

Rise in human activities on the mudflats and Brent Geese (*Branta bernicla*) wintering distribution in relation to *Zostera* spp. beds: a 30-year study

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Abstract Human activities may restrict access of wintering birds to their food resources, but habitat destruction and fragmentation may interact with disturbance to reduce carrying capacity. We analysed the abundance and distribution of wintering Brent Geese (*Branta bernicla*) in a major French wintering site from 1970 to 2000, when they experienced increases in human foreshore activities. We used mixed-effects models to test whether spatial extent of two *Zostera* species, *Z. noltii* and *Z. marina*, influenced the distribution of Brent Geese. The number of geese increased significantly with the area of both *Zostera* species beds. However, the relationship changed in the period after the increase in human activities. More specifically, fragmentation of the most accessible food resource, *Z. noltii*, negatively affected Brent Goose distribution. This

fragmentation was in turn increased by human activities and reduced by the protection of *Z. noltii* (by banning human access). This implies that direct disturbance, although not excluded, might not have been the major cause of changes in Brent Goose distribution, but rather the effects of human activities on food resources. Thus, our results show that establishment of resource protection areas are efficient as conservation measures, and they underline the need for studies of impacts of human activities on resources, in addition to disturbance effects.

Keywords Disturbance · Refuge design · Shell harvesting · *Z. marina* · *Z. noltii*

Introduction

Increasing human population density places increasing pressure on habitats and species, and when animals specialise on a given resource, habitat or food item, human activities may have dramatic effects on their distribution and abundance (Dolman and Sutherland 1995; Rodriguez-Prieto and Fernandez-Juricic 2005). Most avian studies have focused on direct disturbance effects of human activities (Madsen and Fox 1995; Carney and Sydeman 1999; Blumstein et al. 2005; Fernandez-Juricic et al. 2005), which can be exploited (Goss-Custard et al. 2006) to optimise refuge design (Fox and Madsen 1997; Lafferty et al. 2006). Nevertheless, changes in resource extent and quality need to be considered before drawing definitive conclusions about direct human-induced disturbance effects on the distribution and abundance of birds (Percival et al. 1998; Gill et al. 2001a, 2001b).

Dark-bellied Brent Geese (*Branta bernicla bernicla*) traditionally eat eelgrasses *Zostera marina* and *Z. noltii*

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during winter (Ganter 2000). Throughout Europe, *Zostera* spp. beds face threats from physical destruction as well as water quality and climate changes (Phillips and McRoy 1980; Short et al. 1988; Hily et al. 2002) and so have gained high conservation value (Water Framework Directive 2000/60/EC, Habitats Directive 92/43/EEC). Many pressures have the potential to modify the distribution and abundance of *Zostera* spp. and hence the primary food resource of Brent Geese, which are themselves listed in the Birds Directive (79/409/EEC). So the association between Brent Geese and *Zostera* spp. is of high conservation interest. Extensive human modification of coastal ecosystems has caused critical habitat loss to wintering and staging waterbirds (Schekkerman et al. 1994). So human activities may have greater effects on wintering Brent Geese through habitat modification than direct disturbance, for instance by the partial destruction and fragmentation on *Zostera* spp. beds (e.g. from shellfish farming or shell harvesting).

One-third of the world population of Dark-bellied Brent Geese winter in France (Ebbinge et al. 1999), the Gulf of Morbihan (NW of France) being one of the top four French wintering sites (Mahéo 1976; Gillier and Mahéo 1998). Numbers have fluctuated here between 1970 and 2000 (the maximum monthly count fluctuated between 6,100 and 31,600), during which time shellfish farming and clam harvesting have increased. Since the mid-1970s, the Japanese oyster (*Crassostrea gigas*) and, in 1980, the Manila clam (*Ruditapes philippinarum*), have been introduced for shellfish farming, and since free-living stocks of Manila clam appeared in 1991 (Bachelet et al. 1993), harvesting has thrived on the mudflats. Brent Geese primarily forage on the mudflats, creating potential conflicts between human activities and conservation obligations. As a result, patches of *Z. noltii* have been protected, i.e. designated areas have been preserved from human activities as a strategy for conserving these fragile systems.

