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Impact on bird fauna of a non-native oyster expanding into blue mussel beds in the Dutch Wadden Sea

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Abstract

Intertidal mussel beds are important for intertidal ecosystems, because they feature a high taxonomic diversity and abundance of benthic organisms and are important foraging grounds for many avian species. After the introduction of the Pacific oyster (*Crassostrea gigas*) into the European Wadden Sea, many mussel beds developed into oyster dominated bivalve beds. Despite the fact that oysters have been colonizing many European intertidal areas for about two decades, their impact on the ecosystem is still poorly understood. Here, we investigated the impact of oysters on the condition of mussels and on the spatial distribution of birds on 18 bivalve beds with different grades of oyster occurrence throughout the Dutch Wadden Sea. Moreover, in comparing bird densities on bivalve beds with densities expected on the total intertidal area, we could detect which species exhibit a preference for the structured habitat. Overall, 50 different bird species were observed on the beds, of which about half regularly frequent intertidal flats. Most of these species showed a preference for bivalve beds. The condition of mussels decreased with the oyster dominance, whereas the majority of bird species was not affected by the oyster occurrence. However, three of the four species that were negatively affected depend on intertidal mussels as food source. Even though the Pacific oyster is a nonnative species, attempts to fight it may do more harm to avian biodiversity than good.

Keywords

Oyster reef; *Crassotrea gigas; Mytilus edulis*; shorebirds; habitat complexity; species distribution

1. **Introduction**

Shallow intertidal systems are characterized by their high primary productivity and great abundance of benthic primary consumers, including many mollusk, polychaete, and crustacean species. Consequently, these ecosystems are important nursery areas for aquatic secondary consumers such as shrimps, crabs and fishes and are major feeding grounds for many waterbird species that benefit from the high productivity (Pihl and Rosenberg 1982; Zwarts and Wanink 1993; van de Kam et al. 2004). The highest productivity is often found in habitats rich in three-dimensional structure, and one of these complex habitats in shallow intertidal systems is created by blue mussels (*Mytilus edulis*), which aggregate with conspecifics and accordingly form mussel beds. Although mussel beds only account for up to 5% of the intertidal area (Folmer et al. 2014), they represent an important feature of the intertidal ecosystem by providing hard substrate and increasing habitat complexity, reducing hydrodynamics, and modifying the sediment by depositing large amounts of pseudo-feces and other fine particles (Gutierrez et al. 2003). Many studies have shown that these beds have an important effect on the benthic community (Asmus 1987; Dittmann 1990; Markert et al. 2009) and that the beds themselves are important foraging grounds for avian consumers (Zwarts and Drent 1981; Goss-Custard et al. 1982; Nehls et al. 1997; van de Kam et al. 2004).

In the past, intertidal mussel beds were severely overfished on several occasions, such as in the Wash, UK (Atkinson et al. 2003) and in the Dutch Wadden Sea (Ens 2006). The overfishing is in line with the general observation that the degradation of coastal ecosystems is most often due to human exploitation (Lotze et al. 2006). However, more recently, many intertidal systems in Europe are experiencing drastic changes resulting from the invasion of the Pacific oyster (*Crassostrea gigas*). The introduction of *C. gigas*, native to marine waters of Japan and South-east Asia, led to a transformation of many intertidal mussel beds into mixed bivalve beds or even into oyster reefs (Nehls *et al.* 2009; Fey *et al.* 2010; Troost 2010). As a result, bivalve beds in an increasing number of European intertidal areas consist solely of mixed mussel and oyster populations (Nehls et al. 2009). While both species similarly provide hard substrate for sessile species (Kochmann *et al.* 2008), differences between mussels and oysters arise in the three-dimensional structure, heterogeneity and formed micro-habitats, due to the spatial arrangement of shells and individual shell traits (surface area and shell texture) (Gutierrez et al. 2003).

Furthermore, the bed morphology differs between both species, due to different attachment mechanisms. Mussels are adhered to the substratum by a byssus, an assemblage of numerous extracellular, collagenous fibers ending in an adhesive plaque that attaches to the substrate (Bell and Gosline 1996). Byssal threads are temporary features, which generally exhibit longevities of around 8 weeks (Bell and Gosline 1996; Moeser and Carrington 2006). The continuous process of generating new threads leads to flexible and dynamic meshworks of individual mussels (van de Koppel et al. 2005). Lacking a permanent anchorage in the substrate, mussel beds are further subject to a dynamic large scale distribution, being particularly vulnerable to storms and ice scouring (Nehls and Thiel 1993; Büttger et al. 2011; Donker et al. 2015). In contrast, oysters attach themselves permanently by generating an organic-inorganic adhesive (Burkett et al. 2010). Even after the death of individuals, oyster shells often remain anchored in the sediment. The complex of dead and alive oysters serves as settling ground for oyster larvae, which preferably settle on conspecifics (Diederich 2005). In the long run, the process of multiple settlement leads to the creation of rigid and persisting structures (Reise and Beusekom 2008; Walles et al. 2015). For many macroinvertebrate species, the complex structures formed by these two bivalves are likely to provide different resources in terms of nesting sites, shelter from predators and feeding opportunities, thus leading to differences in the species community (Markert et al. 2009). Moreover, the conversion of mussel beds into oyster dominated beds may ultimately lead to a change of the food web structure (Baird et al. 2012) as well as of the feeding opportunities for secondary consumers (Eschweiler and Christensen 2011; Waser et al. 2015).

Intertidal mussel beds are valued and protected because of their contribution to biodiversity, especially avian biodiversity, so it is important to know how the spread of Pacific oysters will affect avian biodiversity. It has been suggested, that molluscivorous species, like the Eurasian Oystercatcher (*Haematopus ostralegus*) and the Common Eider (*Somateria mollissima*) may be particularly negatively affected by the invasion of the oysters (Scheiffarth et al. 2007; Markert et al. 2013), since mussels as their preferred prey are in direct competition with the oysters and therefore may exhibit a reduced body condition (Troost 2009) resulting in a reduced prey profitability for the birds. A consolidation of oysters may additionally hamper access to the mussels. Other waterbird species commonly present on mussel beds, like for example the Eurasian Curlew (*Numenius arquata*), the Common Redshank (*Tringa totanus*), or the Black-headed Gull (*Larus ridibundus*) feed on the associated fauna (Ens and Alting 1996; Nehls et al. 1997; Goss-Custard et al. 2006; Folmer et al. 2010) and might be little affected by the habitat change (Scheiffarth et al. 2007; Markert et al. 2013). Earlier investigations however, compared the bird abundance of the present oyster-transformed beds with historic abundance data on pure mussel beds. Furthermore, these observations were limited in terms of investigated bird species and study sites, only focusing on one locality with a very low number of focal species (Markert et al. 2013) making it difficult to draw general conclusions.

In this study, we investigated the spatial distribution of waterbirds on bivalve beds with different grades of Pacific oyster occurrence. To do so, we studied 18 bivalve beds in the Dutch Wadden Sea in terms of bed properties and linked these to the appearance and number of different bird species between the years 2010 and 2013. In order to ascertain to what extent the different species show a preference for bivalve beds to habitats of less structural complexity, we furthermore used counts of birds during high tide on high tide roosts in the vicinity of tidal flats. Assuming that all birds counted during high tide on a roost will be distributed across the emerging tidal flats closest to that specific roost, it is possible to estimate the mean abundance of the different species during low tide.

The sampling design, together with data on numbers of birds during high tide at high tide roosts allowed us to investigate two main research questions: (a) Which bird species prefer bivalve beds as a low-tide feeding habitat? (b) What is the impact of the composition of the bivalve bed (i.e. the predominance of Pacific oysters) on the avian community?

2. Materials and Methods

2.1 Properties of bivalve beds

The 18 investigated bivalve beds were located throughout the Dutch part of the Wadden Sea (Fig. 1). In this area, three different types of intertidal bivalve beds can be distinguished: mussel dominated beds, where oysters are absent or occur only in very low numbers; beds with a balanced proportion of mussels and oysters and beds where oysters dominate in terms of biomass (van Stralen et al. 2012). In order to identify the proportion between both mussels and oysters, the study sites were mapped and different mussel bed properties were measured twice a year, in spring and autumn, between 2010 and 2013. Firstly, the contours of each bed were determined by walking around the bed with a hand-held GPS device following a common definition of a mussel bed (de Vlas et al. 2005). The contours gave on the one hand the spatial extent (area) of the beds and on the other hand, contours were used to delimit and create a set of multiple random sampling points. All created sample points were visited. Those points that were covered by mussels or oysters were sampled for epibenthos with a rectangular frame of 0.0225 m^{-2} (15 × 15 cm). The samples were sieved (1 mm square meshes) in the field and subsequently sorted for mussels and oysters. These were counted and sized individually using digital calipers, to the nearest 0.01 mm, in the laboratory. In order to estimate the ratio between mussel and oyster biomass, the individual shell length (L) of both mussels and oysters was converted into a volumetric length (V), representing biomass, by a fixed dimensionless shape coefficient (δ_M): $V = (\delta_M \times L)^3$. The shape coefficient is a parameter that relates the real length with the structural length in the context of the dynamic energy budget (DEB) theory (Kooijman 2010) and is well established for oysters (0.175, van der Veer et al. 2006), as well as for mussels (0.297, Saraiva et al. 2011). Based on the assumption, that the density of bivalve flesh approaches the one of water, the volumetric length was further converted into a measure of biomass (wet weight in kg). The precise body condition of mussels was estimated by measuring the ash-free dry mass of the soft tissue ($\mathrm{AFDM_{flesh}}$). To do this, mussels were sorted to discrete shell length classes (every 2.5 ± 0.5 mm beginning with a length of 5 mm, e.g. 5, 7.5, 10, etc.), the soft parts of a random sample of individuals from each length class (max. 15 individuals) was pooled and dried to constant weight, weighed, incinerated and weighed again to obtain by subtraction the $\mathrm{AFDM_{flesh}}$.

Moreover, the tidal elevation of the bivalve beds (m below mean tide level, MTL) was obtained based on the bivalve bed contours and a bathymetric grid (20 × 20 m) of the Dutch Wadden Sea provided by Rijkswaterstaat (Dutch Ministry of Infrastructure and Environment; ‘vaklodingen’; http://opendap.deltares.nl). For each bivalve bed, the mean tidal elevation of all grid-points overlapping with the bed contours was calculated.

2.2 Bird abundance on bivalve beds

All bird species within the contours of the bivalve beds were counted. Counts were usually performed in intervals covering about half of a tidal cycle (from high tide, over outgoing tide to low tide, or from low tide over incoming tide to high tide). Due to logistical reasons or bad weather such interval counts were not always possible. In these cases, one low tide count for a recently exposed bivalve bed was performed. The counts were repeated several times and performed throughout the entire year (Table A.1). In order to obtain seasonal trends of bird numbers throughout the year sinusoidal functions (e.g. Cardoso et al. 2007) were applied to each separate species on all counts made in the four different years of the study period. The overall function was $y = a + b \times sin((x - c)/365 \times 2\Pi)$, in which a, b, and c are parameters for the average, the amplitude and the reference day where the number equals the average, y is the predicted number of birds and x is the Julian day, ranging from 1-365. In some cases bird numbers were low and thus resulting in the sinus function predicting negative values. All of these negatively predicted numbers were set to 0. All sinusoidal functions were fitted using R v3.2.1 (R Development Core Team 2015), with parameters estimated using the Levenberg-Marquardt algorithm implemented in the function nlsLM from the R package minpack.lm (Elzhov et al. 2015). An overview of bird numbers on bivalve beds and the seasonal trends for the species common on intertidal flats is provided in the online supplementary appendix (Fig. A.1 – Fig. A.24).

2.3 Bird abundance on tidal flats

Counts of waterbirds on high-tide roosts adjacent to intertidal flats between July 2010 and June 2014 in combination with the extent of intertidal area were used to estimate average abundance on the intertidal flats (Fig. 1). Three types of counts were used: 1) simultaneous total counts covering all high-tide roosts, excluding the roosts along the North Sea shoreline, of all waterbird species (two counts a year were organized on a trilateral level (the Netherlands, Germany and Denmark), and up to three additional counts on regional level), 2) frequent counts (at least once a month) of all waterbird species in a selection of counting units (see van Roomen et al. 2005 for a detailed description of the high tide roost counts), 3) dedicated aerial counts of Common Eiders in the Dutch Wadden Sea (Cervencl et al. 2015). Bird numbers were investigated per tidal basin by allocating counting units to the nearest tidal basin (van Roomen et al. 2012). When a counting unit was located at the border of two tidal basins bird numbers were divided equally between the two different tidal basins. The estimates on abundance are based on monthly averages. Accounting for missing counts is done with UINDEX (Bell 1995), on the basis of site, month and year factors estimated from the non-missing counts (Underhill and Prys-Jones 1994). The seasonal index, which is the mean of the monthly averages of the four seasons (2010/11-2013/14) was used for further calculations. For Common Eider only, aerial counts between August 2010 and January 2014 were used to calculate an overall seasonal index per tidal basin. The counts were conducted by the Institute for Marine Resources and Ecosystem Studies (IMARES) or by Rijkswaterstaat (RWS) during high tide using a high-winged plane flown along predefined north-south oriented transects covering the entire area of the Dutch Wadden Sea and the adjacent North Sea coastal zone (Table A.2). For each group of Common Eider, the geographical location as well as the number of individuals was determined (see Cervencl et al. 2015, for detailed methods). For further analysis, only groups of Eiders above the intertidal of the Wadden Sea were included. The flocks of Eiders were further grouped to the different tidal basins in order to gain a total number of birds per basin. Per tidal basin, the seasonal trend of Eider numbers was calculated by the sinus function: $y = a + b \times sin((x - c)/365 \times 2\Pi)$, in which a, b, and c are parameters, y is the number of eiders per tidal basin and x is the Julian day, ranging from 1-365. In some cases, Eider numbers were low and thus resulting in negative predictions. All of these negatively predicted numbers were set to 0 (supplementary appendix, Fig. A.25).

2.4 Data analyses

The relationship between body condition and length of mussels was analyzed with linear regressions on a log-log scale. To compare AFDM$_{\text{flesh}}$ between differently sized mussels, we extracted the residual of the different size classes from the linear fits, which reflects the relative AFDM$_{\text{flesh}}$. For representation purposes, we back transformed these residuals into ratios representing the observed body composition relative to the expected value for that length class.

A bootstrap approach was used to estimate relationships between mean abundance on intertidal flats and mean abundance on bivalve beds for the different bird species. 1000 bootstrap samples were taken both from the 10 different tidal basins (e.g. a sample of 10 with replacement) and from the 18 different bivalve beds. Each tidal basin bootstrap sample was summarized by the mean index density, which is given by $\sum^{10} Y / \sum^{10} A$, where Y is the seasonal index and A the area. The bivalve bed bootstrap sample was similarly summarized: $\sum^{18} X / \sum^{18} A$, where X is the seasonal mean of bird numbers and A the area.

The relationships between both Pacific oyster occurrence and the ratio of observed and predicted mussel biomass and oyster occurrence and tidal elevation as well as the effect of oyster occurrence on the abundance of the different avian consumers were tested using Spearman's rank correlations.

Moreover, Spearman's rank correlations were used to explore the relationship between the ratios of observed and predicted mussel biomass and the abundance of birds preying on mussels. All statistical analyses were performed using R v3.2.1 (R Development Core Team 2015).

3. Results

The 18 investigated bivalve beds differed both in their size and composition of bivalve species (Table 1). Eleven beds comprised of very few or mainly small individuals of Pacific oysters, so that the fraction of the total bivalve biomass constituted by the oysters was negligible for most of these beds and overall did not exceed fractions of 6 %. Three beds (W015, E015 and E010) showed intermediate amounts of oyster biomass, resulting in oyster fractions of 18 -26 % of the total bivalve biomass and four beds (W001_A0, W012, W007b and E027) contained considerable amounts of oyster biomass, resulting in fractions of 49 -63 % of the total amount of bivalve biomass. A comparison between all beds showed that the body condition of mussels was negatively correlated with the oyster dominance (Spearman correlation, S = 81131, $\rho = -0.3$, $p = 0.009$, Fig. 2a) and that oysters occurred primarily in lower elevated parts of the intertidal (S = 1314, $\rho = -0.36$, $p = 0.147$, Fig. 2b).

During the entire study period a total of 50 bird species was observed on the different bivalve beds (Table 2). Not all species observed on the beds use intertidal habitats regularly and typically do not forage on these habitats at all or only in very low numbers. Hence, only species commonly foraging in intertidal habitats were considered for detailed analyses of the habitat use (Table 2). Of the species that predominantly forage in the intertidal, most of them were also present on intertidal bivalve beds (Table 3, Fig. 3). Only two species, the Sanderling (*Calidris alba*) and the Common Ringed Plover (*Charadrius hiaticula*), were almost completely absent on bivalve beds and showed an averseness for this habitat. For both species, the comparison of the bootstrap samples indicted that the abundances were in all cases higher on the intertidal than on bivalve beds (Table 3, Fig. 3). Species showing a more or less balanced distribution between bivalve beds and the intertidal were the Great Black-backed Gull (*Larus marinus*), the Mallard (*Anas platyrhynchos*) and the Northern Pintail (*Anas acuta*), where 35 -70 % of the bootstrap samples had a higher abundance on the bivalve beds. All other species were found with higher abundances on bivalve beds (82 -100 %, Table 3, Fig. 3), of which the Little Egret (*Egretta garzetta*) showed the highest preference for bivalve beds with an abundance 47 times higher than on bare intertidal flats (Table 3). Other species showing a relatively high preference for bivalve beds were: Common Eider (*Somateria mollissima*), Common Greenshank (*Tringa nebularia*), Eurasian Whimbrel (*Numenius phaeopus*), Common Redshank (*Tringa totanus*), Ruddy Turnstone (*Arenaria interpres*), Eurasian Spoonbill (*Platalea leucorodia*), and Herring Gull (*Larus argentatus*). These species were, in descending order, between 20 and 11 times more abundant on bivalve beds than on bare intertidal flats (Table 3). The most abundant bird on the bivalve beds, the Eurasian Oystercatcher (*Haematopus ostralegus*), also had a high preference for these beds (bed preference of 9.3, Table 3).

In four species, bed composition significantly affected their abundance: the Eurasian Oystercatcher, the Common Gull (*Larus canus*), the Red Knot (*Calidris canutus*) and the Dunlin (*Calidris alpina*). The abundance of these four species was negatively correlated with the fraction of oysters in the total bivalve biomass (Spearman correlation, all $p < 0.03$, Fig. 4). All other species showed no significant response to the dominance of oysters (Fig. 4). Focusing on the species preying on mussels, a significant relationship between bird abundance and prey quality (ratio of observed and predicted $\mathrm{AFDM}_{\mathrm{flesh}}$) was only observed for the Common Eider (Spearman correlation, S = 378, $\rho = 0.61$, $p = 0.007$, Fig. 5). In contrast, the abundances of the Oystercatcher, the Red Knot and the Herring Gull were not correlated with prey quality (Spearman correlation, all $p > 0.05$, Fig. 5).

