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Feeding grounds for waders in the Bay of the Mont Saint-Michel (France): the *Lanice conchilega* reef serves as an oasis in the tidal flats

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Abstract:

The tube-building polychaete *Lanice conchilega* can form dense populations, often called reefs, which promote benthic community change and constitute feeding grounds for secondary consumers. The aim of this study was to quantify the role of the *L. conchilega* reef of the Bay of the Mont Saint-Michel (BMSM) for feeding waders, by combining macrobenthos data, bird counts and bird diet information. Wader densities in the reef were on average 46.6 times higher than in non-reef areas. According to faecal analyses, waders in the reef mainly selected the accompanying fauna and especially crustaceans. The attractiveness of the reef to feeding birds may be largely explained by the high abundance, richness and biomass of macrobenthic species in the reef compared with the rest of the BMSM.

Introduction

Lanice conchilega is a widespread tubicolous polychaete that can form dense aggregations, considered biogenic reefs (Rabaut et al. 2009; Callaway et al. 2010). Above particular density thresholds, the structures of the tubes as well as the biological activity of the "engineer species" (Callaway 2006; Godet et al. 2008), generate specific sedimentological "structures" (Carey 1987; Feral 1989) and enhance the species diversity and abundance of the associated benthic macrofauna by stabilizing the sediments (Zühlke 2001; Callaway 2006; Rabaut et al. 2007; Van Hoey et al. 2008). These reefs are also important feeding grounds for flatfishes, particularly the juveniles of *Pleuronectes platessa* (Rijnsdorp and Vingerhoed 2001; Rabaut et al. 2010).

Lanice conchilega can be an important item in the diet of several waders (Goss-Custard and Jones 1976; Yates et al. 1993). Godet et al. (2009) showed that oystercatchers may significantly select *L. conchilega* reefs to feed in and that their spatial distribution can change greatly when these reefs disappear. But to our knowledge, the study of Petersen and Exo (1999) in the German part of the Wadden Sea is, so far, the only extensive study investigating the role of large *L. conchilega* dominated tidal flats for waders and gulls. In comparison to the surrounding area, they found higher densities of four bird species feeding in these flats, though the relative biomass consumption on these flats was similar to other regions of the Wadden Sea. Furthermore, the study revealed that gulls tend to feed on *L. conchilega* specimens, while waders rather select the accompanying benthic macrofauna.

The area surveyed by Petersen and Exo (1999) was special because of the spatial dominance of *L. conchilega* sand flats (60% of the 6 680 ha of the study site), and because the remaining area was covered by two other habitat-creating species: *Arenicola marina* (20%) and *Mytilus edulis* (5 to 10%). Despite of the dominance of *L. conchilega*, the tubeworm aggregates did not generate the specific sedimentological structures, typically mounds and depressions, previously described for other *L. conchilega* reefs (e.g. Carey 1987).

The aim of this current study was to quantify the role of *L. conchilega* reefs as potential "oases" for feeding waders; do the reefs constitute a localized and discrete habitat for birds among large and homogeneous tidal flats. Therefore, one of the largest intertidal *L. conchilega* reefs in Europe, located in the Bay of the Mont Saint-Michel (BMSM) (France), was selected. For the first time, a combination of macrobenthos data, bird counts and bird diet information was used to stress the importance of a *Lanice conchilega* reef. Following hypotheses have been tested: i) the benthic macrofaunal composition of the reef clearly differs from the macrofaunal composition of the whole bay; ii) the abundance and composition of waders on the reef is significantly different from the wader abundances and composition at the scale of the whole BMSM. Additionally, the diet of waders feeding on the reef was determined by means of a faecal analysis.

Material and Methods

Study area

The *Lanice conchilega* reef is located in the central region of the BMSM (48°40’45” N-01°41’25” W, south-eastern part of the Normand-Breton Gulf, France) (Figure 1) and in the lower section of the tidal flats. In 2008, the reef covered 105 ha; *i.e.* 0.42% of the sand flats of the BMSM (Godet et al. 2011) (Figure 1). The BMSM is subjected to an extreme megatidal regime (tidal range up to 15.5 m during spring tides), resulting in large tidal flats - covering 25 000 ha - and mainly dominated by a *Macoma balthica* community characterized by low macrobenthic abundances and diversity (Retière 1979; Thorin et al. 2001). The BMSM is an internationally important migration stopover and wintering site for birds (Le Drean-Quenec'hdu et al. 1995), designated as a RAMSAR site and classified as a Special Protection Area (SPA) and a Special Area of Conservation (SAC). More than 50 000 waders over-winter in the BMSM; 12% of the French wintering abundances of waders (Le Drean-Quenec'hdu et al. 1998). At this site, Dunlin *Calidris alpina*, Red Knot *Calidris canutus*, Oystercatcher *Haematopus ostralegus*, Grey Plover *Pluvialis squatarola*, Black-tailed Godwit *Limosa limosa*, and Bar-tailed Godwit *Limosa lapponica* reach international abundance levels in winter (Deceuninck and Mahéo 2000).