Here, we tested whether an increase in human activities on the mudflats could have led to a decrease in Brent Geese abundance in the Gulf of Morbihan and/or changes in their distribution within the Gulf. Brent Geese distribution and abundance often mirror that of their food, *Zostera* spp., as documented in England (Percival et al. 1996). We thus first expected to explain the winter spatial distribution of Brent Geese by the areas of available *Zostera* spp. beds for any given winter. We also expected that the relationship may differ between *Z. noltii* and *Z. marina*, due to their difference in accessibility for Brent Geese. Indeed the latter, despite having larger leaves and potentially being more attractive, was much less accessible for Brent Geese because it was subtidal and seldom out of water. To test for a potential effect (direct or indirect) of an increase in human activities on Brent Geese, we defined two periods in

our 30-year study, separated by 6 years. The first period (nine winters between 1970 and 1983) presented low shellfish farming activity and no clam harvesting, and the second (five winters between 1989 and 2000) much higher shellfish farming activity, developed clam harvesting and protection of some patches of *Z. noltii*. We then tested for differences between the two periods in Brent Geese abundance and distribution, and in *Zostera* spp. characteristics, area and fragmentation, over the whole Gulf and distribution within the Gulf. We finally aimed at linking changes in Brent Geese numbers and distribution to changes in *Zostera* spp. bed characteristics, to *Z. noltii* protection and to human activities. In the case of an indirect effect of human activities on Brent Geese, i.e. effects on food resource, we expected changes in Brent Geese abundance/distribution to be linked with changes in *Zostera* spp. bed characteristics (area, protection status, fragmentation), themselves associated with the presence/absence of human activities (shellfish farming or clam harvesting) on the mudflats. Conversely, if the main effect of human activities was direct disturbance, then we expected to observe changes in Brent Geese abundance and/or distribution unrelated to changes in *Zostera* spp., but mostly linked with the distribution of shellfish farming and/or clam harvesting.

Methods

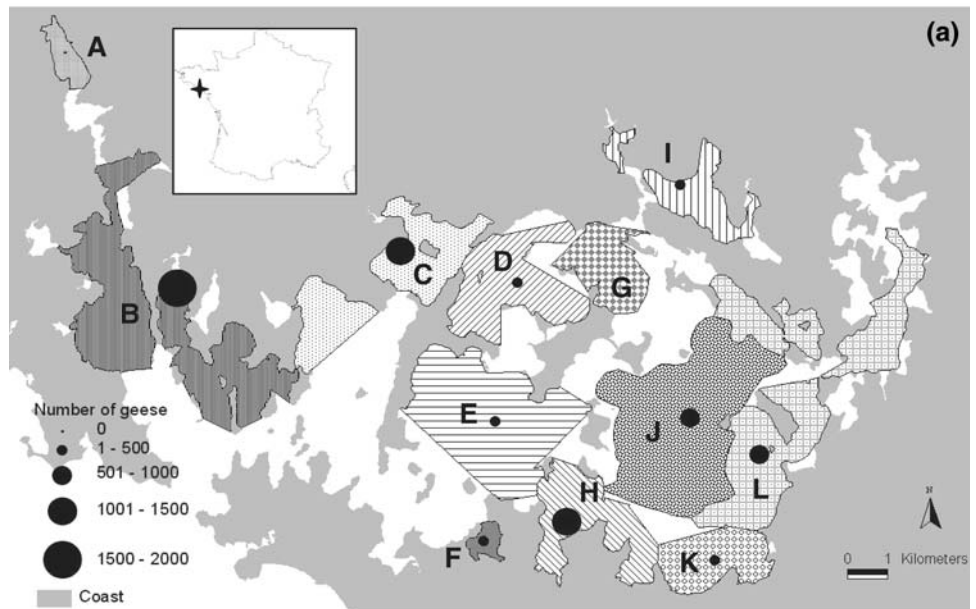
Study area and data collection

The Gulf of Morbihan (South Brittany, France; 47°34'N, 2°45'W; Fig. 1) is an almost fully enclosed sea area of 11,500 ha, connected with the Atlantic ocean by a narrow channel (Mahéo 1976). It is divided into western and eastern basins, separated by two islands. The Gulf comprises 7,000 ha of mudflats, where *Zostera* spp. can develop, of which an average of 4,300 ha is exposed at low tide.