4. Discussion

Epibenthic bivalve aggregations are important structures in shallow intertidal soft-bottom environments. They often feature a higher or different taxonomic diversity and abundance of organisms than surrounding bare flats (Asmus 1987; Buschbaum et al 2009; Markert et al. 2009) and therefore serve as important foraging grounds for many bird species. Indeed, the majority (18 out of 24) of the investigated bird species showed a preference for these biogenic structures. One might argue that we overestimated the number of bird species preferring bivalve beds, because we used bird numbers at high-tide roosts to estimate the abundance on intertidal flats at low tide, instead of direct counts. However, since low tide feeding densities on bare tidal flats on the basis of low tide counts were generally similar to our calculated densities (Folmer et al. 2010; van den Hout and Piersma 2013), we are confident that our procedure did not misjudge the low tide feeding densities leading to a reliable estimate of bird species preferring bivalve beds.

The introduction of the Pacific oyster has led to significant changes of the intertidal systems of the Dutch Wadden Sea. At present, about 50 % of the intertidal mussel beds in the Dutch Wadden Sea contain many oysters and are either a mix of oysters and mussels or dominated by oysters (van Stralen et al. 2012). In line with this, about 40 % (7 out of 18) of the beds investigated in our study contained a considerable amount of oyster biomass. The impacts of the Pacific oyster introduction are manifold, comprising both positive and negative effects. Positive effects of the introduction include numerous important ecosystem services, such as improvement of the water quality, seashore stabilization, carbon burial and habitat provision for other organisms (Grabowski et al. 2012; Katsanevakis et al. 2014). In contrast, the occupancy of the same habitats as native *M. edulis* leads to competition for space and food between the two species. We found that the body condition of mussels generally decreased with increasing oyster dominance. However, some beds featured a low mussel body condition despite oysters being absent or only present in low numbers. Since oysters are intolerant to short inundation times resulting in the failure to grow and persist in higher elevated intertidal areas (Rodriguez et al. 2014; Walles et al. 2016), mussels dominate these high areas. The short inundation times that the mussels face in the high intertidal may result in low body conditions (Goss-Custard et al. 1993).

Yet, our study revealed that the majority of the bird species making use of mussel beds show no clear signs of being affected in terms of feeding density by the changes caused by the oyster introduction. We found no evidence for positive impacts. Negative impacts, indicated by a reduction in abundance, were only evident for four species. These negative impacts are particularly expected for species preying on mussels themselves (Scheiffarth et al. 2007).

Four bird species recorded in our study feed on the mussels: Red Knot, Oystercatcher, Herring Gull and Common Eider. These species may experience changes through the appearance of the invader both in the profitability (Troost 2009; Markert et al. 2009, this study) as well as in the accessibility of the prey (Eschweiler and Christensen 2011, Waser et al. 2015). Therefore, as prey accessibility and prey profitability are important factors determining the fraction of harvestable food for wading birds (Zwarts and Wanink 1993), we expect these species to face a reduction in harvestable prey items leading them to avoid those beds where oysters are prevalent. This was observed for the Oystercatcher and Red Knot, but not for Common Eider and Herring Gull. How can this be explained?

For Oystercatchers, our finding corroborates an earlier study based on observations on one single location before and after oyster invasion that Oystercatchers appear in much lower densities on oyster dominated beds, even though this species is actually able to feed on small-sized oysters (Markert et al. 2013). Although expected, we are not aware of previous reports that Red Knots might be negatively affected by an increased appearance of Pacific oysters. The Knot swallows bivalves whole and is only able to feed on mussels with a length below 20 mm (Zwarts and Blomert 1992). Hence, it only feeds on recently established mussel beds with a preponderance of small mussels. Old mussel beds with many large mussels are not attractive, even in the absence of Pacific oysters, explaining the great range in feeding densities observed on bivalve beds with no or few Pacific oysters.

The reason that densities of Herring Gulls did not decrease with the occurrence of Pacific oysters may be due to the fact that they may not forage exclusively on mussels when they frequent bivalve beds, but may feed on a broad range of resources (Camphuysen 2013). Although mussels represent an important part of their diet, this applies primarily to mussel spat, not older than 1 year and not exceeding lengths of 20 mm (Camphuysen 2013). Since this size range of mussels appears hidden amongst bigger conspecifics in older beds, Herring Gulls typically prey on the mussel spat on young beds only. On older established bivalve beds, Herring Gulls use other resources, such as shore crabs, which are not heavily influenced by the oyster dominance (Markert et al. 2013).

A similar explanation may apply to the Common Eider, as it also feeds on shore crabs (Cramp 1977). In addition, it should be remarked that although Eiders do feed in the intertidal during the period that it is covered with water, they show a strong preference for subtidal areas with high quality food, i.e. mollusks with a high flesh/shell ratio (Nehls 2001; Cervencl et al. 2015). This preference also showed up in a strong correlation between Eider abundance and prey quality. Despite the fact that mussel condition was negatively correlated with presence of oysters, we did not find a negative correlation between Eider abundance and presence of oysters, as already mentioned. This may be due to Eiders feeding on shore crabs instead of mussels on oyster beds, as well as avoiding mussel beds high in the intertidal zone, where no oysters occur, but mussels are of poor quality.

Our study corroborated the prediction of Scheiffarth et al. (2007) that bird species feeding on associated fauna would be little affected by the invasion of Pacific oysters into intertidal mussel beds, except for the Dunlin and the Common Gull, which were clearly negatively affected by an increase in the presence of oysters. The decreasing numbers of Common Gulls might be directly coupled with the decrease of Oystercatchers. Oystercatchers feeding on mussels need to open the shells in order to swallow the soft flesh of the prey (Goss-Custard and Dit Durell 1988), which requires relatively long handling times. As a result, the birds are sensitive to interference and allowing other individuals to steal prey (kleptoparasitism) (Ens and Goss-Custard 1984; Wood et al. 2015). Within avian assemblages, gulls are known to steal food items from several wading bird species (Amat and Aguilera 1990; Ens et al. 1990; Wood et al. 2015). The study of Zwarts and Drent (1981) found that Common Gulls present on mussel beds depended almost entirely on stealing mussels from Oystercatchers, suggesting that the density of Common Gulls reflects the Oystercatcher density. In our study, the densities of Common Gulls and Oystercatchers were indeed correlated with each other (Spearman correlation, $S = 446$, $\rho = 0.54$, $p = 0.021$).

In contrast, the Dunlin does not feed on bivalve covered patches at all, but forages on worms in the open areas in between. While in mussel dominated beds mussels establish hummocks rising above the immediate surrounding, in oyster dominated beds, the between-patch areas often silt up to mud-hummocks higher than the bivalves themselves. This characteristic may decrease their attractiveness as feeding areas for the Dunlin.

Our study demonstrates that mussel beds are very important for avian biodiversity and that the colonization of these beds by Pacific oysters does not improve avian biodiversity, but only has negative impacts, most clearly for three species: Oystercatcher, Common Gull and Knot. One might consider removing the oysters in the hope that the vacant space would be taken by mussels, restoring good feeding opportunities for the affected bird species. However, a complete removal of oyster beds is challenging, since aggregations of oysters are firmly anchored into the sediment and dredging only removes peripheral oysters (Wijsman et al. 2008). After dredging, buried parts of the oyster complex remain in the sediment, providing ideal settling grounds for oyster spat, in the long run leading to a recolonization by Pacific oysters (Wijsman et al. 2008). Moreover, the removal of the oysters has clear negative impacts on the birds, as most species avoid the oyster fished areas (Wijsman et al. 2008) and this is in line with our finding that for the majority of species preferring bivalve beds, high densities of Pacific oysters may not decrease the attractiveness of the bivalve bed as a feeding area. Hence, fishing away the oyster beds would be detrimental for the birds.

As attempts to fight the Pacific oyster, by e.g. fishing away the oysters, will negatively affect the birds using bivalve beds as foraging areas, other measures are needed to mitigate the invasion of the Pacific oyster into intertidal areas. Moreover, the possible effects on avian diversity should be considered when managing the commercial exploitation of Pacific oysters. In the Netherlands it is currently discussed whether fishery of Pacific oysters should be allowed. Hand picking of oysters is the only feasible option on wild beds. Our study shows that it is impossible to visit oyster beds without disturbing birds, but that the number of birds that are disturbed can be minimized by restricting fishery to beds with the highest densities of Pacific oysters.

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Table 1: Overview of some characteristics of the investigated bivalve beds. For each bed, the area on which birds were counted, densities and biomass of oysters and mussels and the fraction of the total bivalve biomass contributed by Pacific oysters are given. Values given are mean ± SE.

Mussel bed	Area (ha)	Mussel density (n m^{-2})	Oyster density (n m^{-2})	Mussel biomass (kg m^{-2})	Oyster biomass (kg m^{-2})	Fraction of oysters of the biomass (%)
W001_A0	1.2	2223 ± 457	326 ± 56	1.67 ± 0.25	2.24 ± 0.34	57.34
W001_A1	6.8	2770 ± 434	25 ± 11	2.07 ± 0.28	0.02 ± 0.02	1.06
W001_A2	3.8	1626 ± 494	5 ± 5	0.78 ± 0.24	0.02 ± 0.02	2.32
W001_B	1.2	1222 ± 305	50 ± 20	1.05 ± 0.31	0.02 ± 0.01	2.16
W012	2.8	1444 ± 206	571 ± 134	2.26 ± 0.25	2.14 ± 0.22	48.70
W013	17.8	1237 ± 98	73 ± 32	1.34 ± 0.18	0.07 ± 0.02	4.73
W017	6.3	1381 ± 230	116 ± 80	2.15 ± 0.22	0.05 ± 0.02	2.40
W015	3.9	1798 ± 108	533 ± 242	1.15 ± 0.14	0.41 ± 0.04	26.43
W007b	9.6	1525 ± 160	622 ± 78	2.47 ± 0.27	4.13 ± 0.77	62.53
E031	11.0	1668 ± 97	113 ± 30	2.92 ± 0.28	0.19 ± 0.04	6.07
E027	17.3	546 ± 74	220 ± 67	1.16 ± 0.16	1.30 ± 0.13	52.95
E024	70.1	7080 ± 1363	0 ± 0	2.54 ± 0.47	0 ± 0	0
E023	56.4	697 ± 317	2 ± 2	0.53 ± 0.14	0.01± 0.01	1.28
E022	34.5	2049 ± 321	37 ± 14	1.57 ± 0.15	0.02 ± 0.01	1.16
E032	30.1	4138 ± 364	1 ± 1	2.11 ± 0.01	0.0002 ± 0.0002	0.01
E015	17.5	815 ± 104	220 ± 76	1.29 ± 0.16	0.29 ± 0.07	18.15
E010	66.8	1290 ± 149	419 ± 188	1.96 ± 0.28	0.65 ± 0.10	24.87
E002	3.7	3505 ± 897	54 ± 51	3.96 ± 0.83	0.02 ± 0.02	0.51

Table 2: Results of the bird counts on bivalve beds. For all bird species that were observed on the beds, the number of beds on which a species was observed, the mean appearance and abundance based on all counts and an indication whether a species was considered to be common on intertidal flats are given. Values given are mean ± SE.

Common name	Scientific name	Number of beds the species was observed on	Mean appearance (%)	Mean abundance (n ha^{-1})	Intertidal species
Great Crested Grebe	*Podiceps cristatus*	7	6.2 ± 2.4	0.012 ± 0.004	
Great Cormorant	*Phalacrocorax carbo*	14	20 ± 4.2	0.084 ± 0.05	
Little Egret	*Egretta garzetta*	9	7.9 ± 2.7	0.009 ± 0.005	X
Grey Heron	*Ardea cinerea*	3	1.2 ± 0.7	0.001 ± 0.001	
Eurasian Spoonbill	*Platalea leucorodia*	17	37 ± 4.9	0.126 ± 0.031	X
Greylag Goose	*Anser anser*	1	0.8 ± 0.8	0.001 ± 0.001	
Dark-bellied Brent Goose	*Branta bernicla*	17	18.6 ± 3.2	0.280 ± 0.107	
Common Shelduck	*Tadorna tadorna*	16	45.2 ± 6.7	1.206 ± 0.383	X
Eurasian Wigeon	*Anas penelope*	12	12.2 ± 2.7	0.493 ± 0.221	
Gadwall	*Anas strepera*	1	0.9 ± 0.9	0.003 ± 0.003	
Common Teal	*Anas crecca*	3	0.9 ± 0.5	0.003 ± 0.002	
Mallard	*Anas platyrhynchos*	14	29.8 ± 5.7	0.332 ± 0.136	X
Northern Pintail	*Anas acuta*	9	7.2 ± 2.1	0.088 ± 0.044	X
Northern Shoveler	*Anas clypeata*	3	1.8 ± 1.2	0.006 ± 0.004	
Common Eider	*Somateria mollissima*	18	73.2 ± 5.5	3.039 ± 1.099	X
Common Goldeneye	*Bucephala clangula*	1	0.8 ± 0.8	0.004 ± 0.002	
Red-breasted Merganser	*Mergus serrator*	10	10.3 ± 3.4	0.047 ± 0.021	
Eurasian Sparrowhawk	*Accipiter nisus*	1	0.6 ± 0.6	0.001 ± 0.001	
Peregrine Falcon	*Falco peregrinus*	10	6.4 ± 1.9	0.004 ± 0.001	
Eurasian Oystercatcher	*Haematopus ostralegus*	18	98.6 ± 1.0	10.702 ± 2.270	X
Common Ringed Plover	*Charadrius hiaticula*	6	5.2 ± 2.2	0.009 ± 0.006	X
European Golden Plover	*Pluvialis apricaria*	9	12.8 ± 4.5	3.064 ± 2.326	X
Grey Plover	*Pluvialis squatarola*	17	40.5 ± 6.1	0.252 ± 0.078	X
Northern Lapwing	*Vanellus vanellus*	1	0.4 ± 0.4	0.001 ± 0.001	
Red Knot	*Calidris canutus*	14	23.2 ± 4.9	1.659 ± 0.871	X
Sanderling	*Calidris alba*	4	1.6 ± 0.8	0.001 ± 0.001	X
Dunlin	*Calidris alpina*	16	40.4 ± 6.9	1.984 ± 0.733	X
Common Snipe	*Gallinago gallinago*	1	0.4 ± 0.4	0.0002 ± 0.0002	
Black-tailed Godwit	*Limosa limosa*	5	2.9 ± 1.2	0.008 ± 0.004	
Bar-tailed Godwit	*Limosa lapponica*	18	54.4 ± 4.3	0.839 ± 0.181	X
Eurasian Whimbrel	*Numenius phaeopus*	15	19.6 ± 3.5	0.133 ± 0.078	X
Eurasian Curlew	*Numenius arquata*	18	99.1 ± 0.6	6.228 ± 1.410	X
Spotted Redshank	*Tringa erythropus*	9	6.9 ± 2.4	0.022 ± 0.015	X
Common Redshank	*Tringa totanus*	18	65.9 ± 6.5	1.748 ± 0.514	X
Common Greenshank	*Tringa nebularia*	18	36.5 ± 4.5	0.194 ± 0.059	X
Ruddy Turnstone	*Arenaria interpres*	18	55.8 ± 4.8	0.371 ± 0.109	X
Parasitic Jaeger	*Stercorarius parasiticus*	1	0.6 ± 0.6	0.00001 ± 0.00001	
Little Gull	*Larus minutus*	1	0.8 ± 0.8	0.002 ± 0.002	
Black-headed Gull	*Larus ridibundus*	18	80 ± 2.7	2.928 ± 0.462	X
Common Gull	*Larus canus*	18	72.3 ± 3.1	0.954 ± 0.280	X
Lesser Black-backed Gull	*Larus fuscus*	14	21 ± 4.9	0.159 ± 0.128	
Herring Gull	*Larus argentatus*	18	89.9 ± 2.8	2.331 ± 0.483	X
Great Black-backed Gull	*Larus marinus*	15	17.6 ± 3.0	0.013 ± 0.005	X
Sandwich Tern	*Sterna sandvicensis*	5	2.4 ± 1.0	0.014 ± 0.012	
Common Tern	*Sterna hirundo*	6	5.1 ± 2.1	0.006 ± 0.004	
Little Tern	*Sterna albifrons*	4	2.0 ± 0.9	0.006 ± 0.005	
Black Tern	*Chlidonias niger*	1	0.8 ± 0.8	0.0003 ± 0.0003	
Carrion Crow	*Corvus corone corone*	8	17.9 ± 7.7	0.044 ± 0.021	
Hooded Crow	*Corvus corone cornix*	2	1.2 ± 0.9	0.003 ± 0.003	
Snow Bunting	*Plectrophenax nivalis*	1	0.4 ± 0.4	0.0001 ± 0.0001	

Table 3: Results of the bootstrap calculations of bird abundance on the intertidal and on bivalve beds. For each species considered to be common on intertidal flats the mean of the total population in the Dutch Wadden Sea (2011-2014), abundances on bare intertidal flats and on bivalve beds, the portion of all bootstrap observations exhibiting a higher abundance on bivalve beds and a comparison between bare intertidal -and bivalve bed abundance (preference factor) are given. The asterisk indicates the part of the population of Common Eider using the intertidal during high tide. Values are given ± SE.