Macrobenthos sampling and treatment at the scale of the *L. conchilega* reef

Benthic macrofauna was sampled from the 10^{th} to the 12^{th} of January 2009 within 1 ha squares of a regular grid (consisting of 150 squares). The *L. conchilega* density within each square was estimated by counting aboveground tubes on pictures of 3 randomly selected 1/4 m^2 quadrats. Samples were only taken in one out of every two squares of each row of the grid, though every square with *L. conchilega* densities ≥ 200 ind. m^{-2} was sampled as well (*i.e.* 80 sampled squares in total) (Figure 2). The number of tubes is highly correlated with the number of individuals in the sediment (e.g. Van Hoey et al. 2006). At every selected square, one macrofaunal core was collected (1/40 m^2, 30 cm deep). Benthic samples were sieved in the field through a 1 mm circular mesh size and the retained biological material was immediately preserved in a 4.5% buffered formalin solution. In the laboratory, samples were sorted and macrobenthos was identified to the lowest possible taxonomic level. Total biomass was estimated by determining the dry mass of all individuals per species (60 °C for 48 h). The ash-free dry mass (AFDM) was calculated as the difference between the dry mass and the ash mass (500 °C for 3 h).

Wader counts at the scale of the BMSM

To assess the total number of waders in the whole BMSM, all waders of the site were monitored 5 times (January ’09, March ’09, May ’09, September ’09 and January ’10) by 10 to 30 people. A standardized protocol to monitor water birds of the BMSM, developed by two ornithological associations, Bretagne-Vivante/SEPNB and GONm, was followed (Beaufils et al. 2009). Waders were counted in their high-tide roosts by people equipped with telescopes and binoculars. Because of the extent of the BMSM, it was divided in sectors assigned to one or two observers. To avoid double counts, surveys in the different sectors were performed on the same day and during the same time interval (20 to 30 min). Additionally, any bird group seen flying from one sector to another was systematically reported with the exact time and flight direction.

Wader counts at the scale of the reef

On the reef, birds were surveyed 21 times from February 2009 to January 2010 (at least once each month, except for November and December), but only while spring tide fully exposed the reef (*i.e.* corresponding to a low tide level of less than 2.5 m above extreme low water spring tide). Birds were counted by two persons equipped with a pair of binoculars and a telescope (magnification respectively 10X and 20-60X). All individuals were counted (in case of a few tens of individuals) or estimated in tens of individuals (if several hundreds or thousands of individuals were present). The observation point, located on a sandbank just outside the study area, ensured visibility of the entire site as well as a minimal bird disturbance.

Estimating the diet of waders feeding on the reef: faeces sampling and treatment

In 2010, faeces of five wader species were collected within the reef: Oystercatcher *H. ostralegus*, Dunlin *C. alpina*, Curlew *Numenius arquata*, Grey Plover *P. squatarola* and Bar-tailed Godwit *L. lapponica*. We selected these species because they: i) are abundant in the reef; ii) feed regularly on the reef; iii) are species for which faeces are easy to collect because they feed in dense and virtually monospecific groups. Faeces of Curlew and Dunlin were collected on the 27th of April 2010, while faeces of Oystercatcher, Bar-tailed Godwit and Grey Plover were collected on the 13th of August 2010, the 9th of September 2010 and the 7th of October 2010 respectively.

Prior to collection, a large monospecific flock of birds feeding on the reef was observed in order to be confident that a dropping came from the target species. After 20 to 30 min (in order to be sure that the collected faeces resulted from a feeding activity on the reef), the entire droppings were scraped off the surface and preserved in 70% ethanol. In the laboratory, the ethanol was removed by pouring the dropping onto a 20-µm sieve. For analysis, the sample was transferred to a 100-ml jar, containing a mix of 80% distilled water and 20% hydrogen peroxide (H_2O_2), for a period of at least 24 h. The samples were shaken regularly and, after sedimentation, the supernatant was poured through a 20-µm sieve. The supernatant remaining on the sieve was transferred to a 25-cm^3 petri dish in order to observe and identify lighter animal parts (e.g. polychaete chaetae) with an inverted microscope. A stereo-microscope was used to screen the entire settled sand fraction for hard remnants of bivalves, polychaete jaws, etc. Prior to investigation, we selected for each of the five bird species 15 faecal samples (except for Curlew: 11 samples).

Although all different items in a faecal sample were quantified, identification to genus or species level was not always possible. Therefore, each unique unidentified animal part was assigned to a morphotype, leading up to the creation of a catalogue consisting of pictures. Finally, for several analyses morphotypes were pooled into taxonomic groups, as mentioned hereafter.

Data and statistical analysis

Macrobenthic density, richness, diversity and production in the reef

Macrobenthic densities (D), species richness (S) and species diversity (H', Shannon Index, Shannon 1948) were calculated. Abundances of macrobenthos in the *L. conchilega* reef were evaluated by summing the numbers of individuals from the different squares. Subsequently, relative abundances were calculated. The annual macrobenthic production in the reef was estimated using an empirical model based on biomass and abundance data (Brey 1999, 2001). The model takes additional data on benthic taxa and environmental variables such as bathymetry and temperature in consideration. Prior to production estimation, benthic biomass in g of AFDM was converted to kJ via conversion factors for aquatic organisms (Brey 2001; Brey et al. 2010).