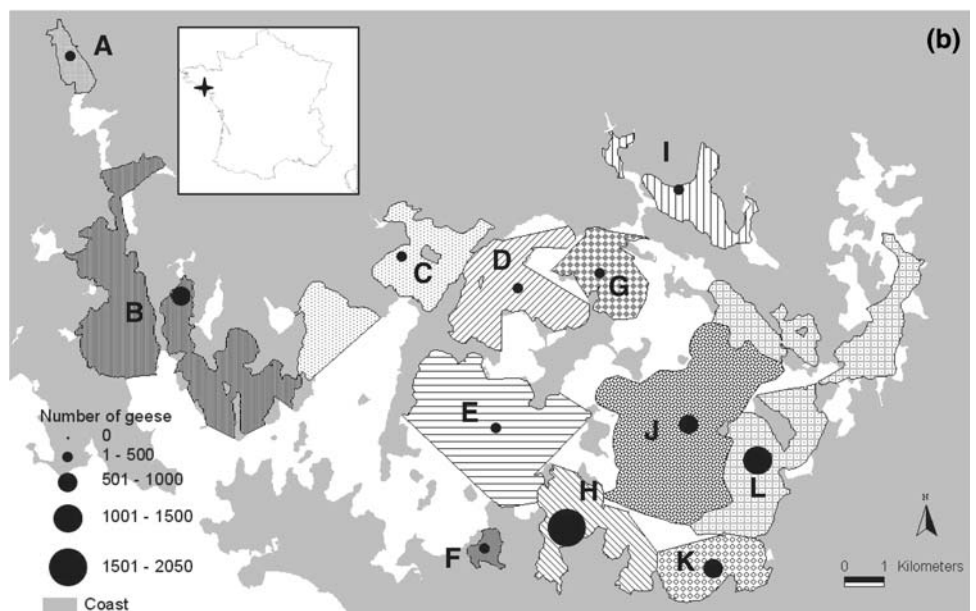
Two eelgrass species grow in the Gulf, the common eelgrass (*Z. marina*) and the dwarf eelgrass (*Z. noltii*). As *Z. noltii* occurs higher on the foreshore and is thus exposed during each low tide, most feeding time spent by Brent Geese is on *Z. noltii* beds, and less on the less accessible *Z. marina* beds. All *Zostera* spp. beds were mapped by ground survey four times between the years 1970 and 2000 (ground surveys were carried out from 1970 to 1972, from 1978 to 1982, in 1990–1991 and in 1999). The intertidal annual ecotype of *Z. marina* (sometimes called *Z. marina* var. *angustifolia*) also occurs in the Gulf, but is less abundant than the perennial one. The two ecotypes were mapped together. Maps of shellfishing activities were available from the local authorities (Affaires Maritimes),

Fig. 1 The Gulf of Morbihan with the 12 census zones and distribution maps of the mean monthly number of Dark-bellied Brent Geese (*Branta bernicla bernicla*): **a** the first period (between 1970 and 1983) and **b** the second period (between 1989 and 2000). Each pattern corresponds to a census zone and black circles indicate the numbers of Brent Geese

(P1: low levels of shellfish farming and harvesting)



(P2: high levels of shellfish farming and harvesting)



especially detailed maps of shellfish farming concessions and sites with clam harvesting. To harvest clams, people were walking on the mudflats, usually pulling half of a sailboard, and scratching the mud with a rake. They also dived in shallow waters to have access to places permanently submerged.

Monthly counts of Brent Geese were carried out by the same two people at falling tide, in 30 winters from October to March during the winters of 1970–1971 to 1999–2000. However, we did not analyse all these count data, because

we wanted to relate them to food abundance. So we dealt only with the winters for which we had information on *Zostera* spp. (i.e. 14 winters out of 30, see below).

Data processing

The study area was divided into 12 census zones (ranging from 56 to 1,277 ha), based on Brent Geese movements during a tidal cycle (Fig. 1). Brent Geese fed in different bays during a single tide cycle, and because not all bays

were counted simultaneously, some were grouped to avoid double counting. As inter-annual variation in *Zostera* spp. bed extent is minimal, we used the first map of *Zostera* spp. beds for the winters 1970–1971 to 1972–1973, the second for the winters 1977–1978 to 1982–1983, the third for the winters 1989–1990 to 1991–1992 and the fourth for the winters 1998–1999 to 1999–2000. We used count data from those years to examine the relationship between *Zostera* availability and Brent Geese distribution. Data between 1970 and 1983 constituted the first period and those between 1989 and 2000 constituted the second.