Species	Population total (mean high water counts)	Abundance intertidal (n ha^{-1})	Abundance bivalve bed (n ha^{-1})	Fraction bird abundance higher on bivalve beds (%)	Preference factor for bivalve beds
Little Egret	15 ± 3	0.0001 ± 0.000002	0.005 ± 0.0001	100	46.7
Common Eider	13037 ± 587 *	0.103 ± 0.001	2.080 ± 0.026	100	20.1
Common Greenshank	1948 ± 478	0.015 ± 0.0001	0.221 ± 0.002	100	15.2
Eurasian Whimbrel	337 ± 104	0.003 ± 0.00002	0.036 ± 0.001	99.9	14.5
Common Redshank	14787 ± 1807	0.111 ± 0.001	1.475 ± 0.020	100	13.3
Ruddy Turnstone	2557 ± 160	0.019 ± 0.0002	0.229 ± 0.003	100	11.9
Eurasian Spoonbill	935 ± 173	0.007 ± 0.0001	0.083 ± 0.001	100	11.8
Herring Gull	29077 ± 1705	0.218 ± 0.001	2.355 ± 0.022	100	10.8
Eurasian Oystercatcher	91766 ± 6171	0.688 ± 0.003	6.371 ± 0.036	100	9.3
Eurasian Curlew	83688 ± 5466	0.627 ± 0.003	5.560 ± 0.038	100	8.9
European Golden Plover	17682 ± 2316	0.132 ± 0.002	0.868 ± 0.019	96	6.6
Red Knot	70549 ± 6686	0.526 ± 0.003	3.068 ± 0.054	92.8	5.8
Common Gull	32080 ± 3566	0.240 ± 0.002	1.312 ± 0.021	99.5	5.5
Common Shelduck	58643 ± 5727	0.434 ± 0.004	2.134± 0.017	99.9	4.9
Black-headed Gull	62483 ± 9379	0.463 ± 0.001	1.958 ± 0.013	100	4.2
Spotted Redshank	835 ± 145	0.006 ± 0.0001	0.020 ± 0.0004	82.3	3.2
Northern Pintail	8408 ± 1225	0.065 ± 0.001	0.131 ± 0.003	70.5	2
Bar-tailed Godwit	62027 ± 5675	0.457 ± 0.005	0.807 ± 0.009	86.5	1.8
Dunlin	231404 ± 16122	1.754 ± 0.015	2.999 ± 0.038	83.7	1.7
Grey Plover	22343 ± 2250	0.173 ± 0.001	0.254 ± 0.002	82.9	1.5
Mallard	17004 ± 1798	0.126 ± 0.001	0.152 ± 0.002	62.7	1.2
Great Black-backed Gull	1577 ± 168	0.012 ± 0.0001	0.010 ± 0.0001	34.6	0.9
Common Ringed Plover	2776 ± 599	0.021 ± 0.0001	0.004 ± 0.0001	0	0.2
Sanderling	9079 ± 702	0.069 ± 0.001	0.001 ± 0.00002	0	0

Fig. 1: Overview of the different tidal basins in the Dutch Wadden Sea. Borders of the tidal basins are represented by thin black lines. Locations of the investigated bivalve beds are indicated by white squares. Beds in the western Dutch Wadden Sea are indicated by a ’W’ and accordingly an ’E’ in a label represents a bivalve bed in the eastern part of the Dutch Wadden Sea. White areas represent water, light grey areas indicate intertidal flats exposed during low tide, intermediate grey indicates bivalve beds and land is represented by dark grey. High-tide roosts of the different bird species are indicated by shaded areas. Bed W001 was subdivided into 4 different sectors which are shown in the detailed map on the bottom right.

Fig. 2: a) The ratio of observed and predicted mean ash-free dry mass of mussel flesh ($\mathrm{AFDM}_{\mathrm{flesh}}$) depending on the oyster fraction of the total bivalve biomass (%) and b) the oyster fraction of the total bivalve biomass (%) depending on the tidal elevation (m below mean tide level, MTL). The coding of the two graphs indicates mean values of the respective bivalve beds.

Fig. 3: Results of the bootstrapping of bird abundances. The bird abundance on bivalve beds (n ha^{-1}) was plotted against the bird abundance intertidal flats (n ha^{-1}). The grey dashed line represents the $x = y$ line. The mean of all bootstrap samples per species is indicated by an encircled $\bar{x}$.

Fig. 4: Relationship between the fraction of oysters on total bivalve biomass and the abundance of the different bird species (n ha^{-1}). Species showing a significant relationship between their abundance and the oyster occurrence are highlighted in bold font.

Fig. 5: Relationship between the body condition of mussels and the abundance of molluscivorous birds. Plotted are the bird abundance of the four bird species (n ha^{-1}) against the relative mean ash-free dry mass of mussels ($\mathrm{AFDM}_{\mathrm{flesh}}$). Species showing a significant relationship between their abundance and the mussel condition are highlighted in bold font.

Figure 1

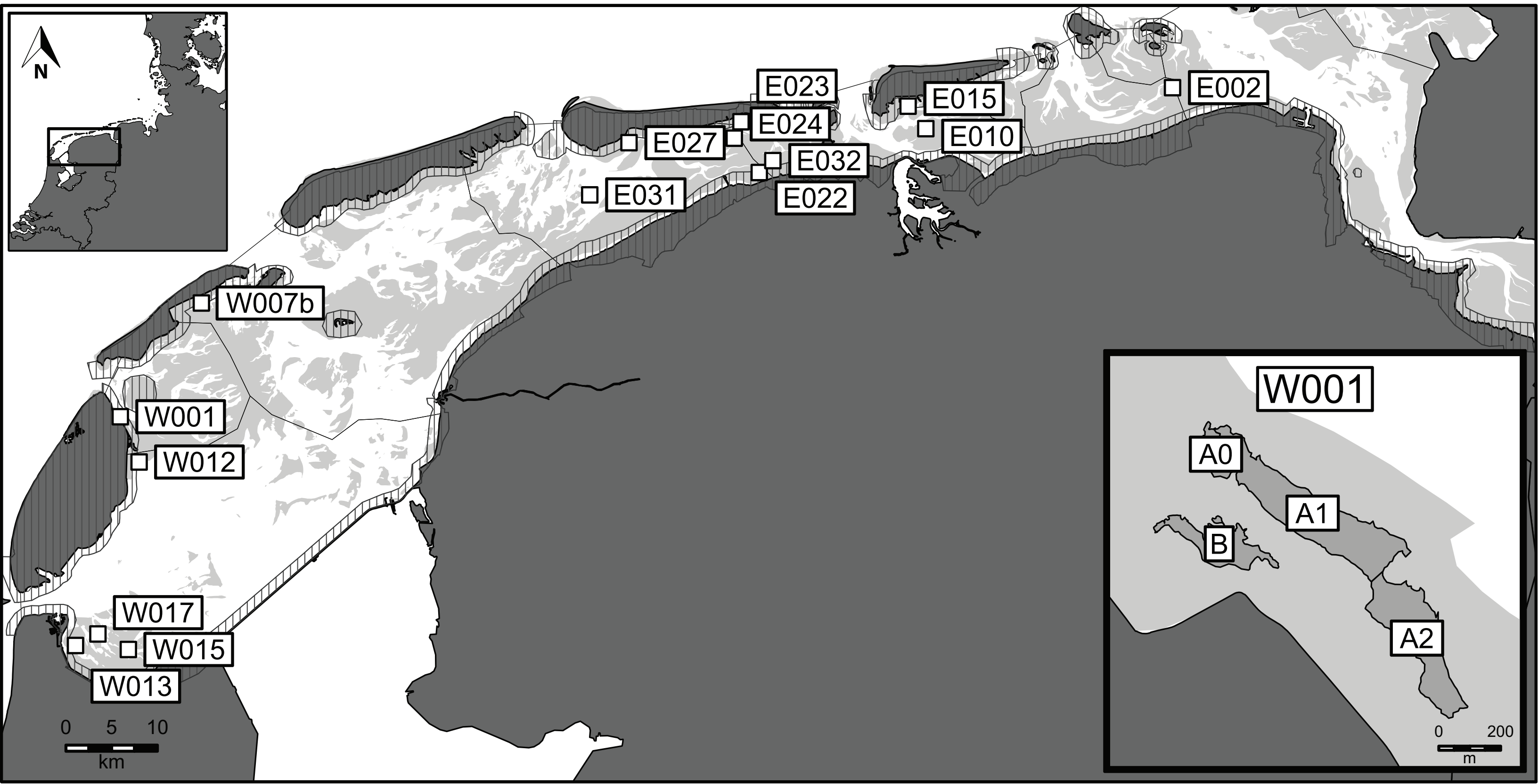

N
E023
E024
E027
E032
E031
E022
E015
E010
E002
W007b
W001
W012
W017
W015
W013
0
5
10
km
W001
A0
A1
B
A2
0
200
m

Figure 2

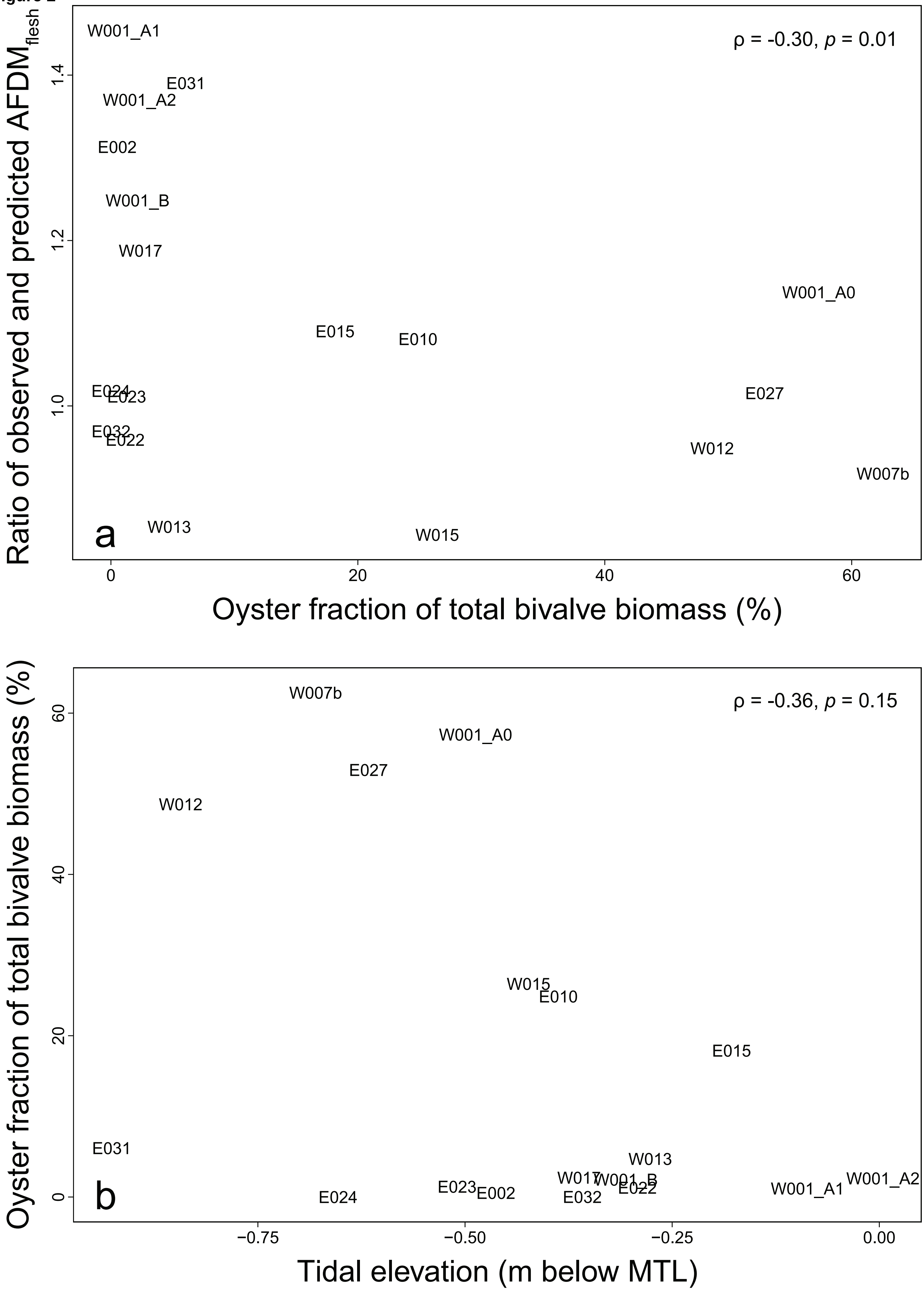

Ratio of observed and predicted AFDM$_{flesh}$
ρ = -0.30, *p* = 0.01
W001_A1
E031
W001_A2
E002
W001_B
W017
W001_A0
E015
E010
E024
E023
E027
E032
E022
W012
W007b
W013
W015
a
1.4
1.2
1.0
0
20
40
60
Oyster fraction of total bivalve biomass (%)
Oyster fraction of total bivalve biomass (%)
ρ = -0.36, *p* = 0.15
W007b
W001_A0
E027
W012
W015
E010
E015
E031
W013
W017
W001_B
W001_A2
E023
E022
E002
W001_A1
E024
E032
b
60
40
20
0
−0.75
−0.50
−0.25
0.00
Tidal elevation (m below MTL)

Figure 3

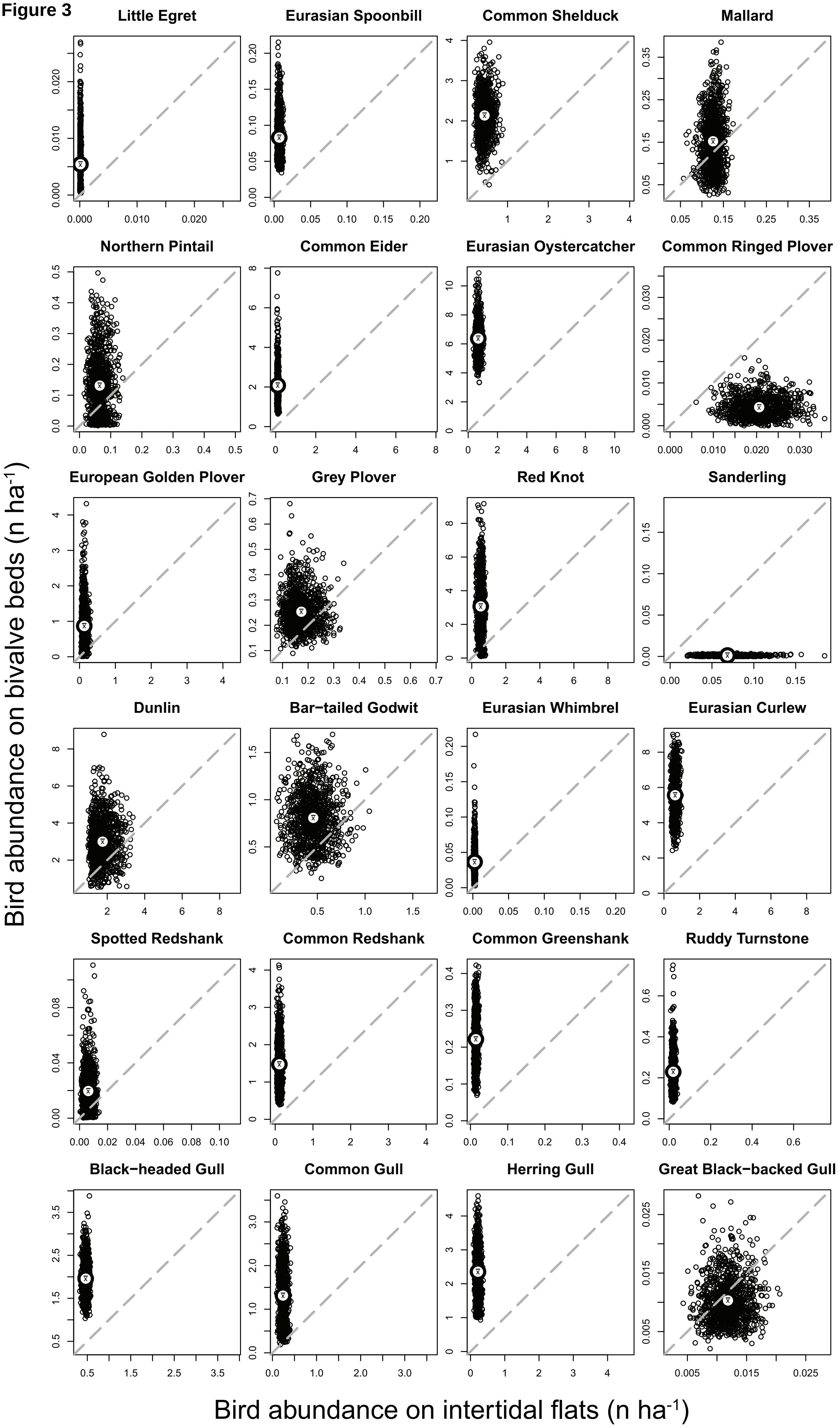

Little Egret
0.000
0.010
0.020
Eurasian Spoonbill
0.00
0.05
0.10
0.15
0.20
Common Shelduck
1
2
3
4
Mallard
0.05
0.15
0.25
0.35
Northern Pintail
0.0
0.1
0.2
0.3
0.4
0.5
Common Eider
0
2
4
6
8
Eurasian Oystercatcher
0
2
4
6
8
10
Common Ringed Plover
0.000
0.010
0.020
0.030
European Golden Plover
0
1
2
3
4
Grey Plover
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Red Knot
0
2
4
6
8
Sanderling
0.00
0.05
0.10
0.15
Dunlin
2
4
6
8
Bar−tailed Godwit
0.5
1.0
1.5
Eurasian Whimbrel
0.00
0.05
0.10
0.15
0.20
Eurasian Curlew
0
2
4
6
8
Spotted Redshank
0.00
0.02
0.04
0.06
0.08
0.10
Common Redshank
0
1
2
3
4
Common Greenshank
0.0
0.1
0.2
0.3
0.4
Ruddy Turnstone
0.0
0.2
0.4
0.6
Black−headed Gull
0.5
1.5
2.5
3.5
Common Gull
0.0
1.0
2.0
3.0
Herring Gull
0
1
2
3
4
Great Black−backed Gull
0.005
0.015
0.025
x̄
Bird abundance on bivalve beds (n ha^{-1})
Bird abundance on intertidal flats (n ha^{-1})