Abundances and community composition of waders on the reef versus the entire BMSM

The community composition of waders was analysed with the PRIMER v6 statistical package (Clarke and Warwick 1994). Analysis of similarity (one-way ANOSIM) was used to describe (dis-)similarities in wader communities between the entire bay and the *L. conchilega* reef. Data were standardized (in order to eliminate the abundance effect) and square root transformed before conducting the analysis. To test whether waders significantly selected the reef at low tide, we compared the abundances of waders present on the reef with predicted wader abundances present on the reef assuming a homogeneous distribution of birds across the entire BMSM during low tide. Because the ratio of the area covered by the reef to the area of the tidal flats is 1:238 (105 ha reef among 25 000 ha of tidal flats), counting n individuals of a species at high tide in the whole BMSM results in a predicted abundance of n/238 individuals of this species on the reef. Only counts which were performed at similar time periods over the entire BMSM and the reef were selected for the analysis; *i.e.* four observation dates (March '09, May '09, September '09, and January '10). The number of days between a count across the BMSM and on the reef varied between 0 and 12 days. *G*-tests for goodness-of-fit were conducted in order to compare predicted and actual abundances of waders on the reef, assuming no selective use of the reef habitat. A significant total *G*-value means that the data do not fit the expected ratio.

Analysing bird faeces data

First, differences in the frequency of occurrence of benthic taxa among wader species were investigated. Therefore, bird faeces data were transformed into presence/absence data, followed by lumping morphotypes into taxonomic groups. Due to diagnostic features of some morphotypes they could be linked to a certain species. Nonetheless, in most of the cases it was not possible to assign a morphotype to a species but only to an order, class, or even phylum. For every wader species, the frequency of occurrence for each taxon *i* (FOi%) was calculated: FOi% = (the number of faecal samples of the wader species *s* where taxon *i* is present / the total number of faecal samples of the wader species *s*) * 100. Second, to determine which taxa are preferentially found in faecal samples of particular wader species, the proportion of different taxonomic groups (Ni%) per faecal sample was calculated: Ni% = (Number of items in taxonomic group *i* / total number of items in the faecal sample) * 100. To test whether relative abundances of higher taxonomic groups and the most abundant lower taxonomic groups differed significantly among bird species, a generalized linear model (GLM) was used in the SAS 9.2 software package (Glimmix procedure). Because the response variables are percentage data, the residual error structure was tested against a binomial distribution. When overdispersion became apparent in the model output, the model was rerun, taking the overdispersion into account by adding an overdispersion component (random residual) to the variance function. Accordingly, underestimation of the standard errors was avoided. Because the predictor and the mean response are not linearly related to each other, the relationship was specified by a log link function.

Results

Macrobenthic density, richness, diversity, biomass and production in the *Lanice conchilega* reef

In 2009, 13 806 macroinvertebrates belonging to 61 different taxa were sampled on the reef. Excluding *L. conchilega* itself, the macrobenthic abundance was dominated by the bivalves *Macoma balthica* and *Cerastoderma edule* and the polychaete *Nephtys hombergii*. Taking into account *L. conchilega*, the mean density of macrobenthic species was 6 903 ± 5 339 ind. m^{-2}, N = 80; mean species richness was 11.8 ± 4.7 species per square and mean species diversity (H') was 2.1 ± 0.5. At the phylum level, the benthic community within the reef was dominated by annelids (59%), followed by molluscs (38%) and arthropods (1.8%). More than 99.9% of the annelids in the reef belonged to the class Polychaeta. Moreover, this taxon was dominated by *L. conchilega* (69%). The average *L. conchilega* density was 200 ± 351 ind.m^{-2}, N = 150, and a maximum density of 1985 ind.m^{-2} was reached. Within the phylum of Mollusca, the most abundant species were *M. balthica* (55%) and *C. edule* (44%). Crustaceans were the most abundant taxon within the phylum of the arthropods (99.6%). The order of the amphipods (71%) dominated the crustaceans within the reef. Cumaceans, isopods and decapods (crabs) constituted respectively 14.7%, 7.8%, and 6.5% of total abundances. The mean benthic biomass in the reef was 49.7 ± 50.4 g of AFDM.m^{-2}. The annual macrobenthic production in the reef (95% confidence interval) was estimated at 1552.9 (1368.5-1762.3) kJ.m^{-2}.$year^{-1}$ or 70.6 g AFDM.m^{-2}.$year^{-1}$ (60.2-80.1).

Wader density and community composition in the BMSM and on the reef

Across the entire BMSM, 22 wader species were counted, representing a mean density of 1.03 ± 0.58 birds ha^{-1}, N = 5. The five most abundant species were: Dunlin (42%), Red Knot (18%), Oystercatcher (13%), Grey Plover (9%) and Curlew (7%). On the reef, 15 wader species were counted, representing a mean density of 51.38 ± 19.11 birds ha^{-1}, N = 5. Dunlin (39%) was the most abundant species on the reef followed by Red Knot (20%), Grey Plover (14%), Oystercatcher (13%), Bar-tailed Godwit (8%) and Curlew (5%).

The one-way global ANOSIM test failed to detect a significant difference in the wader community in the two habitats ($p > 0.05$; $R = 0.108$). Unlike bird composition, bird counts revealed that all wader species together exhibited a high proportion of individuals in the reef in relation to the whole BMSM (Table 1). The frequency of waders in the reef was on average 46.6 times higher than expected assuming a random distribution of waders over the entire BMSM. The same was observed for the five wader species selected for the faecal analysis. Focussing on each of the 5 wader species separately revealed frequencies ranging from 31.1 times (Curlew) up to 112.3 times (Bar-tailed Godwit) higher than expected. Consequently, the observed numbers of these 5 species in the reef were significantly higher than their predicted numbers (assuming that the total number of waders counted at high tide have a homogeneous distribution in the BMSM at low tide) (for each species, G-test, $p < 0.001$).