All the data were integrated into a geographic information system (ArcView 3.2). The following layers were built: (1) census zones, (2) spatial distribution of *Zostera* spp. ($n = 8$, four by species, i.e. one for each distribution map of each *Zostera* species), (3) shellfish farming concessions and (4) areas of highest densities of clam harvesters. This allowed us to generate new variables which we subsequently used in the analysis: the area and number of beds of each *Zostera* species in each census zone for each mapped year, the area of shellfish farming concessions per census zone, the census zones where there was clam harvesting ($n = 4$ census zones with, B, H, K and L, and $n = 8$ without) and the census zones where there was some *Z. noltii* protection ($n = 3$, H, K and L, corresponding to three out of four census zones with clam harvesting). It has to be pointed that *Z. noltii* protection was not applied to the entire beds, but on average to 60% of them (which represent about 25% of each respective census zone).

Statistical analyses

We analysed the determinant of goose numbers per census zone per month per winter ($n = 642$, with 326 values for the first period and 316 for the second) using mixed-effects models. The numbers were log-transformed for all analyses unless specified. The census zone, the winter and the month were included in the model as random effects to account for repeated measures, and the areas of each eelgrass species (covariate) and the period (factor) were included as fixed effects. We also included as a fixed effect covariate the world population of Brent Geese to account for between year differences in Brent Geese numbers. We used the ‘lmer’ function in the MASS package (Venables and Ripley 2002) in R 2.1.0 (R Development Core Team 2003), and performed a manual backward stepwise selection of the variables, based on their significance (kept when $P < 0.05$). We tested for the presence of spatial autocorrelation in both the raw data and the residuals of the final model, using variograms, and found none.

To test for changes in the numbers of Brent Geese between the two periods over the whole Gulf and changes

in distribution within the Gulf, we performed another mixed-effects model with the number of geese as a dependent variable ($n = 620$). The random effects were again the census zone, the winter and the month. The world population of Brent Geese, the period and the interaction between the period and the census zone were included as fixed effects. In the case of changes in Brent Geese abundance for the whole Gulf, we expected the period to be significant, and in the case of changes in Brent Geese distribution within the Gulf, we expected the interaction between the period and the census zone to be significant.

We also tested for changes between the two periods in total areas and distributions within the Gulf of areas of each *Zostera* species, by performing two generalised linear models (GLMs, one for each *Zostera* species) with a negative binomial error, with the area of *Zostera* spp. per zone as dependent variable ($n = 48$, for each *Zostera* species). We included the period, the census zone and the interaction between them as explanatory variables. Then, to test for changes in *Zostera* spp. fragmentation (i.e. numbers of patches) over the whole Gulf and inside the Gulf, we performed two GLMs (one for each *Zostera* species) with a ‘quasipoisson’ error, with the number of patches of *Zostera* spp. per zone as dependent variable ($n = 48$ for each *Zostera* species). As previously, we included the period, the census zone and the interaction between them as explanatory variables.

We then tested for a significant relationship between differences in numbers of Brent Geese in each census zone and significant differences in *Zostera* spp. characteristics (i.e. area and/or fragmentation) on the one hand and between differences in numbers of Brent Geese in each census zone and variables related to human activities on the other hand. The variables related to human activities were, per census zone: the presence/absence of clam harvesting, the presence/absence of *Z. noltii* protection and the proportion of the census zone covered by shellfish farming concessions. We performed two mixed-effects models with the difference between the two periods in mean numbers of Brent Geese per month per census zone as dependent variable ($n = 61$). The month and the census zone were included as random effects. The fixed effects were the differences in *Zostera* spp. characteristics on the one hand and the variables related to human activities on the other hand.

Finally, for differences in *Zostera* spp. significantly linked with differences in numbers of Brent Geese, we tested for a relationship between these differences and the variables related to human activities. We performed GLMs with a ‘quasipoisson’ error, and the focused differences in *Zostera* spp. as dependent variables ($n = 12$). The explanatory variables were those related to human activities, i.e. the presence/absence of clam harvesting, the

presence/absence of *Z. noltii* protection and the proportion of the census zone covered by shellfish farming concessions.

Results

Relationships between Brent Geese and *Zostera* spp. areas and changes between the two periods

We found no significant relationship between the number of Brent Geese and the world population nor the period alone. However, the number of Brent Geese increased significantly with the areas of *Z. noltii* and *Z. marina*, and the period had a significant effect through the interaction with the areas of *Z. noltii* and *Z. marina* (Table 1). The relationship between the number of geese and *Z. noltii* area was positive, meaning that Brent Geese were more numerous in the census zones with larger areas of *Z. noltii*. The slope of the relationship was steeper during the second period (slope = 0.012 ± 0.002 SE; Table 1) than during the first period (slope = 0.004 ± 0.002 SE; Table 1). So, for the same increase in *Z. noltii* area, the number of Brent Geese increased more in the second period than in the first period. The pattern was different for *Z. marina* as the number of Brent Geese increased significantly with the area of *Z. marina* beds during the first period (slope = 0.008 ± 0.003 SE; Table 1), but the slope was not significantly different from zero in the second period (slope = 0.000 ± 0.003 SE; Table 1).