Figure 4

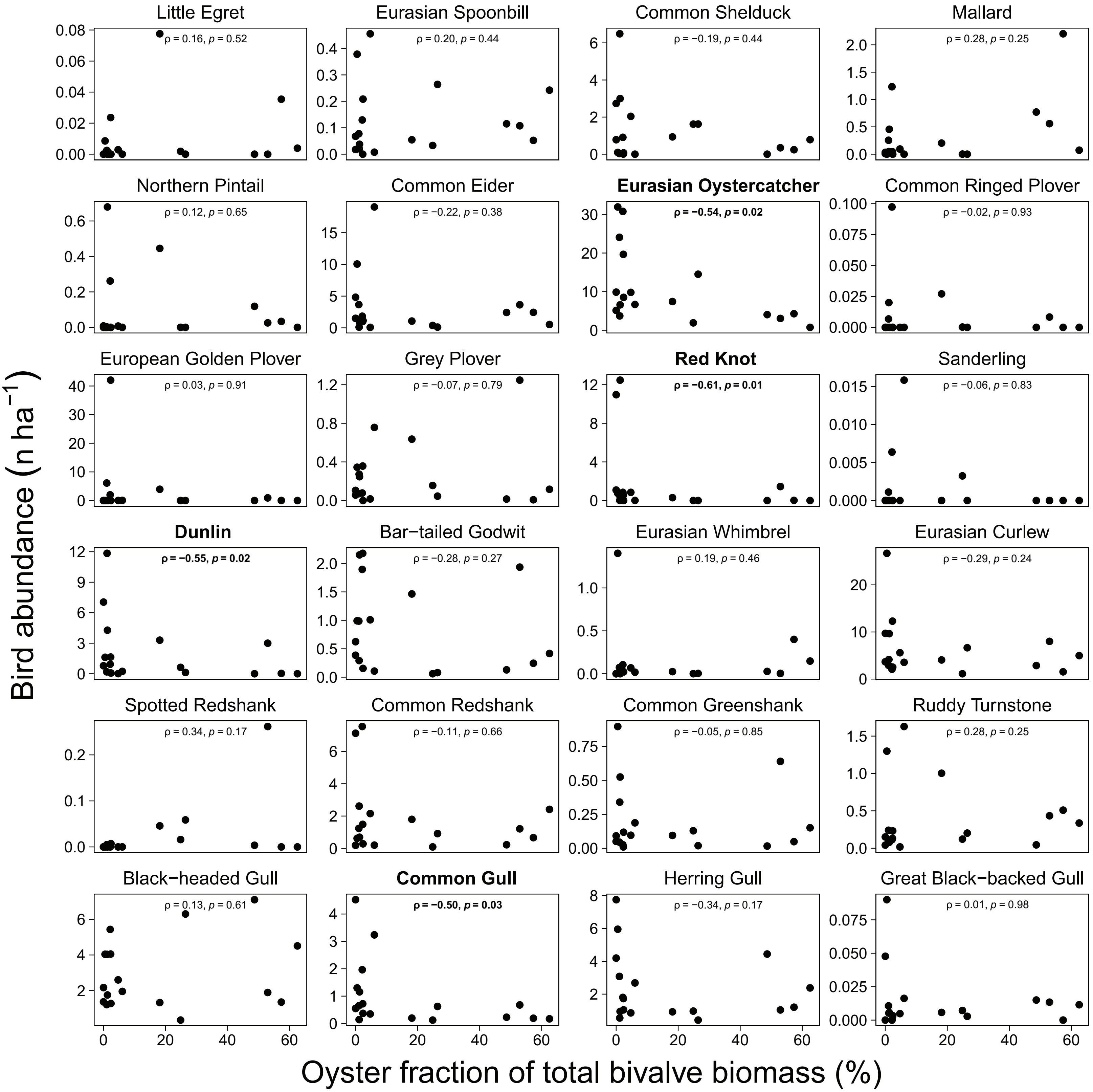
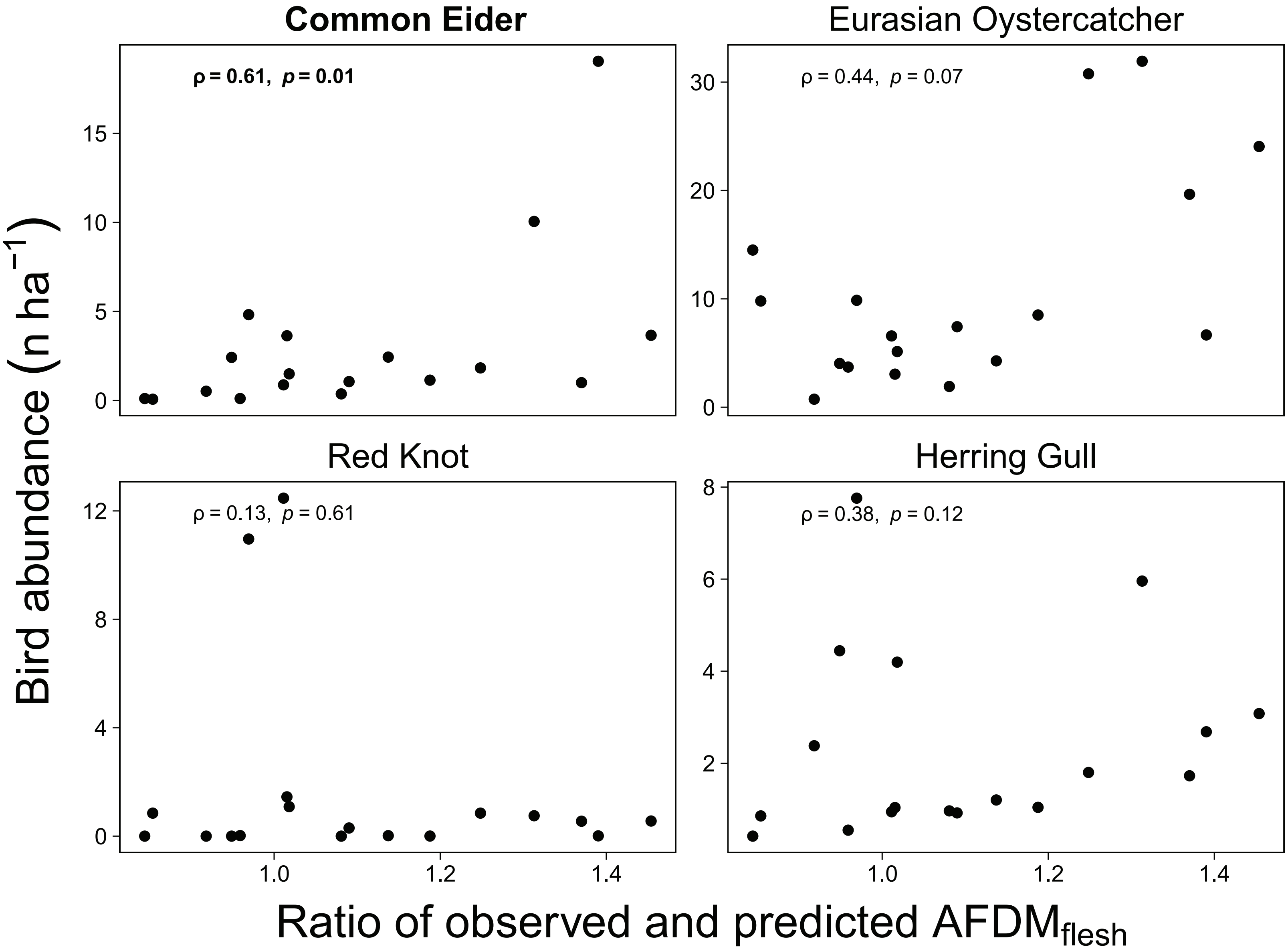

Little Egret
ρ = 0.16, p = 0.52
Eurasian Spoonbill
ρ = 0.20, p = 0.44
Common Shelduck
ρ = −0.19, p = 0.44
Mallard
ρ = 0.28, p = 0.25
Northern Pintail
ρ = 0.12, p = 0.65
Common Eider
ρ = −0.22, p = 0.38
Eurasian Oystercatcher
ρ = −0.54, p = 0.02
Common Ringed Plover
ρ = −0.02, p = 0.93
European Golden Plover
ρ = 0.03, p = 0.91
Grey Plover
ρ = −0.07, p = 0.79
Red Knot
ρ = −0.61, p = 0.01
Sanderling
ρ = −0.06, p = 0.83
Dunlin
ρ = −0.55, p = 0.02
Bar−tailed Godwit
ρ = −0.28, p = 0.27
Eurasian Whimbrel
ρ = 0.19, p = 0.46
Eurasian Curlew
ρ = −0.29, p = 0.24
Spotted Redshank
ρ = 0.34, p = 0.17
Common Redshank
ρ = −0.11, p = 0.66
Common Greenshank
ρ = −0.05, p = 0.85
Ruddy Turnstone
ρ = 0.28, p = 0.25
Black−headed Gull
ρ = 0.13, p = 0.61
Common Gull
ρ = −0.50, p = 0.03
Herring Gull
ρ = −0.34, p = 0.17
Great Black−backed Gull
ρ = 0.01, p = 0.98
Bird abundance (n ha⁻¹)
Oyster fraction of total bivalve biomass (%)
0
20
40
60

Figure 5



Common Eider
ρ = 0.61, p = 0.01
Eurasian Oystercatcher
ρ = 0.44, p = 0.07
Red Knot
ρ = 0.13, p = 0.61
Herring Gull
ρ = 0.38, p = 0.12
0
5
10
15
0
10
20
30
0
4
8
12
2
4
6
8
1.0
1.2
1.4
1.0
1.2
1.4
Bird abundance (n ha^{-1})
Ratio of observed and predicted AFDM$_{flesh}$

Electronic appendix

Table A.1: The number of counting days of birds on the studied intertidal mussel beds in the Dutch Wadden Sea for the study years.

Mussel bed	2010	2011	2012	2013
W001_A0	9	6	3	7
W001_A1	10	6	3	7
W001_A2	10	2		
W001_B	9	6	3	6
W012		5	3	5
W013		4	4	5
W017			3	4
W015		4	4	5
W007b		4	2	1
E031		4	5	1
E027		5	4	4
E024				5
E023			1	4
E022	1	3	6	3
E032			1	8
E015	1	5	7	6
E010	2	2	4	2

Table A.2: Overview of the aerial counts of Common Eider in the Dutch Wadden Sea performed by IMARES and Rijkswaterstaat (RWS). Asterisks indicate counts which only covered the western part (holding about 90% of the total Dutch population) of the tidal area of the Dutch Wadden Sea.

Season	Date	Institution
2010/2011	14.8.2010 *	IMARES
	15/16/19.11.2010	IMARES
	10/11/12.12.2010	IMARES
	22/23.1.2011	RWS
	18/19.2.2011	IMARES
	11/12.3.2011	IMARES
	8/9.4.2011	IMARES
2011/2012	7/8.8.2011	IMARES
	14/15.1.2012	RWS
	11.2.2012 *	IMARES
	26/27.2.2012	IMARES
	17.3.2012 *	IMARES
2012/2013	24/25.1.2013 *	RWS
2013/2014	15/16.11.2013	RWS
	4/5.1.2014	RWS

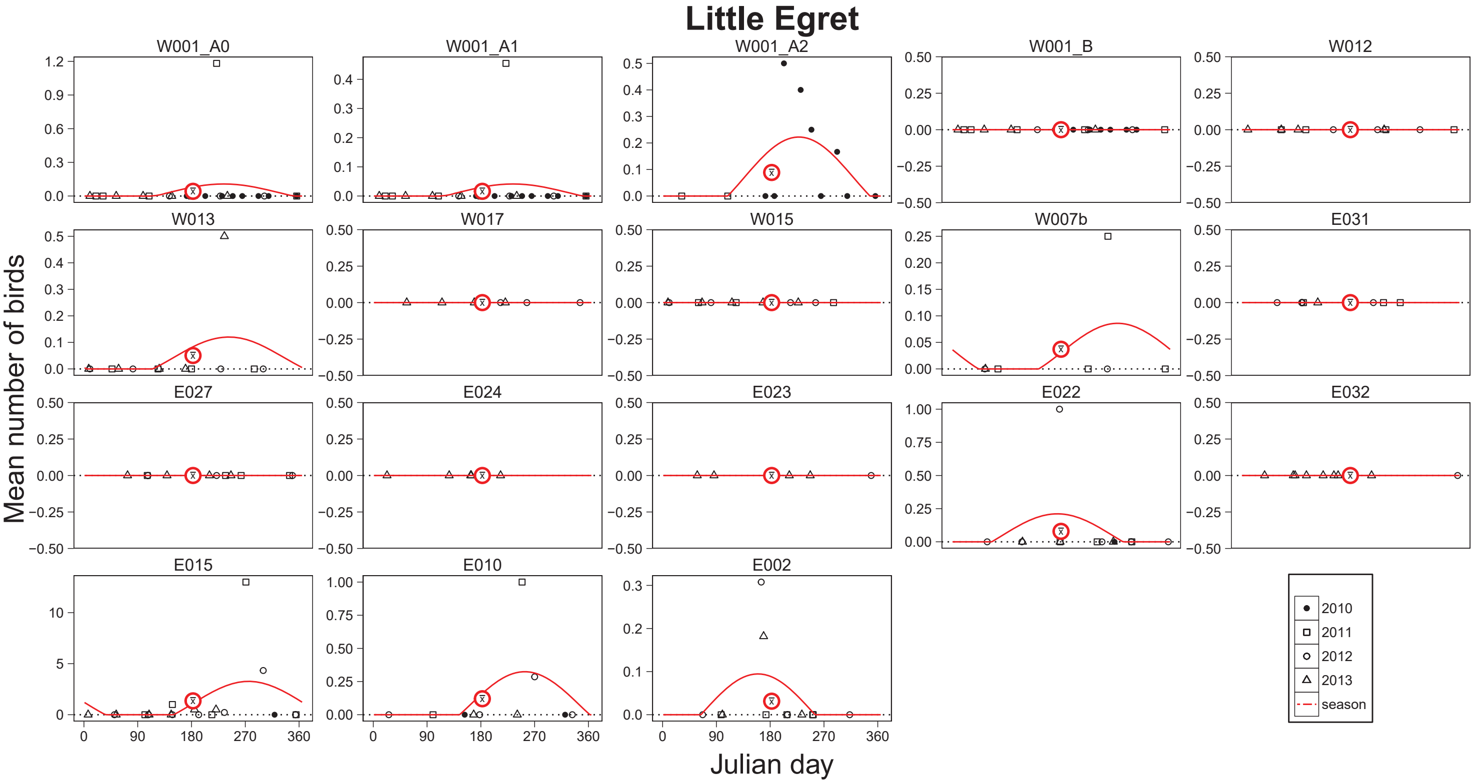


Fig. A.1: Numbers of the Little Egret (*Egretta garzetta*) on bivalve beds.

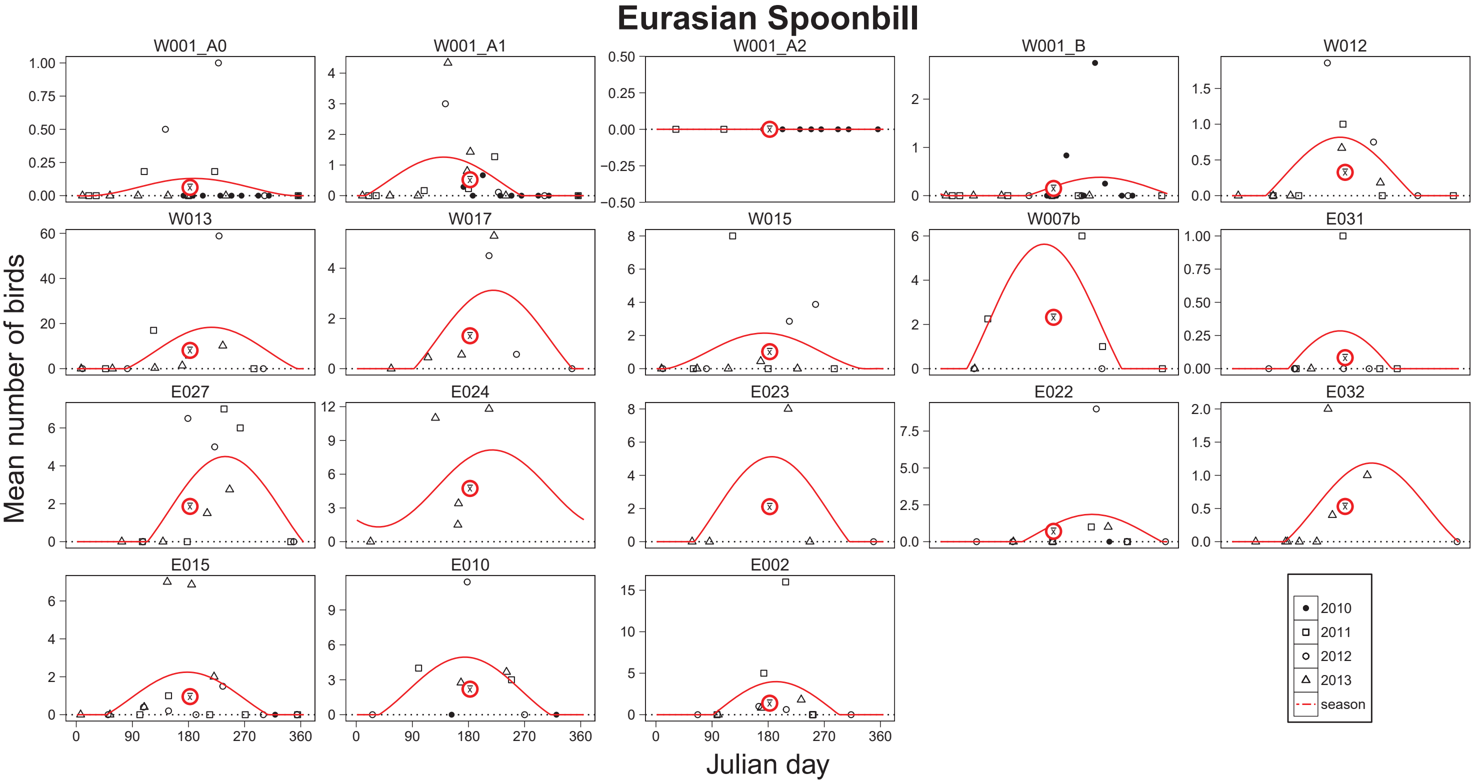


Fig. A.2: Numbers of the Eurasian Spoonbill (*Platalea leucorodia*) on bivalve beds.