Diet of waders feeding on the reef

In general, the frequency of occurrence (FO%) of higher taxonomic groups in the faeces did not differ much among different bird species (Table 2). Crustaceans were present in all faecal samples of all birds except for Bar-tailed Godwit (FO% = 93.3%). Both polychaetes and bivalves were present in all bird species but polychaetes in a much higher percentage of the faeces (ranging from 72.7% in Curlew to 93.3% in Dunlin) than bivalves (ranging from 13.3% in Oystercatcher and Grey Plover to 45.5% in Curlew). *Lanice conchilega* was eaten by all birds though it never exceeded a FO% of 63.6%. Other polychaetes were scarce. Crabs, amphipods and ostracods - the most abundant crustacean groups in the faeces - were encountered in all bird species and reached the highest FO% in Curlew (respectively 81.8%, 45.5% and 90.9%). The three most frequently occurring bivalve species among all bird species were *Abra alba*, *C. edule* and *M. balthica*, although they never exceeded a FO% of 6.7%, 36.4%, and 20% respectively.

Based on the relative abundances of taxonomic groups in each of the 5 bird species a diet composition can be displayed for the 5 bird species examined (Table 3). Relative abundances of all higher taxonomic groups differed significantly ($p < 0.05$) among the 5 wader species (GLM, $p < 0.05$, Table 4). Globally, polychaetes differed significantly among species of birds, though no significant pairwise differences were detected. Crustaceans were more frequently eaten by Curlew than by Oystercatcher or Bar-tailed Godwit, while bivalves were eaten more frequently by Dunlin than Curlew. Significant differences in the relative abundances of *L. conchilega* (GLM, $p < 0.0001$) and 'Other polychaetes' (GLM, $p < 0.0001$) were detected among bird species (Table 5). According to pairwise tests, *L. conchilega* was eaten more frequently by Oystercatcher than by Dunlin and Curlew. Additionally, Bar-tailed Godwit ate *L. conchilega* more frequently than Dunlin, but less than Curlew. Within the group of crustaceans, 'Crabs' differed significantly among bird species (GLM, $p = 0.005$), although no significant pairwise differences were detected. Lastly, no bivalve species showed a significant difference among waders (GLM, $p > 0.05$).

Discussion

Our study showed that the *Lanice conchilega* reef of the BMSM is remarkable because of the wader density which easily exceeds the expected frequency. In the entire BMSM a total of 22 wader species was observed and counted during the study period, while only 15 species were observed in the *L. conchilega* reef. Since the entire BMSM is almost 240 times bigger than the reef area, the observed difference in species richness is not surprising keeping in mind the species-area relationship (Connor and McCoy 1979). Consequently, species that were rarely counted at the scale of the entire BMSM are not likely to be observed at the scale of the reef. Despite this difference, both areas were mainly dominated by the same species: Dunlin, Red Knot, Grey Plover, Oystercatcher and Curlew. Eybert et al. (2003) already demonstrated that 96% of the wintering shorebird community in the entire BMSM was represented by 7 species: Dunlin, Oystercatcher, Red Knot, Curlew, Grey Plover, Bar-tailed Godwit and Black-tailed Godwit. Overall, the composition of waders can be considered the same in the entire BMSM and the reef.

However, when abundances are included, the composition of waders clearly differed between the two study sites. The observed frequency of total waders on the *Lanice*-reef was on average 5 799 birds, which is approximately 46.6 times higher than expected assuming a uniform distribution of the birds in the BMSM. Petersen and Exo (1999) observed higher than expected bird abundances in *L.*

conchilega dominated tidal flats of the Wadden Sea, although densities were only 6 times higher than expected. Similar counting surveys in the Chausey archipelago (France) and preliminary counts in the BMSM already showed the attractiveness of the *L. conchilega* reefs for birds and consequently their potentially important role in the conservation of the avifauna (Godet et al. 2008). The results of the current study prove that within a site of international importance for birds, several wader species are able to select preferentially habitats generated by *L. conchilega*.

In general, the attractiveness of *L. conchilega* reefs can be attributed to the good food supply, i.e. the high diversity, abundance and biomass of associated macrobenthic invertebrates, as proven by several authors in different study areas (e.g. Zühlke et al. 1998; Zühlke 2001; Callaway 2006; Rabaut et al. 2007; Van Hoey et al. 2008). The situation in the *L. conchilega* reef of the BMSM seems to be alike. In our study, the macrofaunal density is 4.4 times higher than in a study of Trigui (2009), which investigated the general characteristics of the benthic macrofauna of the entire intertidal zone of the BMSM in 2003. Trigui's survey is, with 176 sampled stations, the most extensive benthic survey ever done in the BMSM. Comparison with current research reflects well the fact that the reef does accommodate a more abundant fauna (6 903 ± 5 339 ind.m^{-2}) than the average macrobenthic assemblage in the entire BMSM (1 568 ± 299 ind.m^{-2}). As part of a study of Leloup et al. (2008), biomasses of different trophic groups which make up the BMSM were modelled. The biomass of carnivorous and necrophagous macrobenthic fauna in combination with intertidal filter feeders was transformed according to weight-to-weight conversion factors proposed by Ricciardi and Bourget (1998). Comparing the resulting biomass (2.88 g AFDM. m^{-2}) to the reef biomass (49.69 g AFDM.m^{-2}) revealed a reef biomass which is more than 17 times higher. Therefore, the reef area can be considered a high productivity area in the bay. Nevertheless, the importance of the whole BMSM for the productivity and functioning of the reef cannot be neglected.