When performing the analysis with census zone and period as fixed effects, controlling for the Brent Geese world population, the interaction between census zone and period was significant ($F_{10,598} = 2.52, P = 0.006$). This means that Brent Geese changed their distribution between

census zones between periods as well as changed their relationship with *Zostera* spp. beds (Fig. 1).

For *Z. marina*, we found no significant difference in area, nor fragmentation between the two periods, but differences in areas and fragmentation between census zones (Table 2; Fig. 2). For *Z. noltii*, however, we found significant changes between periods: the distributions of area and fragmentation (i.e. number of patches per census zone) within the Gulf significantly differed between the two periods, and the fragmentation over the whole Gulf was significantly higher in the second period than in the first.

Links between changes in Brent Geese numbers, *Zostera* spp. beds and human activities

The only *Zostera* spp. characteristics for which there were significant differences between the two periods were the distributions of *Z. noltii* area and number of patches. Because differences in areas and in numbers of beds were not significantly correlated, $r_s = 0.374, df = 10, P = 0.227$, we were confident that this increase in number of patches corresponded to an increase in fragmentation. So, we included only those two variables in the models and found that just the fragmentation of *Z. noltii* had a significant effect (slope = -165.9, SE = 58.3, $t = -2.85, P = 0.006$). The number of Brent Geese increased more/ decreased less in the census zones, where the fragmentation increased less.

Concerning the variables related to human activities, we found that Brent Geese increased more in the census zones with *Z. noltii* protection and less where there was clam harvesting (Table 3). We also found that the fragmentation of *Z. noltii* increased more with increasing proportion of the census zone covered with shellfish farming concessions (Fig. 3) and less in census zones with protection (Table 3).

Table 1 Relationship between Dark-bellied Brent Geese (*Branta bernicla bernicla*) (BG) and *Zostera* spp.: results of a mixed-effects model on log-transformed monthly number of Brent Geese per census zone ($n = 642$), with census zone (12), winter (14 between 1970 and 200) and month (6 per winter) as random variables and the world population of Brent Geese, area of *Zostera noltii* (Zn), area of *Zostera marina* (Zm) and period as fixed effects

	df	t	P
Intercept	635	4.43	<0.001
BG world population	635	-0.73	0.464
Period	635	1.68	0.094
Zn area	635	2.10	0.036
Zm area	635	3.32	<0.001
Zn area × period	635	4.51	<0.001
Zm area × period	635	-3.15	0.002

