na wybrzeżu Francji, sugerują, że większość ptaków leci po sezonie lęgowym najpierwna Wyspy Brytyjskie, a dopiero potem część z nich przelatuje do Francji. Tylko niewielka liczba ptaków leci bezpośrednio do Francji

Appendix 1. Size of functional unit (feeding area over roost area) for waders and surface area of protected areas in the 19 Channel-Atlantic survey sites participating in the Observatory of Coastal Shorebirds (numbered from 1 to 16), and the other main wintering sites (letters A-C), with their relative importance for Black-tailed Godwits in winter (mean number ± SD January 2000 to 2010).

Site	Location on Fig. 1B	Area of the functional or length of coastline	Area of Nature Reserve included	Area preserved of hunting activities included	Area of mud-sandflat	Mean unit number of Godwits in January
Channel						
Platier d'Oye	1	485 ha	391 ha	-	242 ha	occasional
Canche Bay	2	4000 ha	505 ha	750 ha	1000 ha	occasional
Somme Bay	3	7000 ha	2800 ha	-	2800 ha	163 ± 100
Seine Estuary	4	21900 ha	8528 ha	-	1703 ha	occasional
Veys Bay	5	4500 ha	505 ha	135 ha	3375 ha	occasional
Vauville Cove	6	10 km	62 ha	-	-	occasional
Mt St-Michel Bay	A	24000 ha		3000 ha	20000ha	1126 ± 316
Saint-Brieuc Bay	7	3000 ha	1140 ha	-	2895 ha	occasional
Molène Archipelago	8	752 ha	39 ha	76 ha	Absent	occasional
Atlantic Coast						
Groix Island	9	25 km	98 ha	-	200 ha	occasional
S Brittany						
Morbihan Gulf	10	18705 ha	410 ha	7358 ha	5460 ha	1068 ± 552
Guérande Peninsula	B	3000 ha	-	-	-	1997 ± 1563
Loire Estuary	C	22000 ha	-	4560 ha	1000 ha	146 ± 162
Bourgneuf Bay	11	5000 ha	181 ha	4200 ha	4200 ha	510 ± 686
Pertuis Charentais						
Aiguillon Bay & Lay Estuary	12	7535 ha	4900 ha	1035 ha	6135 ha	6188 ± 2003
Ré Island	13	6850 ha	369 ha	-	5250 ha	3000 ± 921
Yves Bay	14	3192 ha	192 ha	2000 ha	3000 ha	505 ± 786
Marennes-Oléron Bay	15	18000 ha	6720 ha	-	10000 ha	2000 ± 1375
Arcachon Bay	16	19000 ha	3766 ha		12290 ha	220 ± 152