Faecal analysis conducted in this study revealed information on the diet composition of waders in the reef. Polychaetes were represented in all bird species and they occurred in a high percentage of the faecal samples, which can probably be attributed to the dominance of polychaetes in the reef benthos. *Lanice conchilega* was the most abundant species and polychaete in the reef, which was partially reflected in the faecal samples since *L. conchilega* was the only identifiable polychaete species present in all bird species. Nevertheless, based on the relative abundances on the reef it could be expected that *L. conchilega* counted as a larger part of a bird's diet. The fact that the tube-building polychaete is large (up to 30cm; Hartmann-Schröder 1996), sturdy and buried quite deeply in the sediment (Jones and Jago 1993) can lead to a lower accessibility and possibly explains the lower than expected portion of *L. conchilega* in the diet of waders. Additionally, the fact that the energy content of polychaetes in temperate waters is high (Dauvin and Joncourt 1989), in combination with the high biomass of *L. conchilega* in the reef, might lead to the great contribution of one individual to the nutritional demands of birds. The bivalves *Macoma balthica* and *Cerastoderma edule* were, next to *L. conchilega*, the most abundant macrobenthic species in the reef. However, the general occurrence and portion of these two species in the diet of the investigated bird species was low. Even in Oystercatchers, which are specialized bivalve feeders (e.g. Hulscher 1982), bivalves were underrepresented. A feeding strategy avoiding the uptake of bivalve shell pieces, as described by Hulscher (1982), and hence the low detection success of shell remains in the faeces of Oystercatchers, is the most plausible explanation. Crustaceans, and in particular crabs and ostracods, were the most frequently occurring and abundant taxonomic group in the faeces of all bird species. However, relative abundances of crustaceans in the reef benthos were very low (1.77% of the total abundance), particularly for crabs. The observed ubiquity of crabs (and crustaceans in general) in the faecal samples implies a selective feeding behaviour of waders for this benthic group, which may be due to the fact that the stimuli associated with crustaceans, can have properties which make them particularly perceptible to the avian eye (Goss-Custard 1977).

Based on relative abundances of taxonomic groups, bird species that largely dominate the wader community on the reef exhibited significant differences in their dietary composition. Differences in polychaetes, and especially *L. conchilega*, contributed highly to differences in the wader diets. Differences in diets due to bivalves were rather low and in all probability largely overshadowed by an inability to trace back bivalve shells in faeces. For crustaceans, differences in the relative abundance between waders were the result of significant differences in crabs, though no significant pairwise tests were noted. Nevertheless, it can be visually seen that crabs reached much higher abundances in the faeces of Curlew compared to other waders (Table 3), which is in accordance with studies revealing that crabs are a major food source of Curlew (e.g. Goss-Custard and Jones 1976).

Considering the frequency of occurrence of taxonomic groups in the diet, waders foraging within the reef can be seen as opportunistic feeders, while focusing on the relative abundance gives the impression of a more selective feeding strategy. Based on current wader diet analysis, the actual strategy in the reef probably lies somewhere in between these two extremes. In general, waders feeding on the reef tend to feed on the associated fauna, and especially crustaceans, rather than specifically on *L. conchilega*. This result confirms the investigations of Petersen and Exo (1999), providing evidence that *L. conchilega*, within *L. conchilega* dominated tidal flats, was a less important food source for birds (mainly waders) than the accompanying macrobenthos. However, *L. conchilega* was of overriding importance for a few species, especially for gulls (Petersen and Exo 1999).

As experienced in this current study, investigating bird faeces can give us better insights into the diet of waders feeding in the reef. However, faecal analysis is hampered by a high proportion of unidentified prey items and is unlikely to reveal all prey taken by the predator (Barrett et al. 2007). Despite some shortcomings, faecal analysis is a valuable and easily applicable technique for which samples can be obtained all-year round without causing harm to the birds. Moreover, this approach can reveal the presence of prey species which could not be noticed by means of visual observations. Nevertheless, to get a more complete view on a wader's diet, the use of complementary approaches (e.g. visual observations) is recommended (Scheiffarth 2001). In this study morphotypes were counted, which cannot be compared with specimens. Since morphotypes are mostly parts of animals and can belong to one or several specimens of the same species or taxonomic group, caution regarding the interpretation of the results is recommended. Faecal samples of the wader species were collected on different dates ranging from the end of April 2010 until the beginning of October 2010. It is known that the diet composition of waders, as well as the nutritive value of some macrobenthic organisms, can change seasonally (e.g. Scheiffarth 2001; Braeckman et al. 2012). Furthermore, sexual differences in the diet composition have been demonstrated for several birds (e.g. Bar-tailed Godwit; Scheiffarth

2001). As neither sexual nor seasonal variations in the diet composition of waders were taken into account in our study, comparing wader diets is restricted. Additionally, future studies should try to compare diet composition of waders both inside and outside the *L. conchilega* reef.

Evaluating the importance of *Lanice conchilega* reefs as trophic resources for waders is not merely fundamental to gain knowledge on the feeding ecology, but is also essential for predicting the effects of a possible loss of the reef habitat in the future. Overall, the *L. conchilega* reef of the BMSM can be considered an oasis within the tidal flats composed of a similar composition of waders but with much higher bird densities compared to the non-reef areas of the BMSM. This result clearly demonstrates that birds are attracted by the reef. According to faecal analyses, waders in the *L. conchilega* reef tend to feed on the associated fauna, and especially crustaceans, rather than specifically on *L. conchilega* itself. Within the BMSM, which is characterized by low species diversity and low macrofaunal abundances, the *L. conchilega* reef constitutes a rich feeding area. For future studies, the use of complementary techniques to study a wader's diet is recommended, as well as the inclusion of information on the alimentary regime of waders in the BMSM.