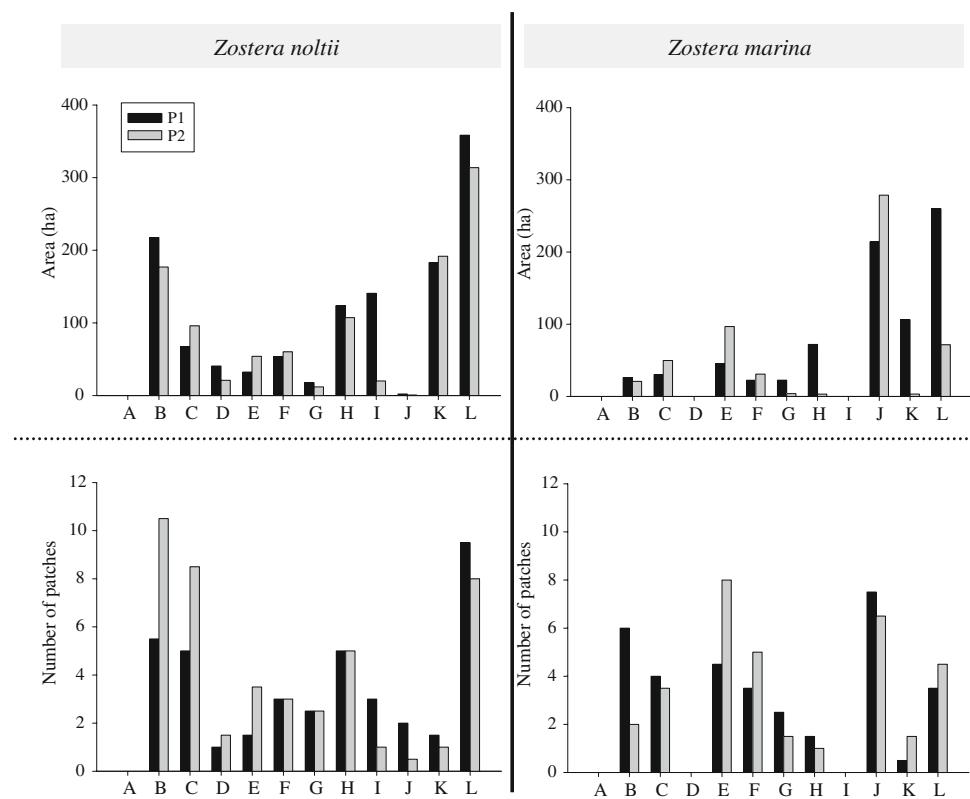
Discussion

Relationship between Brent Geese and *Zostera* spp.

As we expected, areas of food resources had a significant effect in determining the spatial distribution of Brent Geese; greater numbers of geese were found in census zones with greater areas of *Zostera* spp. These results are in accordance with results found in California for staging Black Brant *Branta bernicla nigricans* (Moore et al. 2004) and in England for wintering Brent Geese (Tubbs and Tubbs 1983; Percival et al. 1996). However, these studies focused on intertidal *Zostera* spp., whereas here we also assessed the role of the subtidal perennial ecotype of *Z. marina*. Our results strongly suggest that, although *Z. marina* is much less accessible to wintering Brent Geese,

Table 2 Changes in *Zostera* spp. area and fragmentation: GLMs on areas and numbers of patches per census zone ($n = 48$ for each GLM), with period, census zone and interaction between them as explanatory variables

Response variable	Explanatory variable	Area			Fragmentation		
		df	F	P	df	F	P
Changes in <i>Z. noltii</i>	Period	1	-0.04×10^{-13}	1.000	1	5.54	0.027
	Census zone	11	24.07	<0.001	11	16.40	<0.001
	Period \times census zone	11	2.65	0.022	11	4.31	0.001
Changes in <i>Z. marina</i>	Period	1	-0.02×10^{-11}	1.000	1	-0.04×10^{-13}	1.000
	Census zone	11	8.46	<0.001	11	3.28	0.007
	Period \times census zone	11	2.07	0.067	11	0.48	0.895

Fig. 2 Mean area and fragmentation of each *Zostera* species per census zone for the first period (P1) and the second (P2)**Table 3** Results of GLMs on changes in number of Brent Geese (*BG*, $n = 61$) and changes in *Z. noltii* fragmentation (i.e. number of patches, $n = 12$), with human activities related variables as explanatory variables

Response variable	Explanatory variable	Slope	SE	df	t	P
Changes in number of BG	Protection of <i>Z. noltii</i>	1,636.31	430.78	57	3.80	<0.001
	Clam harvesting	-935.75	411.95	57	-2.27	0.027
	Shellfish farming	338.35	915.25	57	0.37	0.713
Changes in <i>Z. noltii</i> fragmentation	Protection of <i>Z. noltii</i>	-1.49	0.52	8	-2.87	0.020
	Clam harvesting	0.70	0.38	8	1.83	0.104
	Shellfish farming	4.13	1.50	8	2.76	0.024

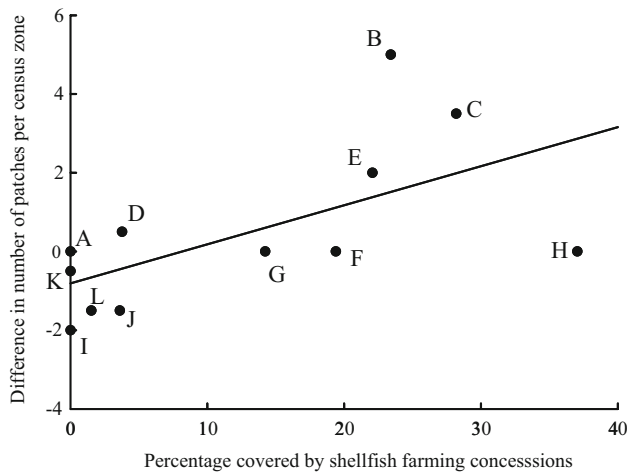


Fig. 3 Changes in *Z. noltii* fragmentation in relation to the percentage of census zone covered by shellfish farming concessions (letter of corresponding census zone is indicated next to each point of the graph)