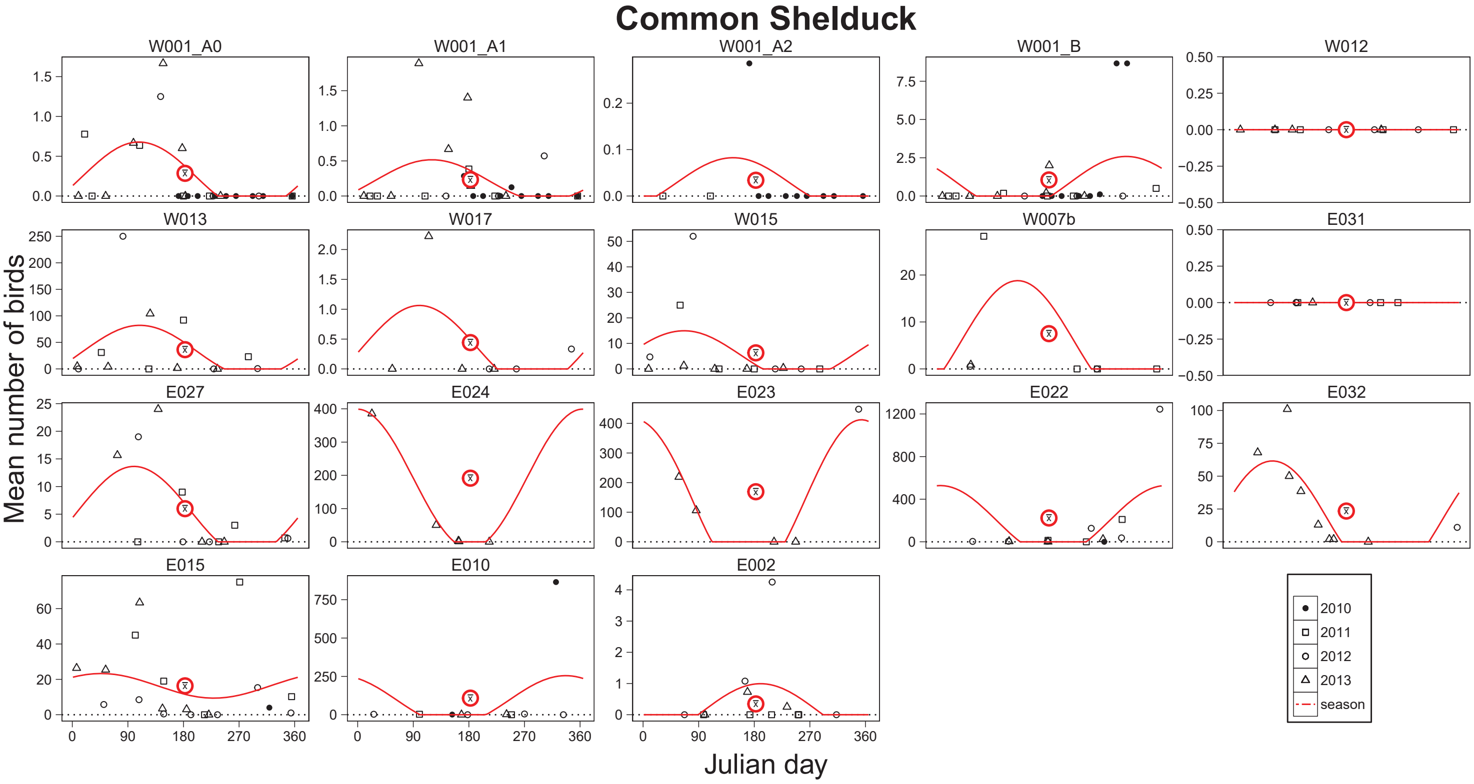


Fig. A.3: Numbers of the Common Shelduck (*Tadorna tadorna*) on bivalve beds.

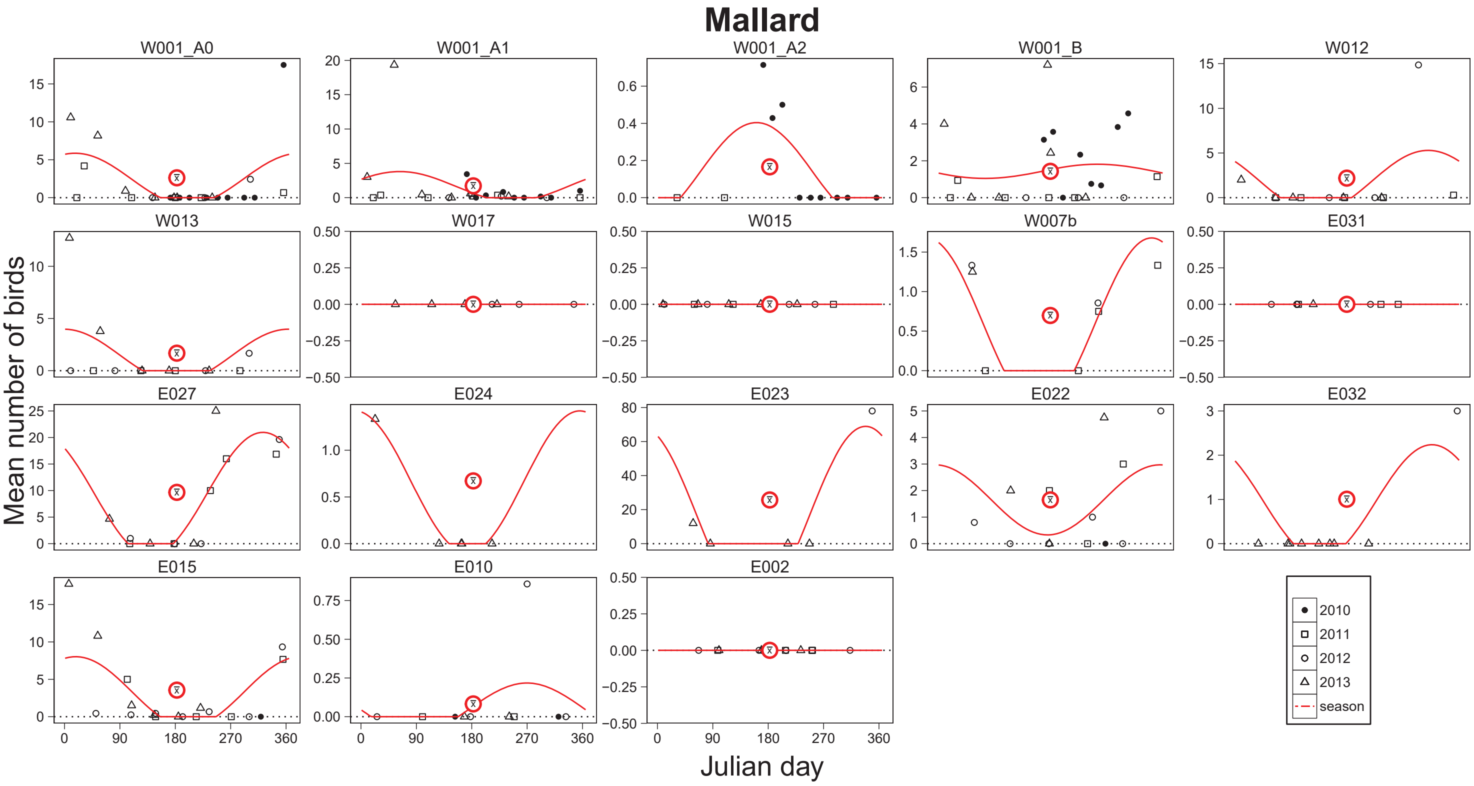


Fig. A.4: Numbers of the Mallard (*Anas platyrhynchos*) on bivalve beds.

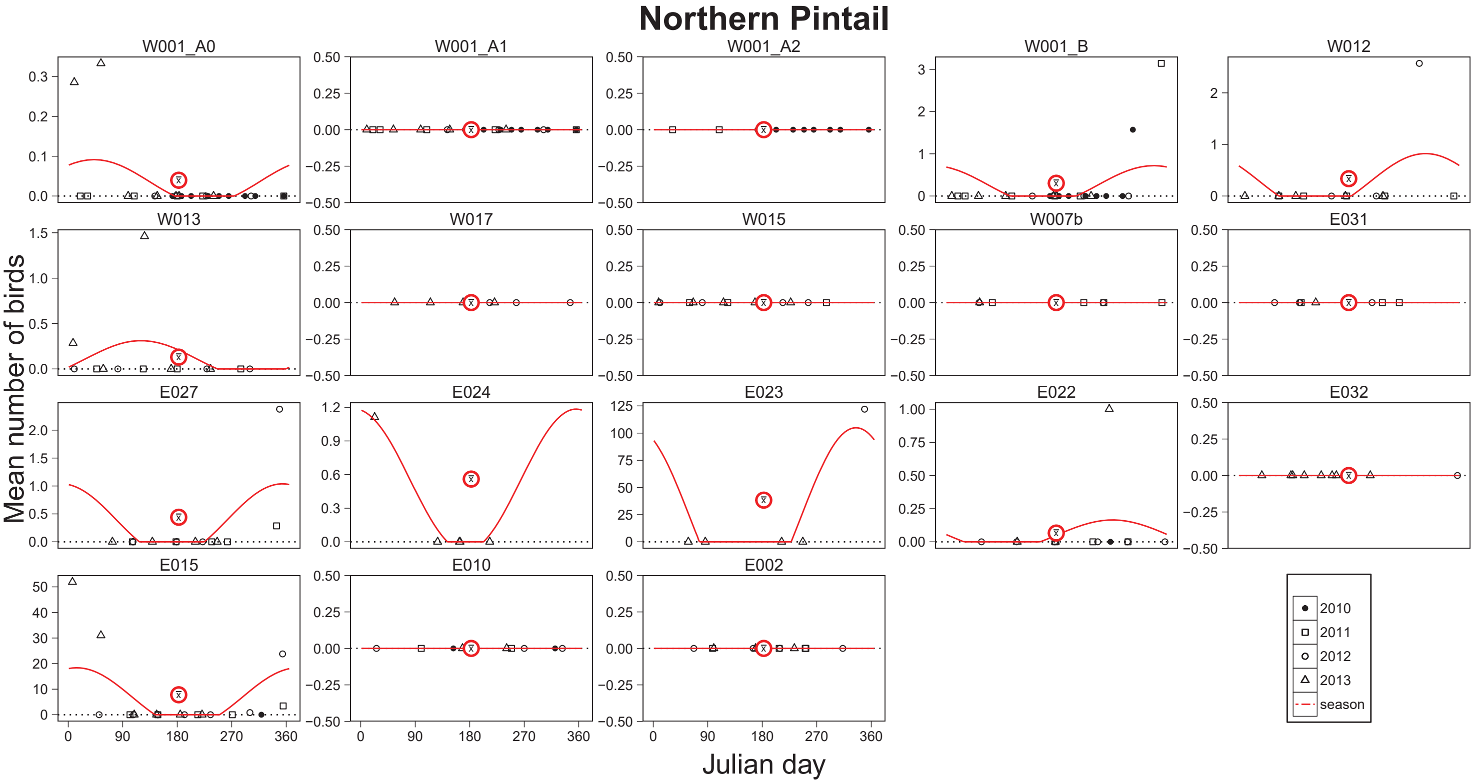


Fig. A.5: Numbers of the Northern Pintail (*Anas acuta*) on bivalve beds.

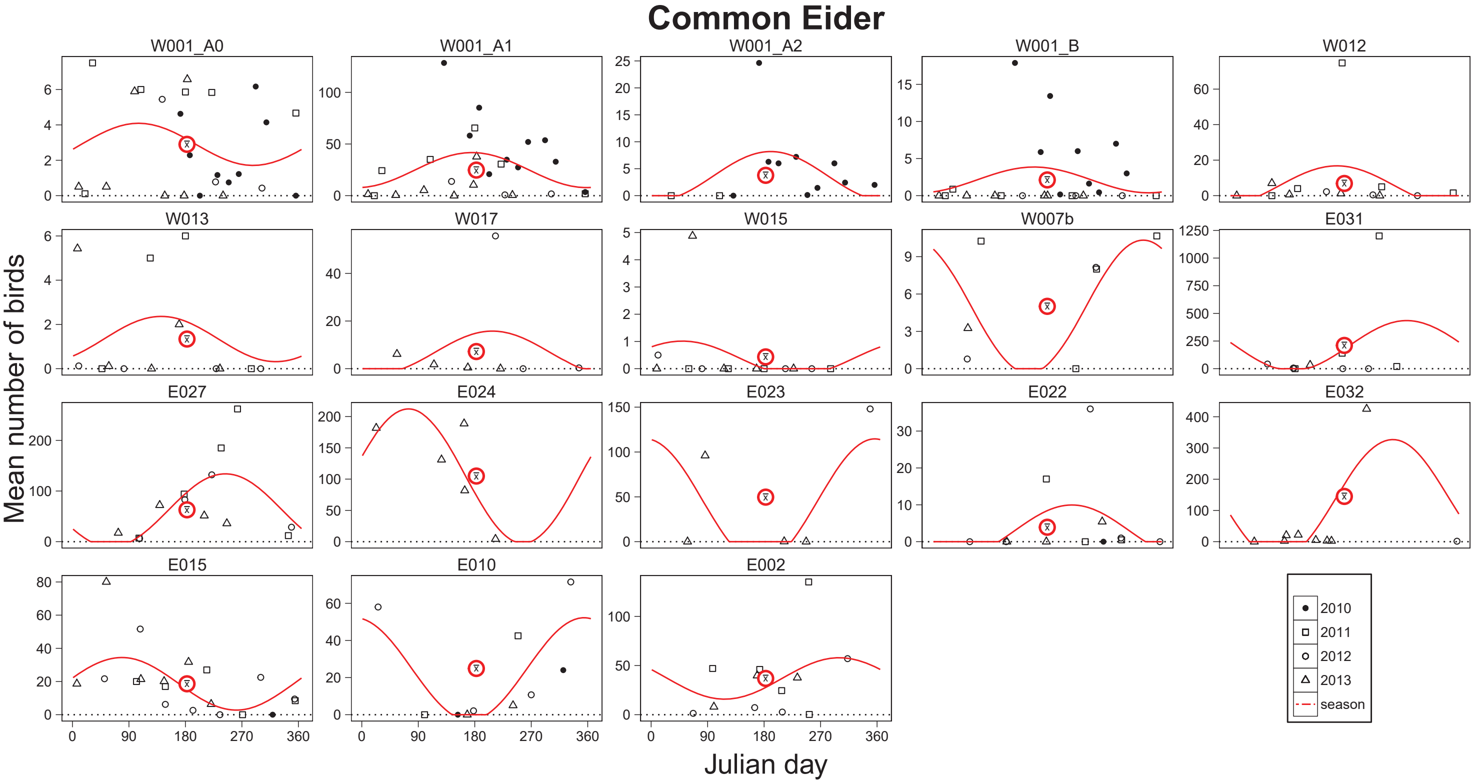


Fig. A.6: Numbers of the Common Eider (*Somateria mollissima*) on bivalve beds.

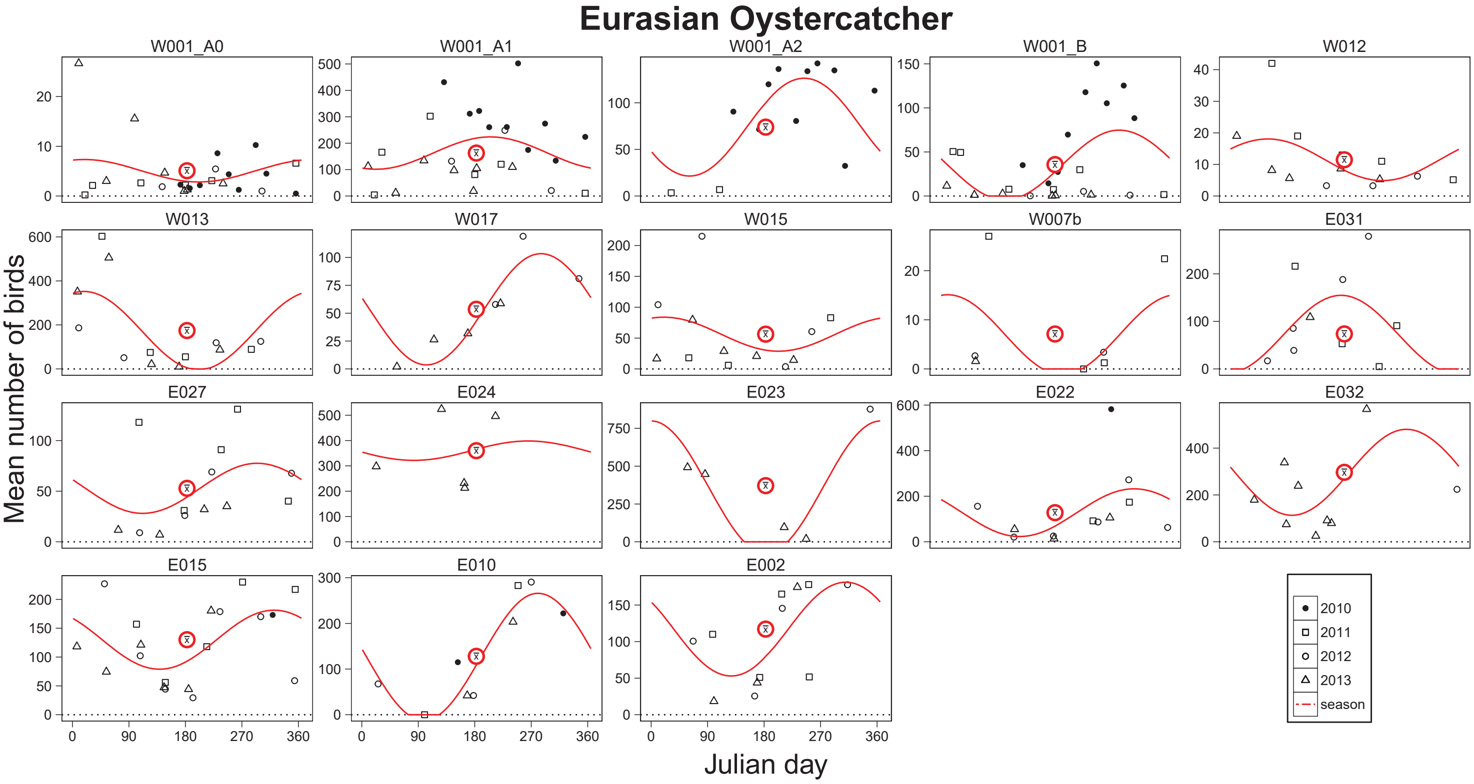


Fig. A.7: Numbers of the Eurasian Oystercatcher (*Haematopus ostralegus*) on bivalve beds.