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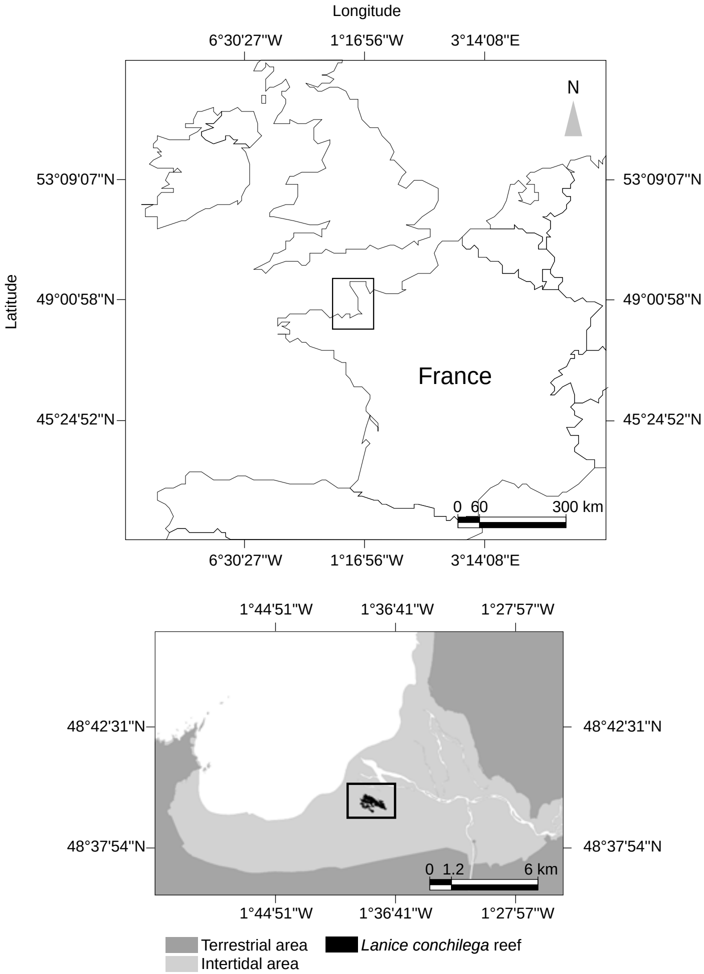
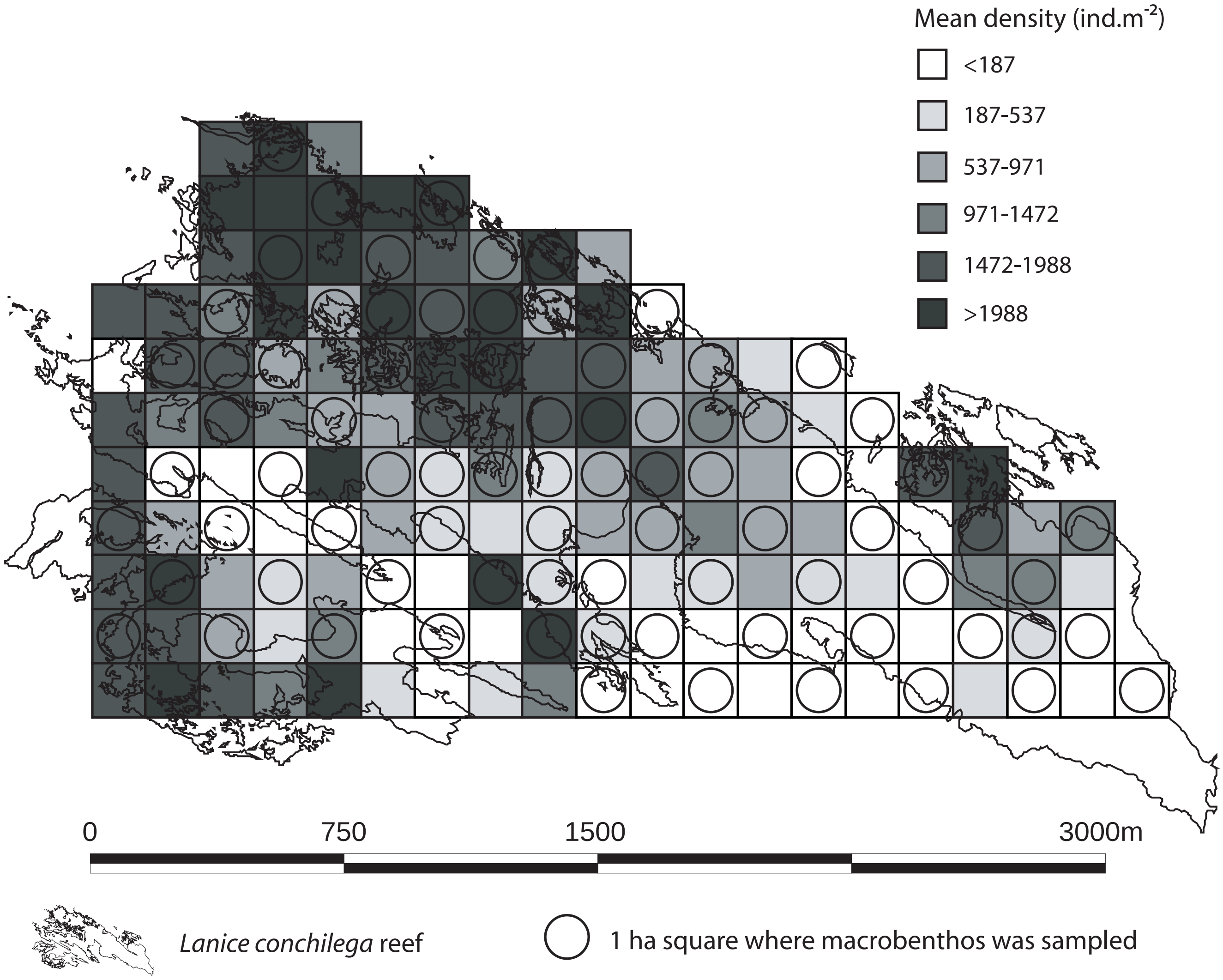
Figure Legends