it also influences their spatial distribution, hence contributing to the quality of wintering sites. Indeed, during the first period, the relationship between Brent Geese and *Z. marina* was tighter than between Brent Geese and *Z. noltii* (slopes 0.008 vs 0.004). Although the leaves of *Z. marina* are much larger and the calorific values of the two plants do not seem to differ (Percival and Evans 1997), not enough is known to determine if *Z. marina* was preferred by Brent Geese or if the relationship resulted from a lack of *Z. noltii*. The relative influence of the two *Zostera* species may in fact reflect the differences in their characteristics as food sources, in availability and in accessibility. This can be compared to the situation of staging Brent Geese in Denmark (Clausen 2000). There, they alternate between feeding on submerged *Z. marina* beds and salt-marshes, and the switch between habitats is partly determined by accessibility and availability of *Z. marina*.

The relationship between Brent Geese and their food resources changed in the second period; it was tighter with *Z. noltii* (slope 0.012) and did not exist any more with *Z. marina*. However, there were no significant differences between the two periods, either in overall numbers of Brent Geese or in whole Gulf areas of *Zostera* spp. Nevertheless, without excluding a potential effect of direct disturbance by human activities, these changes in relationship could be linked to changes in other characteristics of *Zostera* spp.

Changes between the two periods and links with human activities

The reason for changes in the relationship between Brent Geese and areas of their food resources could be linked

with human activities, which was one of the initial concerns from local conservation bodies, and one of the questions of this study. Although Brent Geese distribution followed that of their resources, the degree of changes in Brent Geese distribution in fact mostly followed changes in *Z. noltii* fragmentation; the number of geese increased more where the fragmentation of *Z. noltii* decreased. These differences in fragmentation were related to shellfish farming (number of patches increased more with increasing proportion of census zone covered by shellfish farming concessions) and *Z. noltii* protection (number of patches tended to decrease in the census zones with protection). By limiting fragmentation, the protection may have had several positive effects and thus increased the attractiveness of the sites to foraging Brent Geese: (1) it may have maintained patches large enough to accommodate large groups of gregarious feeders, such as Brent Geese (patches were significantly larger in sites with protection—84.6 ha ± 9.2 SE—than without—11.4 ha ± 2.9 SE, $W = 5$, $P = 0.001$, and numbers of geese per patch were significantly greater in sites with protection—494 ± 68 SE—than without—140 ± 43 SE, $W = 3,384.5$, $P < 0.001$); (2) it may have maintained the most selected part of the beds in relation to tide edge, hence in fact have limited the reduction in actual usable bed area; and (3) it could have allowed an increase in *Z. noltii* biomass, i.e. both shoot density and leaf length (Auby and Labourg 1996). Trampling by people and clam harvesting can have negative effects on *Zostera* spp. beds by decreasing or stopping their increase in biomass (Cabaço et al. 2005; Alexandre et al. 2005). So resource protection could have played an important role in determining Brent Geese distribution through mitigating resource degradation. However, more specific data are needed to verify this hypothesis and we cannot exclude a possible disturbing effect of human activities. Indeed, we also found that the number of Brent Geese increased significantly more in the census zones with *Z. noltii* protection than in those without and decreased significantly more when there was clam harvesting. However, in the only census zone with clam harvesting and without *Z. noltii* protection, the number of patches doubled, whereas the area decreased. So we could fairly suppose that the overall available abundance of food resource decreased, leading to the avoidance of this census zone by Brent Geese independently of any disturbance by clam harvesters. Thus, the direct effect, i.e. disturbance, of human activities does not appear central in explaining differences between census zones. Nevertheless, it could have had an influence within the census zones. Indeed, by feeding on the *Z. noltii* protected patches, Brent Geese could have remained more than several 100 m away from clam harvesters.

Although correlative, these results suggest that both shellfish farming and clam harvesting have had an effect on Brent Geese changes in distribution, probably mostly by indirect effects on food resources. More generally, these results highlight the importance of the indirect effects of human activities due to exploitation of food resources, as has been shown to affect shorebird populations elsewhere (Norris et al. 1998; Stillman et al. 2001; Atkinson et al. 2003, 2005).