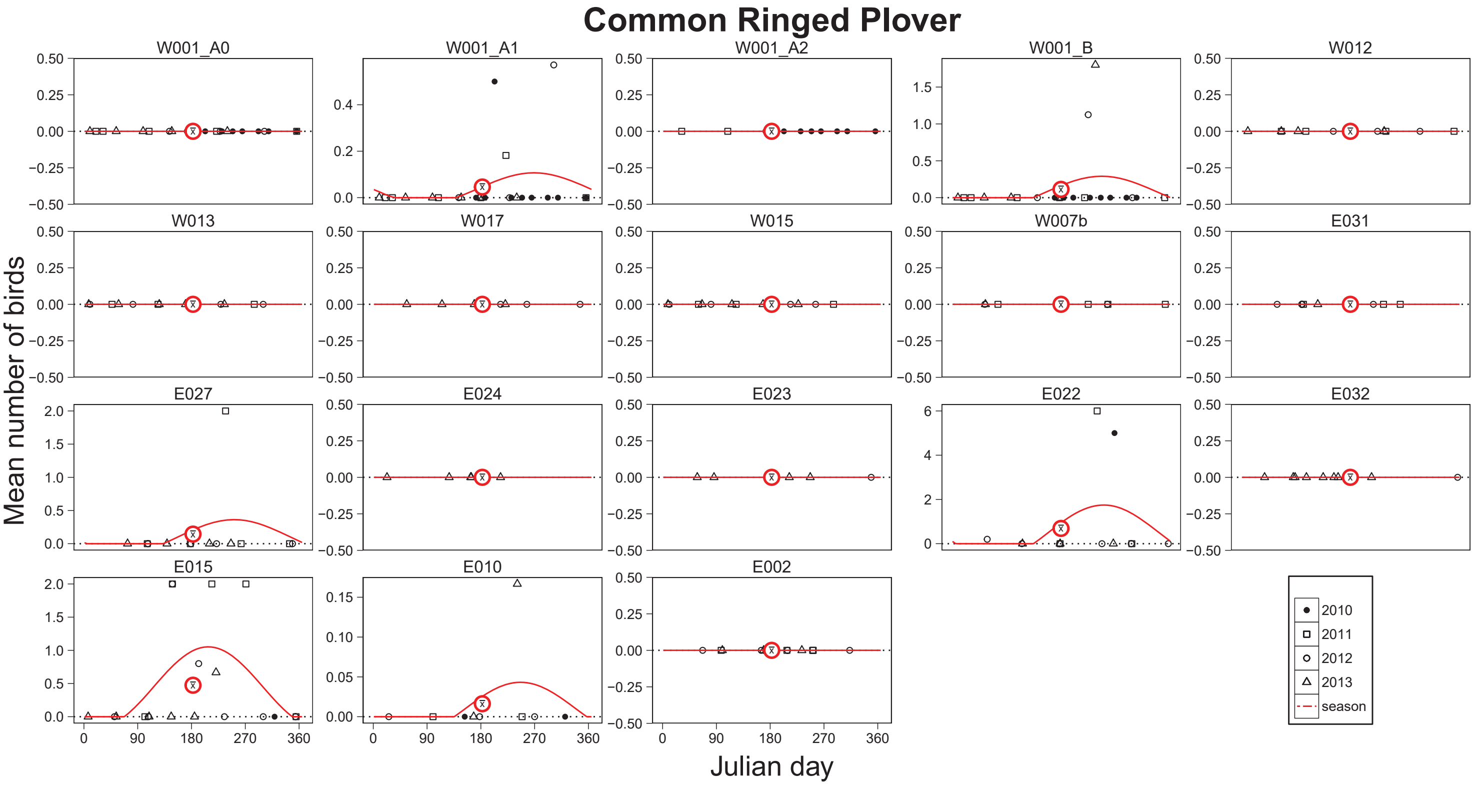


Fig. A.8: Numbers of the Common Ringed Plover (*Charadrius hiaticula*) on bivalve beds.

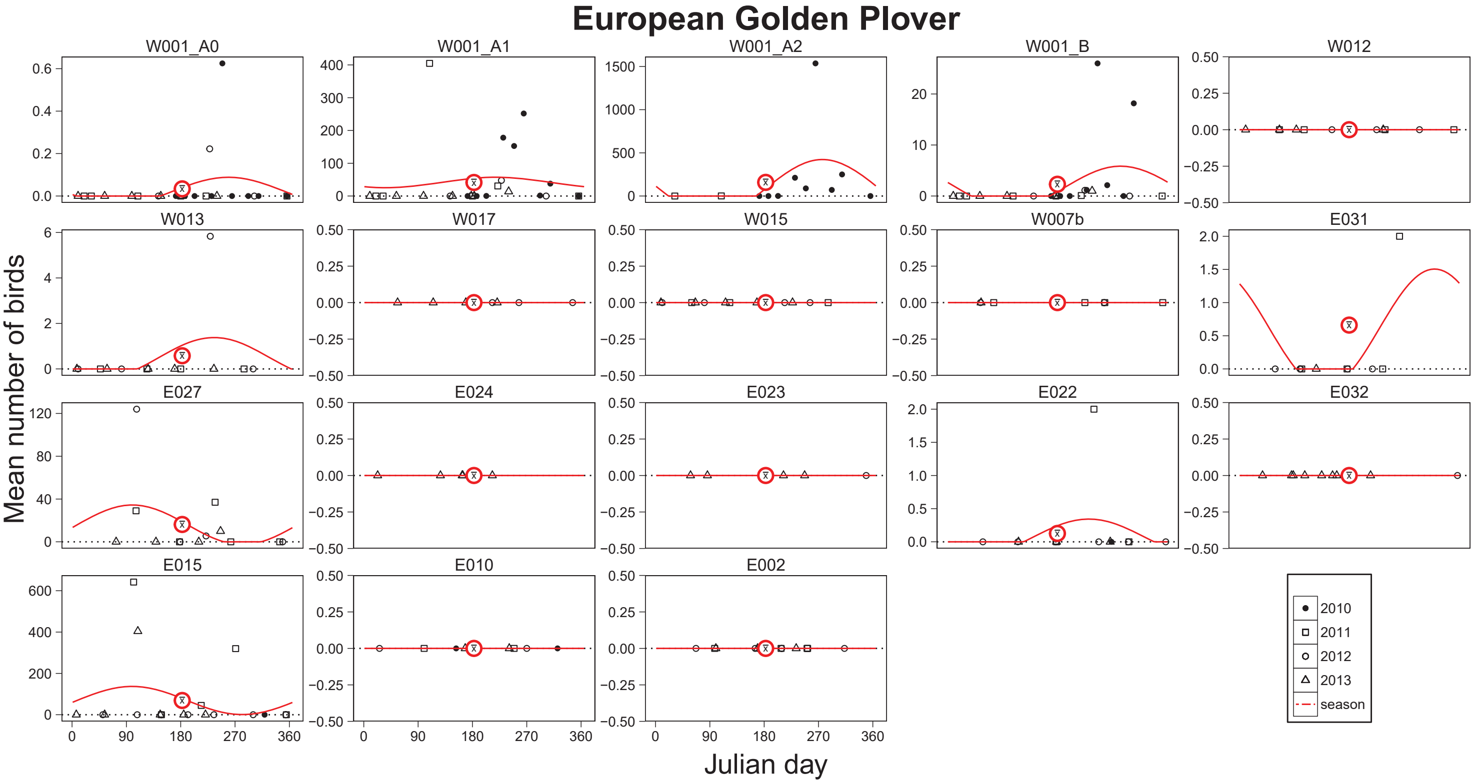


Fig. A.9: Numbers of the European Golden Plover (*Pluvialis apricaria*) on bivalve beds.

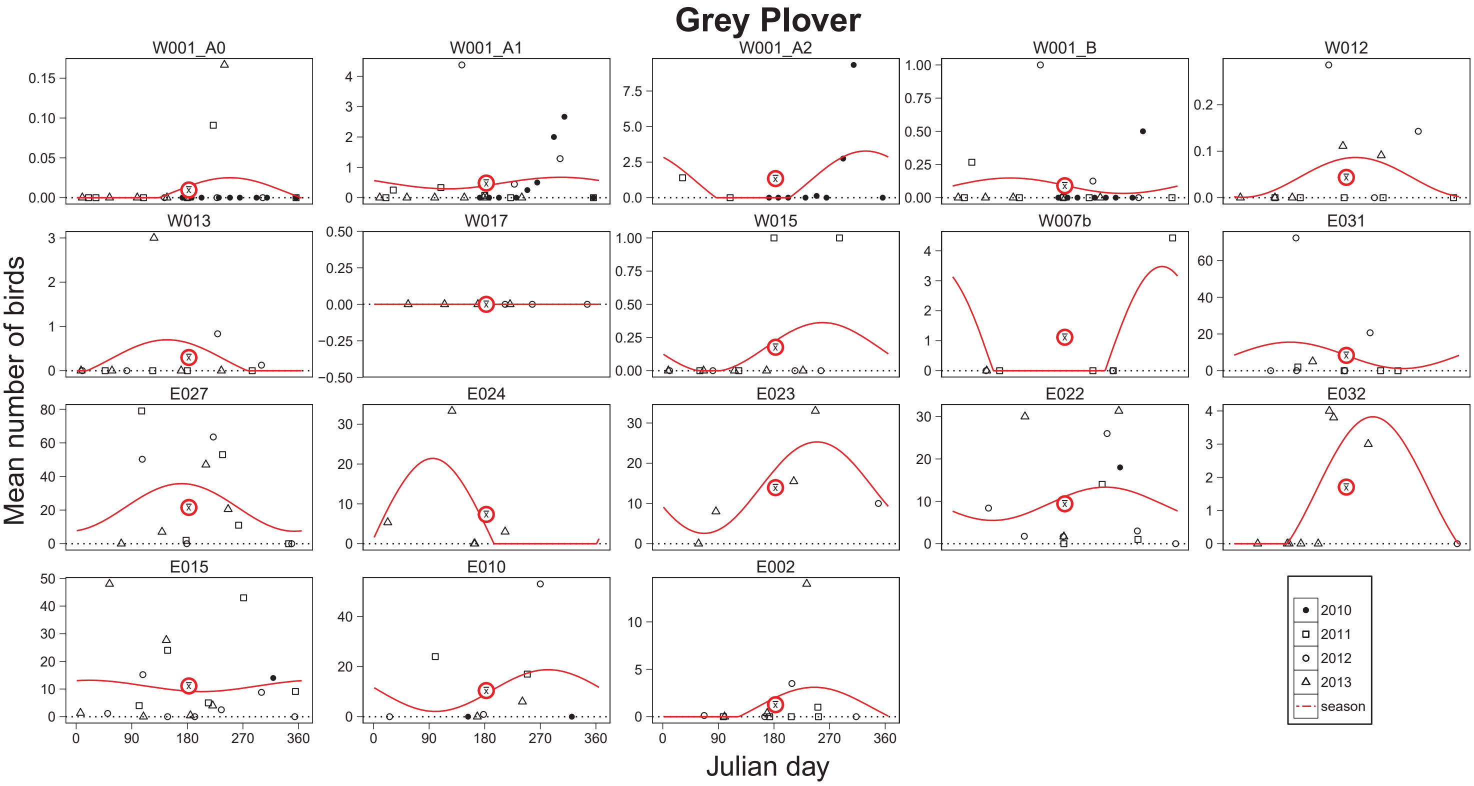


Fig. A.10: Numbers of the Grey Plover (*Pluvialis squatarola*) on bivalve beds.

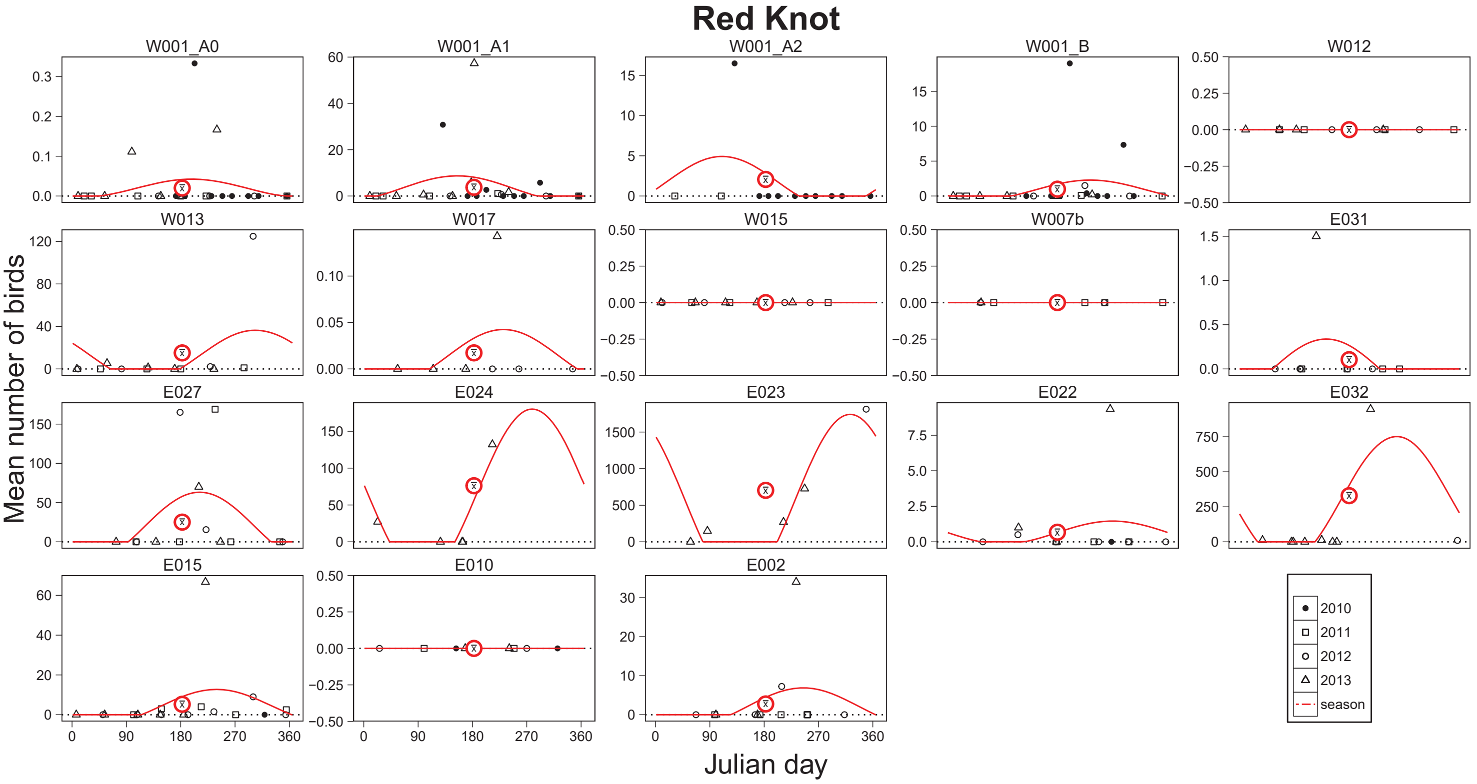


Fig. A.11: Numbers of the Red Knot (*Calidris canutus*) on bivalve beds.

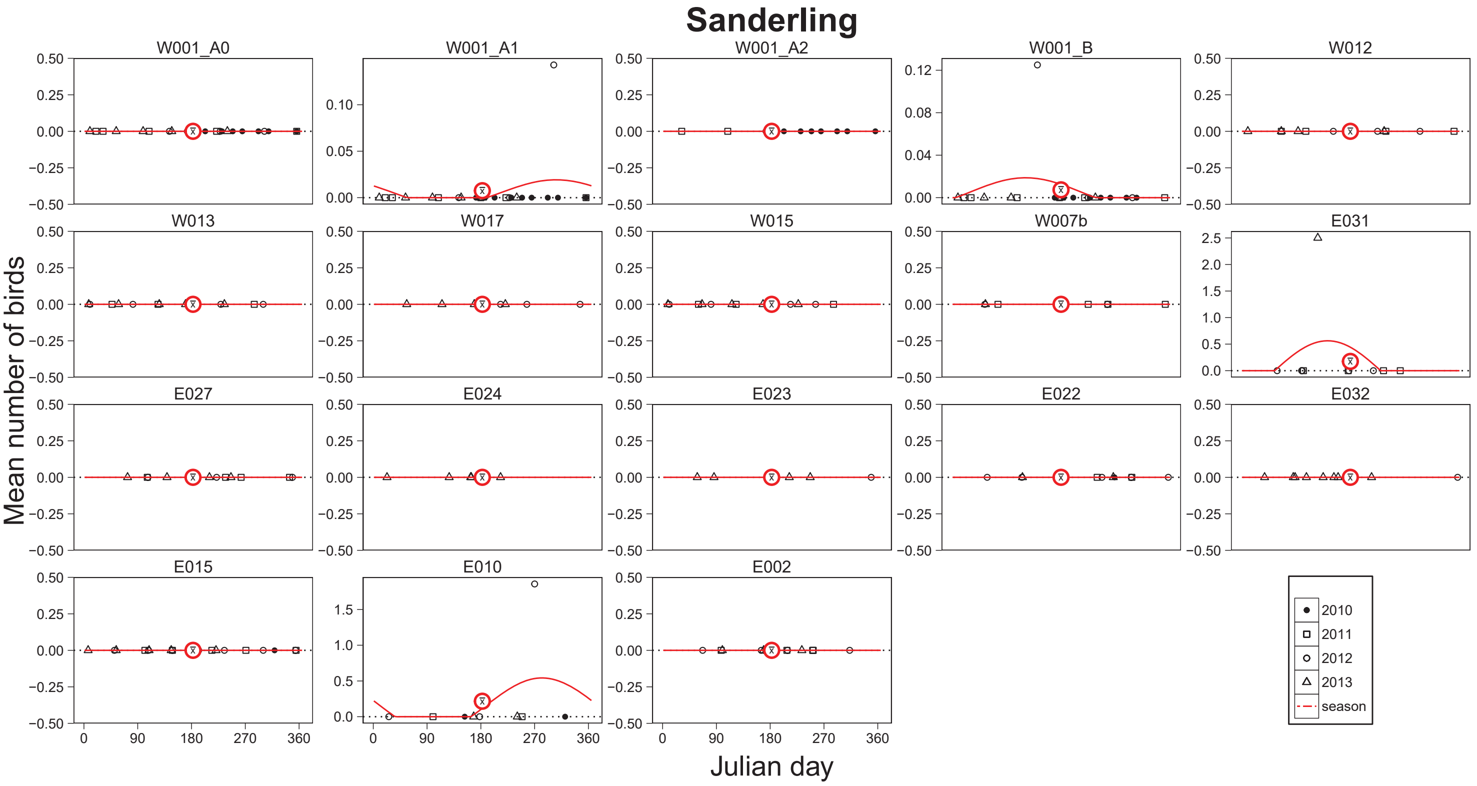


Fig. A.12: Numbers of the Sanderling (*Calidris alba*) on bivalve beds.