Fig. 1 Location of the Bay of the Mont Saint-Michel (BMSM, France) and the *Lanice conchilega* reef within the bay

Fig. 2 Macrobenthic sampling design and mean *Lanice conchilega* densities on the *L. conchilega* reef in the Bay of the Mont Saint-Michel (BMSM) from 2005 to 2008. Macrobenthic samples were taken at alternating squares of each row of the grid (consisting of 150 squares). In addition, every square with a mean *L. conchilega* density ≥ 200 ind. m^{-2} was sampled as well, resulting in 80 sampled squares in total


Longitude
6°30'27"W
1°16'56"W
3°14'08"E
N
53°09'07"N
49°00'58"N
45°24'52"N
Latitude
France
0 60 300 km
1°44'51"W
1°36'41"W
1°27'57"W
48°42'31"N
48°37'54"N
0 1.2 6 km
Terrestrial area
Intertidal area
Lanice conchilega reef



Mean density (ind.m^{-2})
<187
187-537
537-971
971-1472
1472-1988
>1988
0
750
1500
3000m
Lanice conchilega reef
1 ha square where macrobenthos was sampled

Table 1 Overview of the mean observed and mean expected bird frequencies, and the ratios of these frequencies, for the entire Bay of the Mont Saint-Michel (BMSM) and the *L. conchilega* reef; total G-values, and p-values (G-test) of different groups of birds. Observed frequencies in the BMSM and the *L. conchilega* reef were derived from bird counts in March ’09, May ’09, September ’09, and January ‘10

	BMSM			*Lanice*-reef				
	Obs. freq. ± SD	Exp. freq. ± SD	Ratio	Obs. freq. ± SD	Exp. freq. ± SD	Ratio	Total *G*-value	p-value
Total waders	23928 ± 15976	29602 ± 17513	0.81	5799 ± 1994	124 ± 74	46.64	140976	< 0.0001
5 Species	17651 ± 10761	21830 ± 12882	0.81	4271± 2444	92 ± 54	46.58	101915	< 0.0001
Dunlin	9853 ± 9478	12080 ± 11337	0.82	2278 ± 1972	51 ± 48	44.90	53565	< 0.0001
Oystercatcher	3381 ± 1963	3916 ± 2502	0.86	551 ± 614	16 ± 11	33.52	12206	< 0.0001
Grey Plover	2315 ± 884	3157 ± 1476	0.73	856 ± 798	13 ± 6	64.52	23768	< 0.0001
Curlew	1734 ± 1171	1984 ± 1340	0.87	259 ± 274	8 ± 6	31.08	5642	< 0.0001
Bar-tailed Godwit	369 ± 400	694 ± 819	0.53	327 ± 425	3 ± 3	112.34	10697	< 0.0001

Table 2 Frequency of occurrence (FOi%) of higher and the most abundant lower taxonomic groups for all five investigated waders, based on faecal analysis. N = the number of faecal samples investigated. 100% = present in all droppings

Taxon	*C. alpina* (Dunlin) N = 15	*H. ostralegus* (Oystercatcher) N = 15	*N. arquata* (Curlew) N = 11	*P. squatarola* (Grey Plover) N = 15	*L. lapponica* (Bar-tailed Godwit) N = 15
Polychaeta	**93.3**	**73.3**	**72.7**	**73.3**	**86.7**
Lanice conchilega	40	60	63.6	13.3	33.3
Nereis sp.	6.7	0	9.1	0	0
Eteone longa	0	0	9.1	0	0
Other polychaetes	93.3	73.3	72.7	60	73.3
Crustacea	**100**	**100**	**100**	**100**	**93.3**
Crab sp.	73.3	53.3	81.8	80	46.7
Amphipoda sp.	33.3	33.3	45.5	26.7	33.3
Ostracoda sp.	80	73.3	90.9	53.3	40
Isopoda sp.	0	0	9.1	0	6.7
Cumacea sp.	0	0	9.1	0	6.7
Copepoda sp.	0	13.3	0	33.3	20
Other crustaceans	100	100	100	100	93.3
Bivalvia	**33.3**	**13.3**	**45.5**	**13.3**	**26.7**
Abra alba	0	6.7	0	6.7	6.7
Aequipecten opercularis	0	0	9.1	0	0
Cerastoderma edule	0	0	36.4	6.7	0
Macoma balthica	20	0	9.1	0	0
Mysella bidentata	0	0	0	0	6.7
Nucula sp.	0	6.7	0	0	0
Scrobicularia plana	0	0	0	0	6.7
Spisula subtruncata	0	0	18.2	0	0
Other bivalves	26.7	0	18.2	0	6.7
Other	**100**	**100**	**100**	**100**	**100**