Conclusions and conservation implications

The spatial distribution of wintering Brent Geese in the Gulf of Morbihan appears mostly to rely on the distribution of food resources, as found by Clausen et al. (1998) for Light-bellied Brent Geese (*Branta bernicla hrota*) in a more northern part of Europe (Denmark) between 1980 and 1994, and by Rowcliffe et al. (1999) for Dark-bellied Brent Geese feeding on green algae in eastern England. Even though disturbance by human activities cannot be excluded, the two activities considered here (clam harvesting and shellfish farming) clearly seem to affect the characteristics of the food resources, either by reducing *Zostera* spp. biomass density or by increasing bed fragmentation, possibly leading to a medium- or long-term decrease in food availability. Both theoretical models (Dolman and Sutherland 1995; Goss-Custard et al. 1995a, b) and empirical evidence (Burton et al. 2006) indicate that winter habitat loss could have dramatic consequences on bird populations. Therefore, our results raise concerns about the influence of ongoing human activities on wintering habitats in the Gulf of Morbihan and its long-term impact on Brent Geese populations. The deterioration of resources at wintering sites, directly or indirectly related to human activities, should be brought back into focus to investigate the possible reason for the downward trend of the world Dark-bellied Brent Geese population in the last decade (Wetlands International 2006). Even though climate-driven changes in the high arctic should have a major influence on breeding success, the decrease in the trophic function of wintering, staging and stop-over sites may well also impair the fitness of individuals, as suggested by Ebbs and Spaans (1995) for females' breeding success. Indeed, they found that female Brent Geese returning to wintering sites with offspring were on average heavier in spring than those failing to raise offspring.

Our results also suggest that the perennial subtidal *Z. marina*, although less accessible, could be as important as *Z. noltii* in determining Brent Goose distribution. Consequently, we suggest that areas of resource protection should also consider both ecotypes of *Z. marina*, to take into account the gradient of food resources used by Brent Geese.

Our results address a key conservation issue, underlining once more the importance of understanding the influence of changes in food resources on changes in wintering birds' distribution before making conclusions about the disturbance effects of human activities. Human impacts on food resources can easily be taken for disturbance effects when food resources are not considered. However, conservation measures should differ depending on whether human activities induce direct disturbance or have effects through impacts on food resources. Places with abundant food resources could be selected for refuge design, even if they are close to human activities, whereas they would not be chosen if the main human effect was disturbance. Further, human presence could be authorised provided it does not affect food resources.

Zusammenfassung

Zunehmende menschliche Aktivität im Schlickwatt und die Winterverbreitung von Ringelgänsen *Branta bernicla* auf Seegraswiesen: eine 30-jährige Studie

Menschliche Aktivitäten können den Zugang überwinternder Vögel zu ihren Nahrungsressourcen einschränken, aber Habitatzerstörung und -fragmentierung können mit Störungen interagieren, um die Tragekapazität zu reduzieren. Wir haben die Abundanz und Verbreitung überwinternder Ringelgänse in einem bedeutenden französischen Überwinterungsgebiet von 1970 bis 2000 analysiert. In diesem Zeitraum nahm dort die menschliche Aktivität im Uferbereich zu. Wir verwendeten gemischte Modelle, um zu testen, ob die räumliche Ausdehnung zweier Seegrasarten, *Zostera noltii* und *Z. marina*, die Verbreitung der Ringelgänse beeinflusste. Die Anzahl der Gänse nahm mit der Fläche der Wiesen beider *Zostera*-Arten signifikant zu. Diese Beziehung änderte sich jedoch in dem Zeitraum nach dem Anstieg der menschlichen Aktivität. Die Fragmentierung der am leichtesten zugänglichen Nahrungsressource, *Z. noltii*, wirkte sich negativ auf die Ringelgansverbreitung aus. Diese Fragmentierung wurde wiederum durch menschliche Aktivitäten verstärkt und durch den Schutz von *Z. noltii* (durch Sperrung dieses Gebietes für Menschen) vermindert. Dies bedeutet, dass direkte Störungen, wenn auch nicht ausgeschlossen, nicht der Hauptgrund für Veränderungen in der Verbreitung der Ringelgänse gewesen sein dürften, sondern eher die Einflüsse menschlicher Aktivitäten auf die Nahrungsressourcen. Daher zeigen unsere Ergebnisse, dass die Einrichtung von Ressourcenschutzgebieten als Schutzmaßnahme wirksam ist, und sie unterstreichen den Bedarf an Studien über den Einfluss menschlicher Aktivitäten auf Ressourcen, zusätzlich zu Störungseffekten.

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