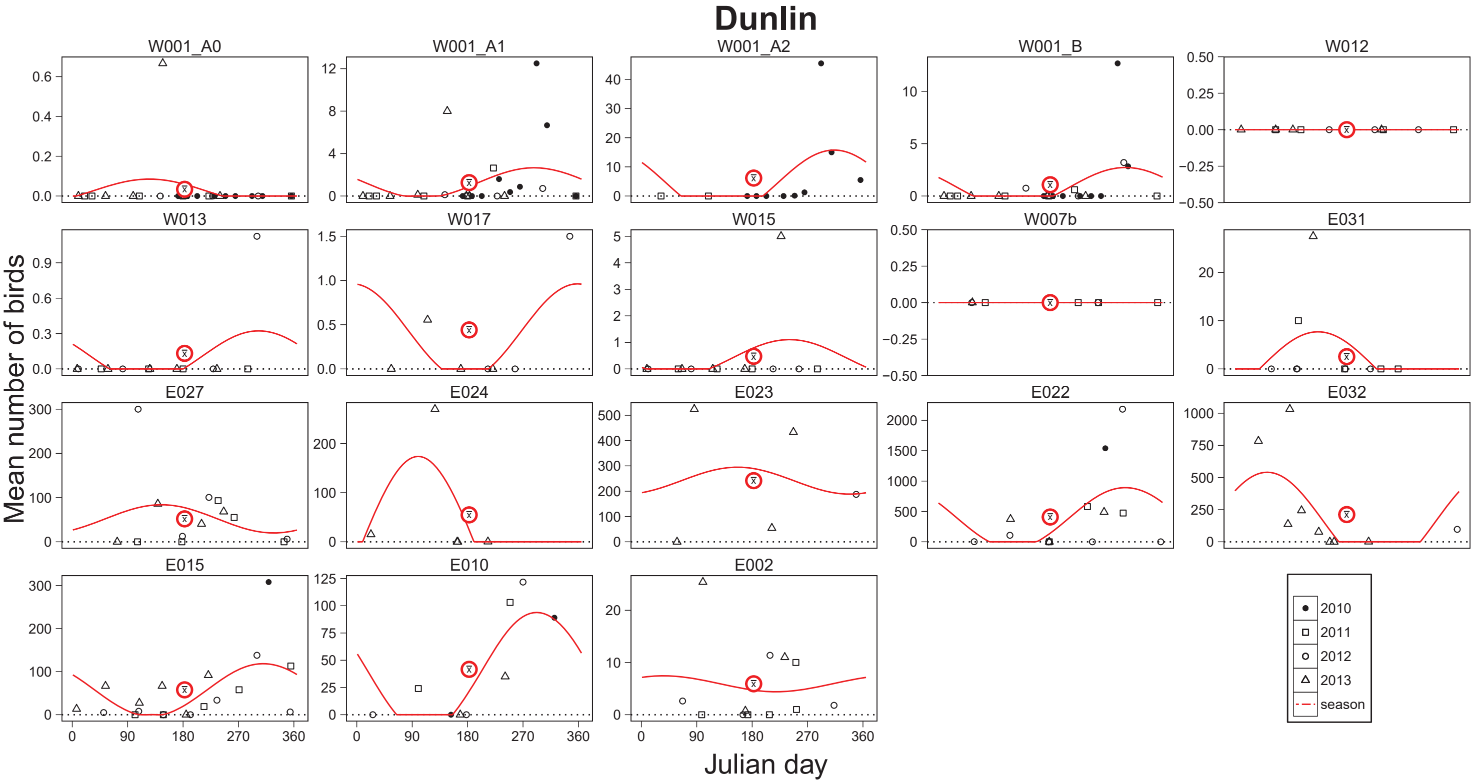


Fig. A.13: Numbers of the Dunlin (*Calidris alpina*) on bivalve beds.

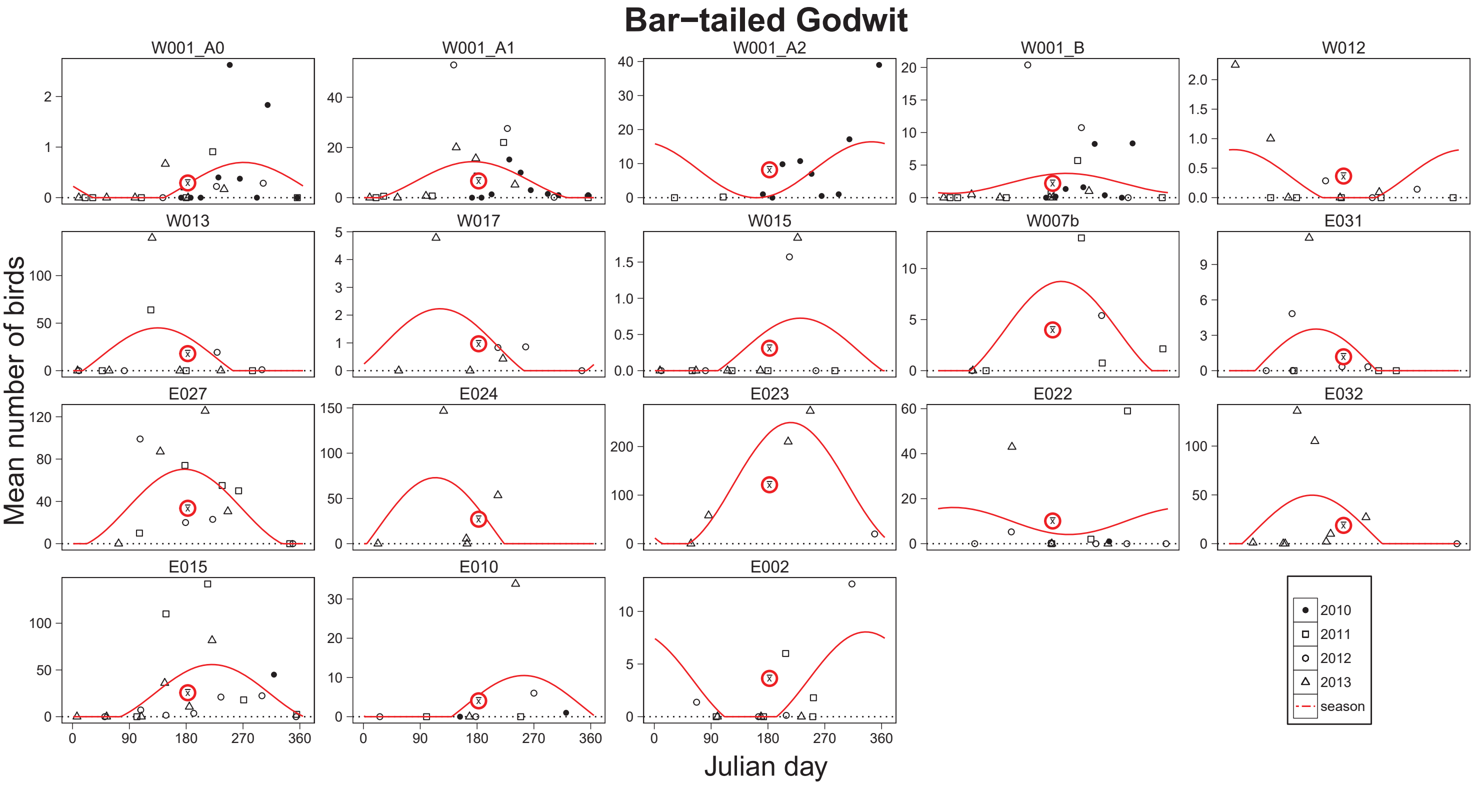


Fig. A.14: Numbers of the Bar-tailed Godwit (*Limosa lapponica*) on bivalve beds.

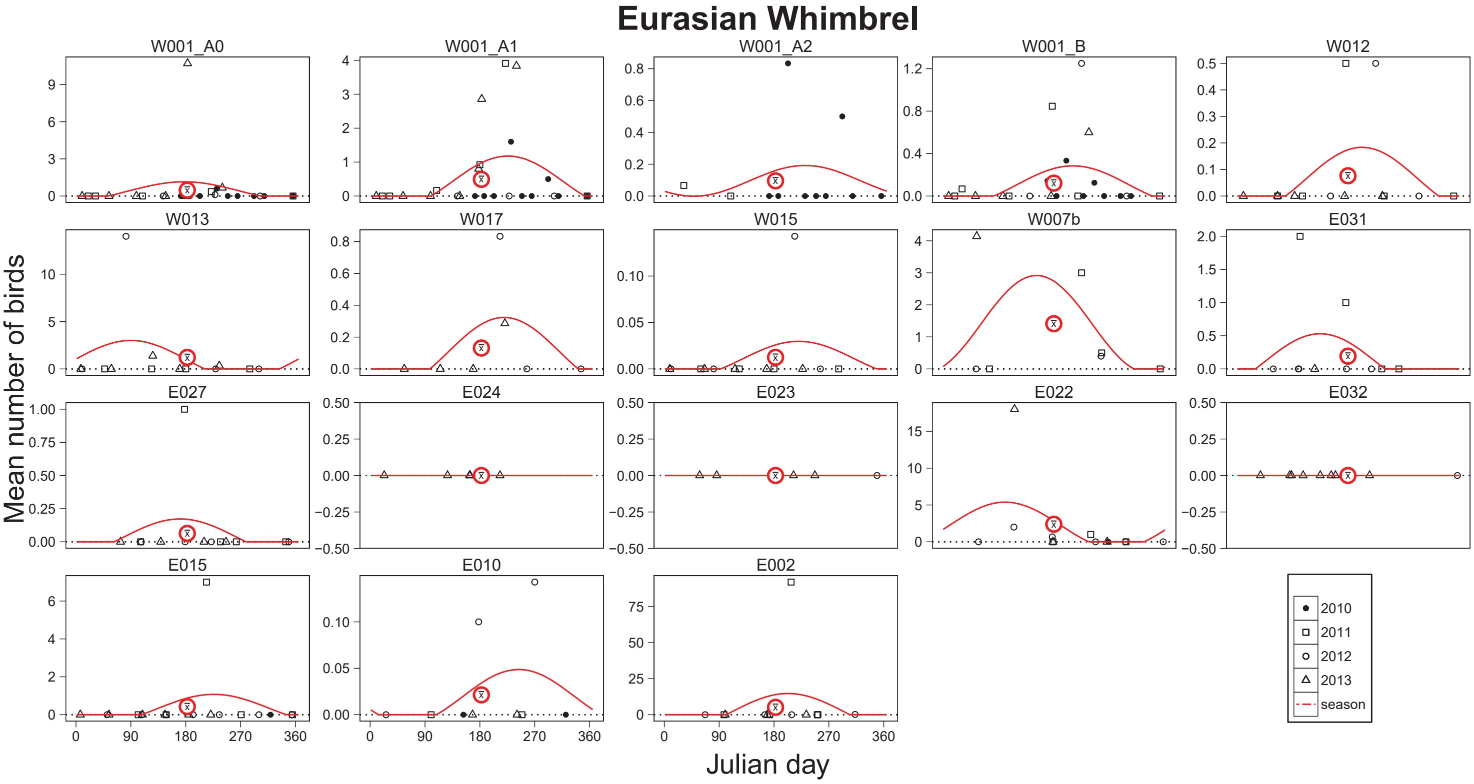


Fig. A.15: Numbers of the Eurasian Whimbrel (*Numenius phaeopus*) on bivalve beds.

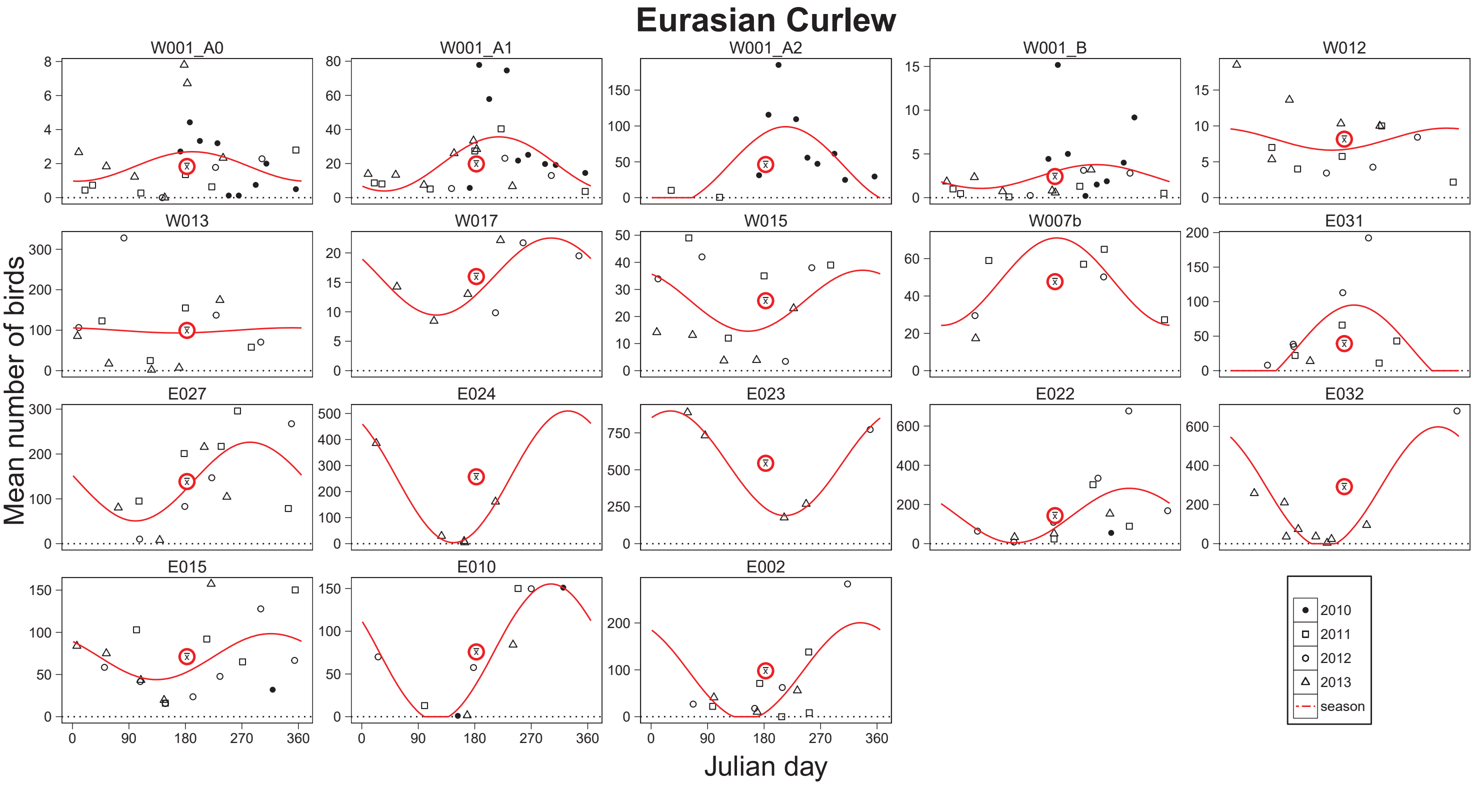


Fig. A.16: Numbers of the Eurasian Curlew (*Numenius arquata*) on bivalve beds.

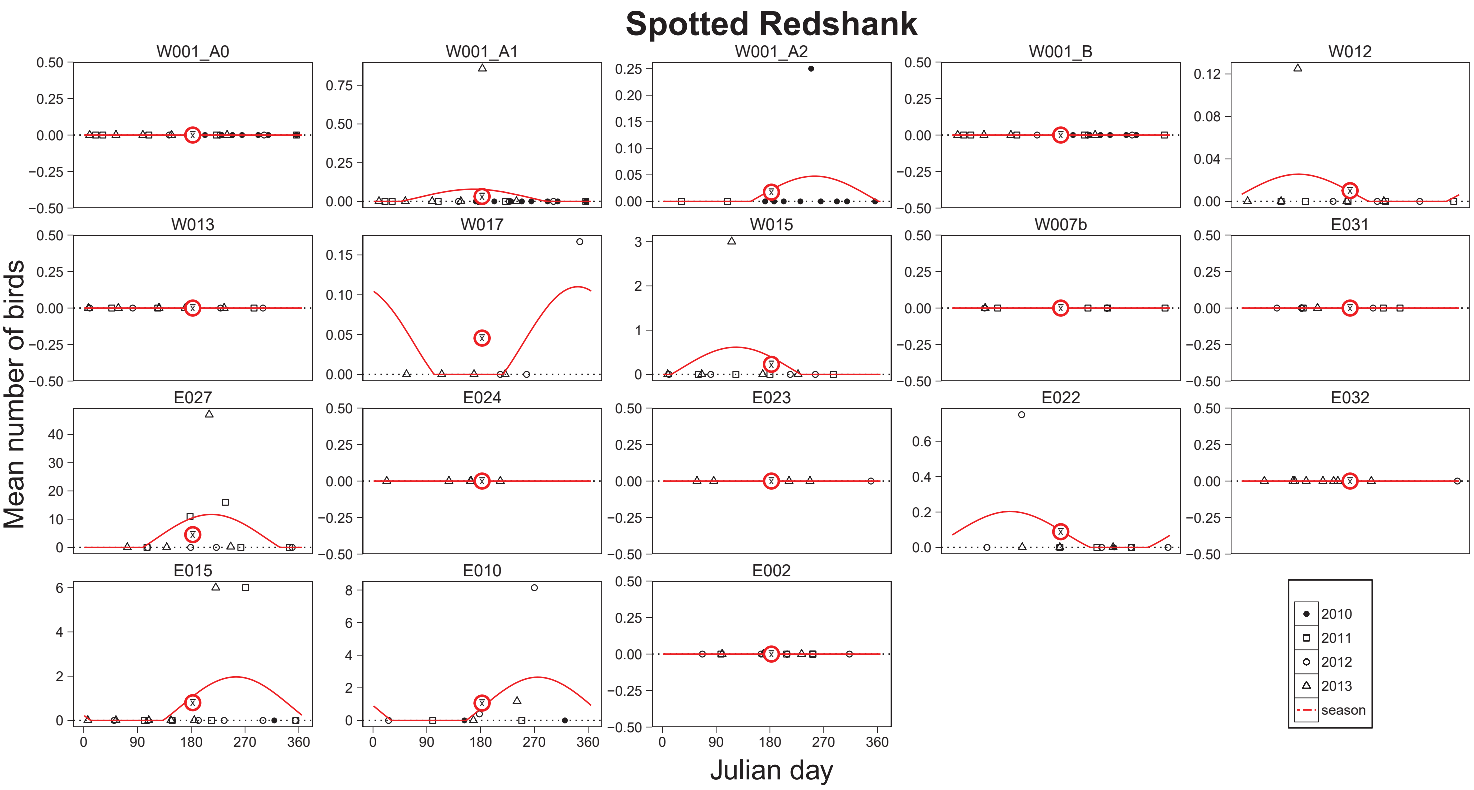


Fig. A.17: Numbers of the Spotted Redshank (*Tringa erythropus*) on bivalve beds.