Table 3 Relative abundance (± SD) of all higher and the most abundant lower taxonomic groups in the diet composition of all five investigated wader species, based on faecal analysis. N = the number of faecal samples investigated

		C. alpina (Dunlin) N = 15		*H. ostralegus* (Oystercatcher) N = 15		*N. arquata* (Curlew) N = 11		*P. squatarola* (Grey Plover) N = 15		*L. lapponica* (Bar-tailed Godwit) N = 15	
	Taxon	%	± SD	%	± SD	%	± SD	%	± SD	%	± SD
Higher taxa	Polychaeta	17.56	17.57	15.15	24.86	18.17	29.61	5.98	9.59	8.93	18.59
	Crustacea	43.31	24.49	26.75	18.16	60.46	35.11	47.26	25.39	18.46	9.65
	Bivalvia	0.23	0.40	0.03	0.10	0.07	0.17	0.01	0.03	0.02	0.05
	Other	38.90	24.57	58.06	26.07	21.30	26.64	46.75	24.63	72.58	21.24
Polychaeta	*L. conchilega*	6.81	12.19	39.79	32.34	20.10	33.57	18.18	40.45	19.68	36.95
	Nereis sp.	0.48	1.78	0	0	0.02	0.05	0	0	0	0
	E. longa	0	0	0	0	1.01	3.03	0	0	0	0
	Other poly.	92.71	12.03	60.21	32.34	78.88	33.32	81.82	40.45	80.32	36.95
Crustacea	*Crab* sp.	4.60	5.86	5.12	7.25	32.84	34.00	18.10	18.13	10.06	17.18
	Amphipoda sp.	0.81	1.36	1.30	2.34	6.25	19.06	0.46	0.93	5.69	10.23
	Ostracoda sp.	9.18	15.06	13.36	17.84	15.81	19.30	8.17	22.37	9.15	13.90
	Isopoda sp.	0	0	0	0	0.83	2.74	0	0	0.71	2.67
	Cumacea sp.	0	0	0	0	0.001	0.003	0	0	0.71	2.67
	Copepoda sp.	0	0	0.92	2.90	0	0	0.41	0.78	1.64	3.56
	Other crust.	85.40	19.00	79.30	18.51	44.26	28.28	72.86	25.66	72.04	23.76
Bivalvia	*A. alba*	0	0	50.00	70.71	0	0	50.00	70.71	25.00	50.00
	A. opercularis	0	0	0	0	2.86	6.39	0	0	0	0
	C. edule	0	0	0	0	49.52	47.57	50.00	70.71	0	0
	M. balthica	34.50	44.17	0	0	2.86	6.39	0	0	0	0
	M. bidentata	0	0	0	0	0	0	0	0	25.00	50.00
	Nucula sp.	0	0	50.00	70.71	0	0	0	0	0	0
	S. plana	0	0	0	0	0	0	0	0	25.00	50.00
	S. subtruncata	0	0	0	0	18.10	26.17	0	0	0	0
	Other bivalves	65.50	44.17	0	0	26.67	43.46	0	0	25.00	50.00

Table 4 Global p-values (GLM) and adjusted p-values of the pairwise tests (Tukey-Kramer) to check differences in the relative abundances of higher taxonomic groups among the five investigated waders. In case of significant differences ($p < 0.05$) p-values are in bold. D=Dunlin, O=Oystercatcher, C=Curlew, G=Grey Plover, B=Bar-tailed Godwit

	Global	D - O	D - C	D - G	D - B	O - C	O - G	O - B	C - G	C - B	G - B
Polychaetes	**0.0254**	0.509	1.000	0.951	0.398	0.197	0.242	1.000	0.894	0.095	0.183
Crustaceans	**<0.0001**	0.100	0.531	1.000	0.069	**0.0010**	0.124	1.000	0.354	**<0.001**	0.087
Bivalves	**0.0013**	0.307	**0.004**	0.294	0.182	0.999	1.000	0.994	0.998	0.999	0.992
Other	**0.0009**	0.833	0.063	0.894	0.898	**0.002**	1.000	1.000	**0.002**	**0.002**	1.000

Table 5 Global p-values (GLM) and adjusted p-values of the pairwise tests (Tukey-Kramer) to check differences in the relative abundances of lower taxonomic groups (*Lanice conchilega*, Other polychaetes, Crabs and Other crustaceans) among the five investigated wader species. In case of significant differences ($p < 0.05$) p-values are in bold. D=Dunlin, O=Oystercatcher, C=Curlew, G=Grey Plover, B=Bar-tailed Godwit

	Global	D - O	D - C	D - G	D - B	O - C	O - G	O - B	C - G	C - B	G - B
L. conch.	**<0.0001**	**0.039**	1.000	0.997	**0.023**	**0.0003**	0.675	0.992	0.997	**0.0003**	0.607
Other poly.	**<0.0001**	**0.036**	1.000	0.997	**0.022**	**0.0003**	0.672	0.992	0.996	**0.0003**	0.604
Crab	**0.005**	1.000	0.070	0.769	1.000	0.570	0.950	1.000	0.135	0.468	0.950
Other crust.	**<0.0001**	0.830	**0.0001**	0.704	0.896	0.094	1.000	1.000	**0.0002**	**0.045**	1.000