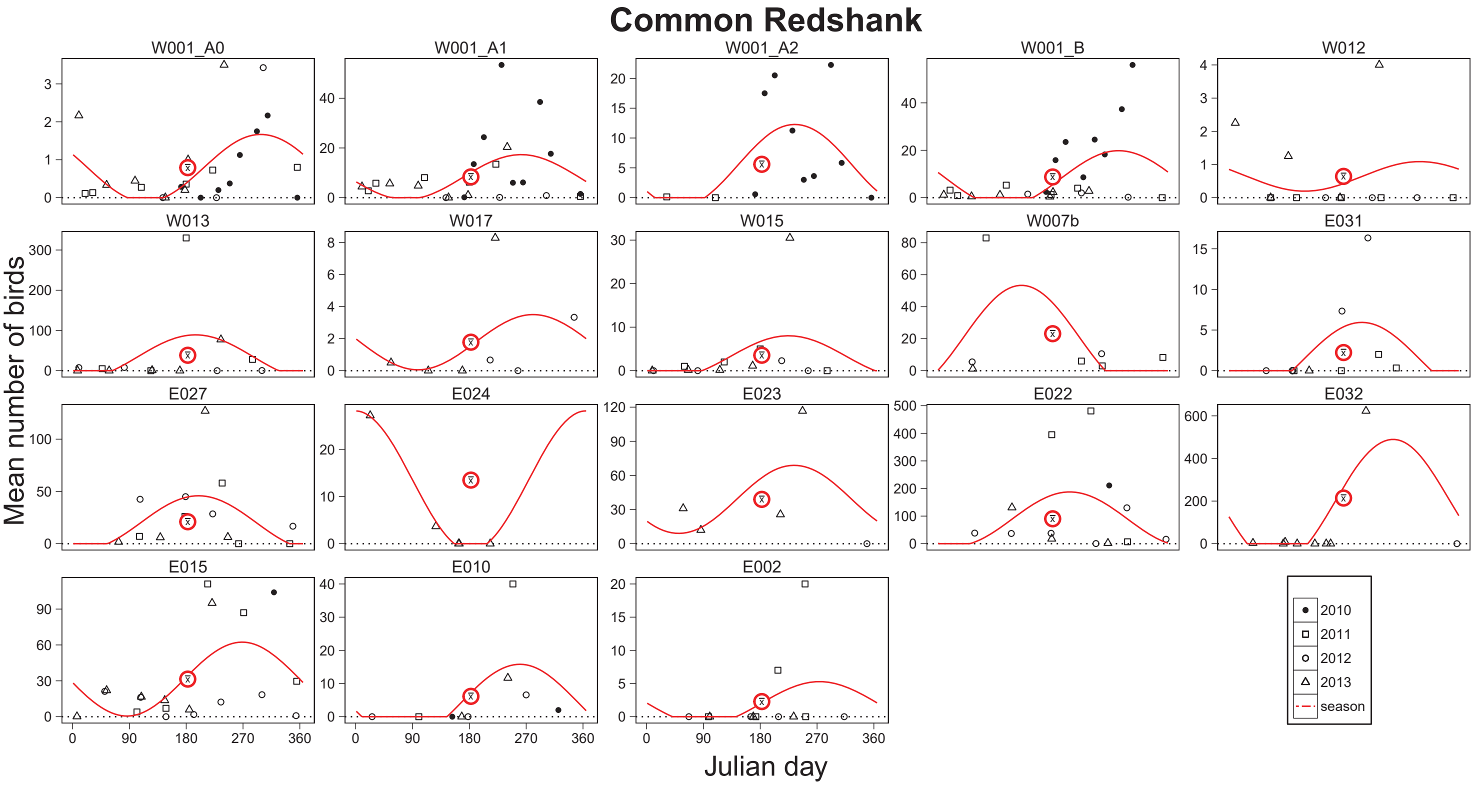


Fig. A.18: Numbers of the Common Redshank (*Tringa totanus*) on bivalve beds.

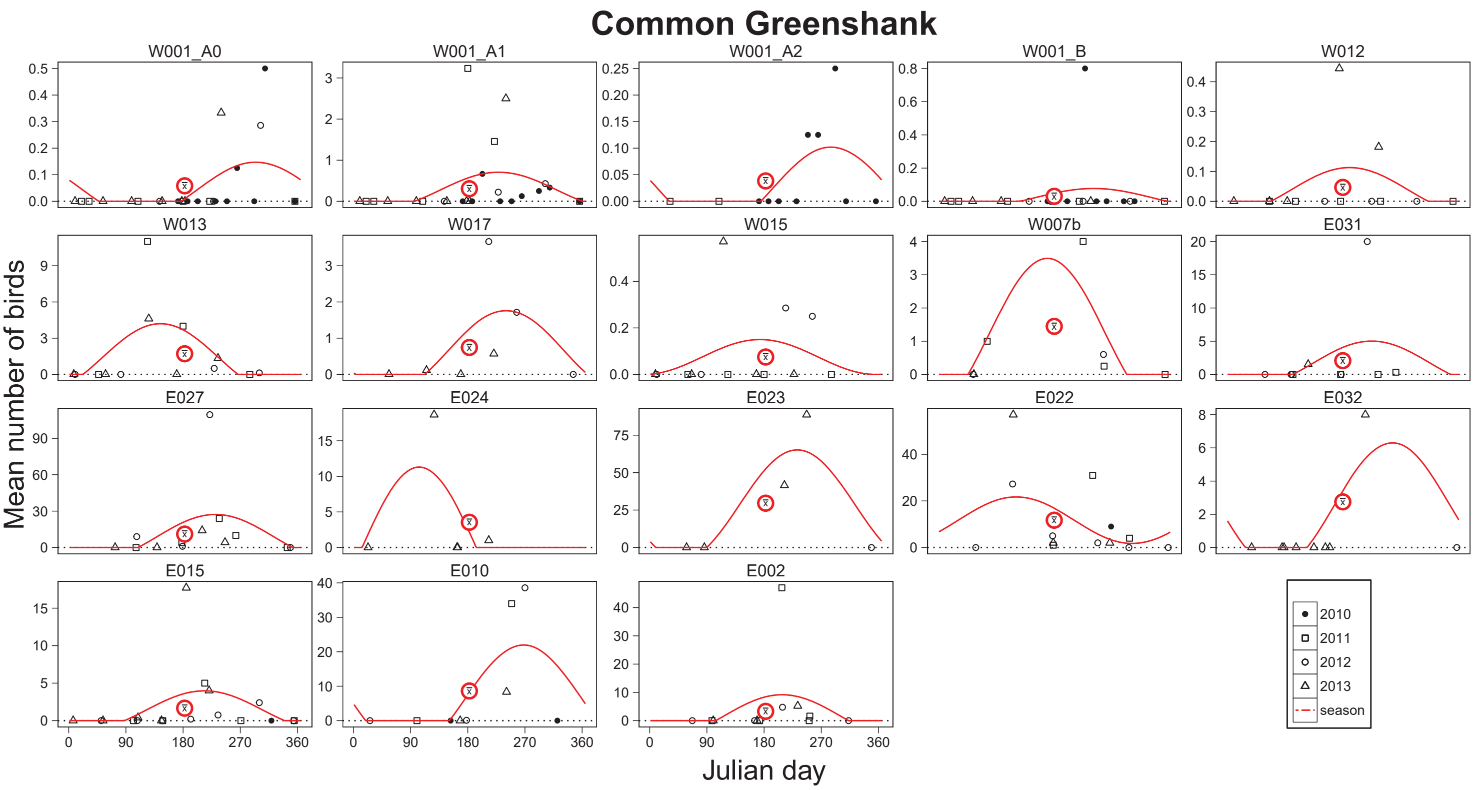


Fig. A.19: Numbers of the Common Greenshank (*Tringa nebularia*) on bivalve beds.

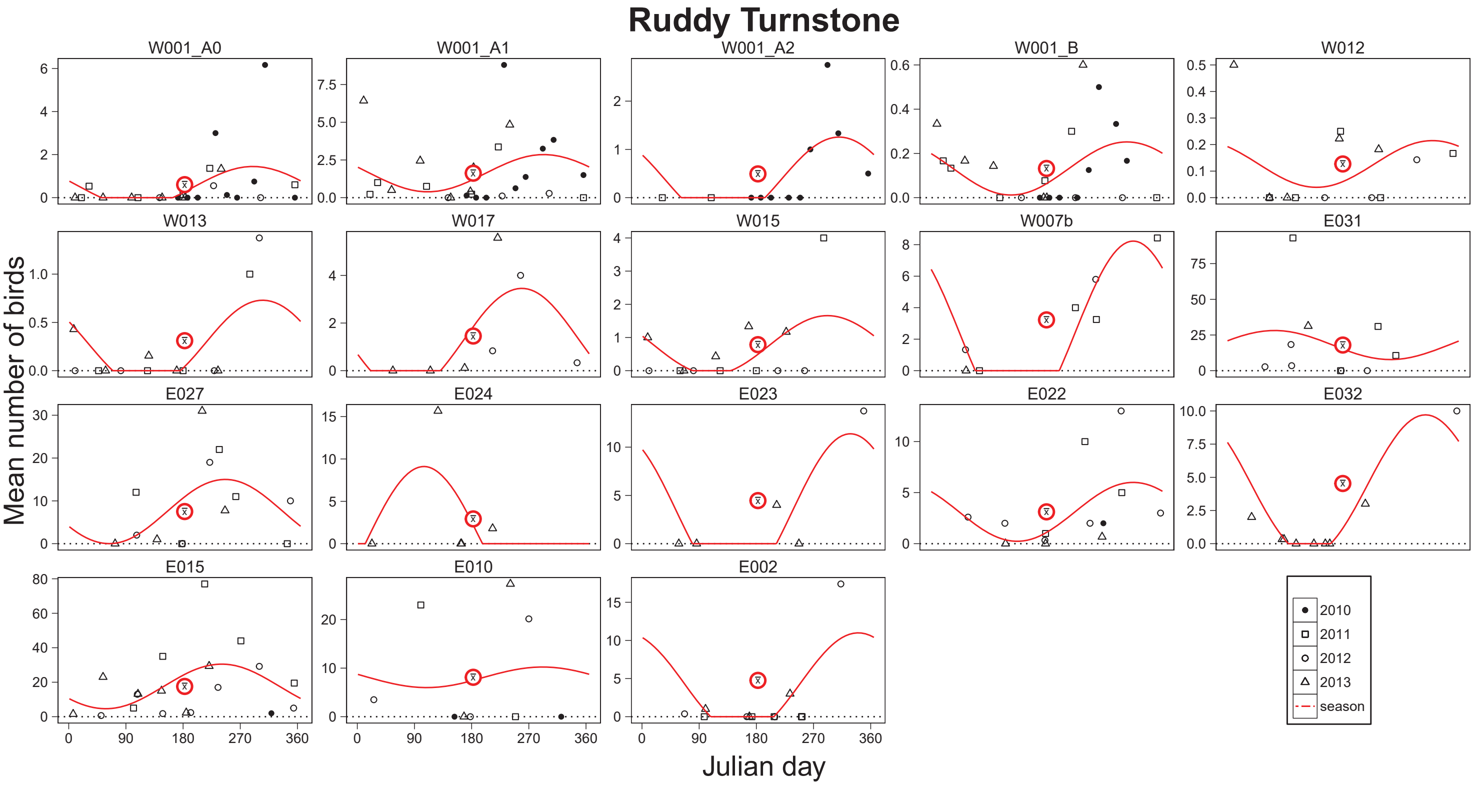


Fig. A.20: Numbers of the Ruddy Turnstone (*Arenaria interpres*) on bivalve beds.

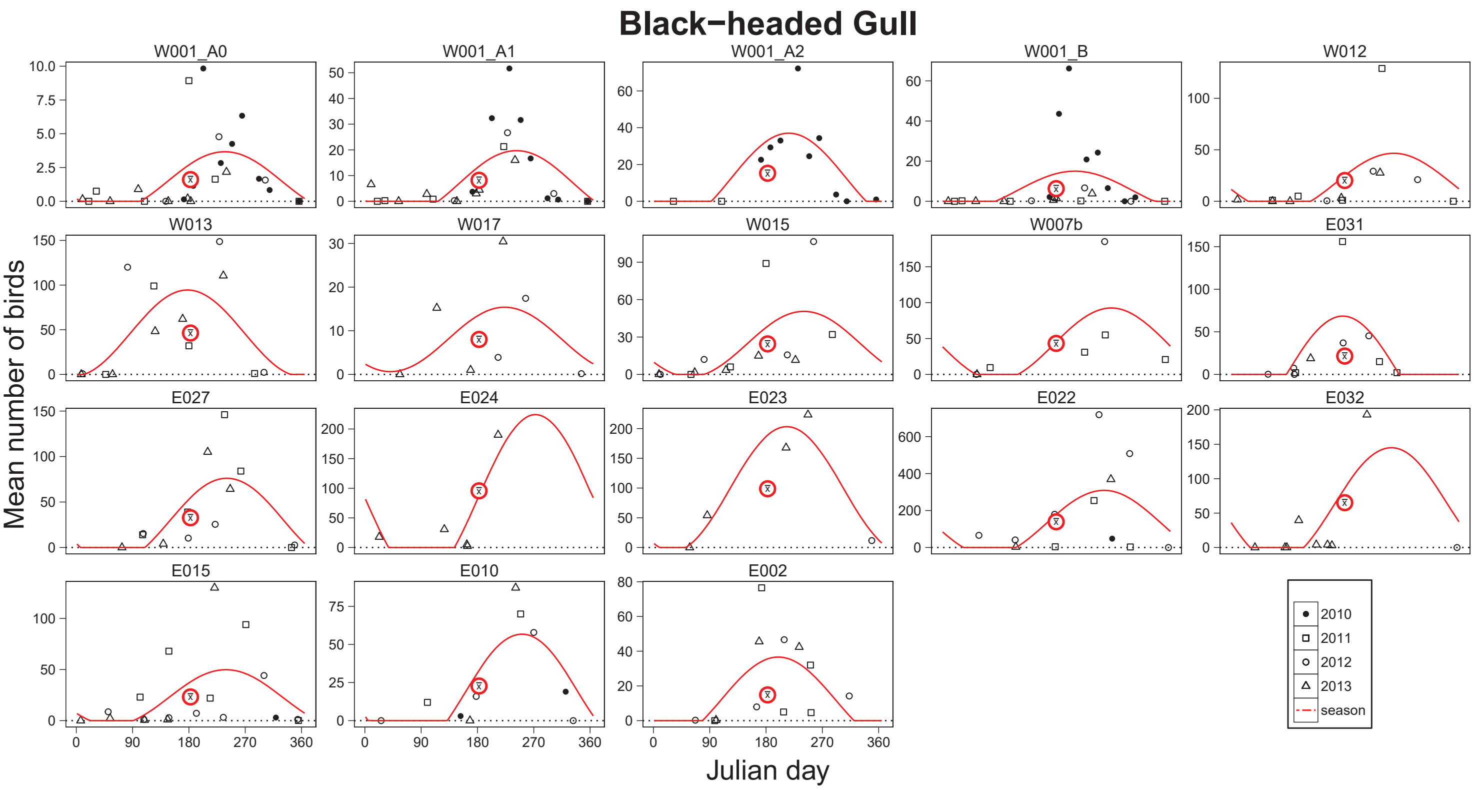


Fig. A.21: Numbers of the Black-headed Gull (*Larus ridibundus*) on bivalve beds.

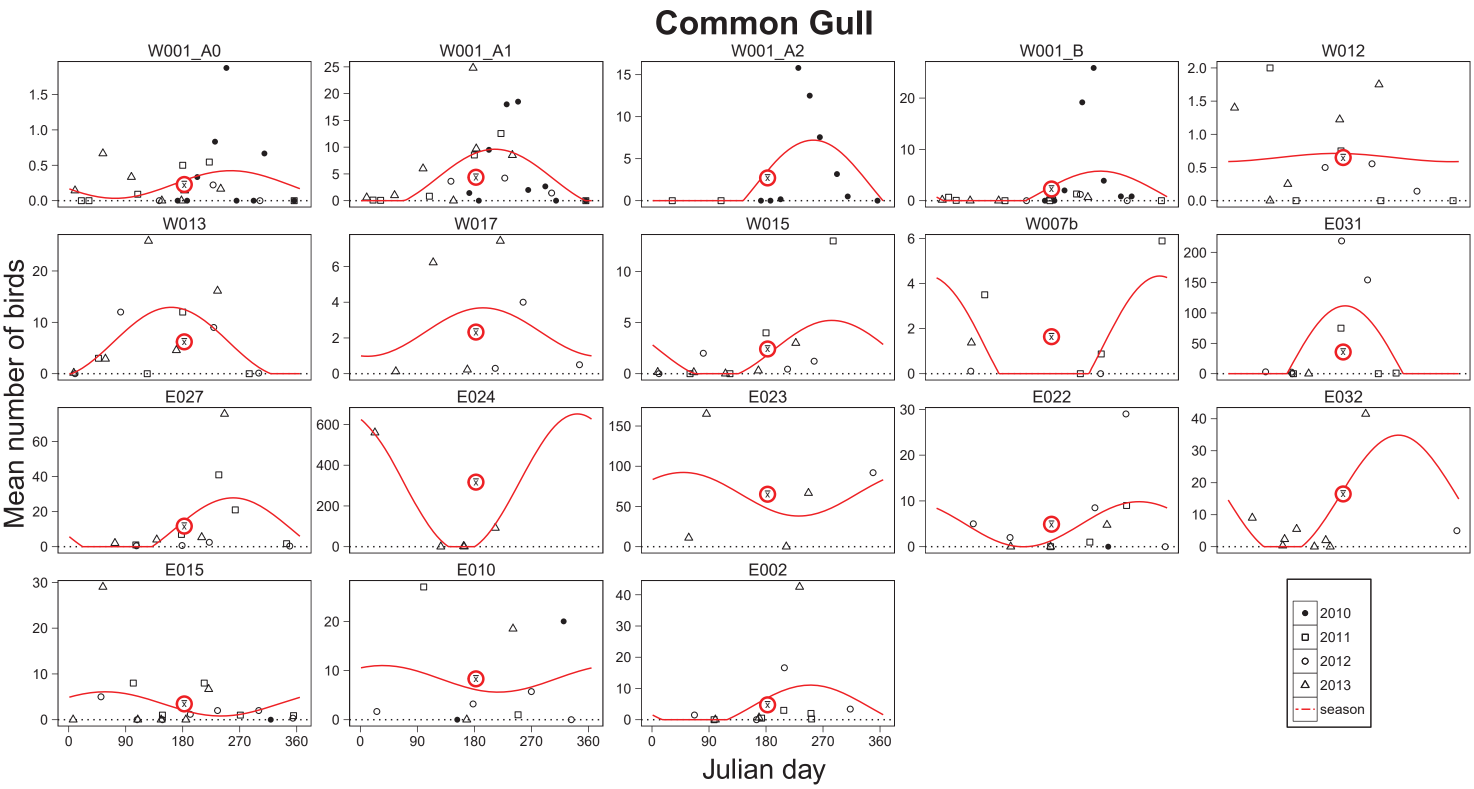


Fig. A.22: Numbers of the Common Gull (*Larus canus*) on bivalve beds.

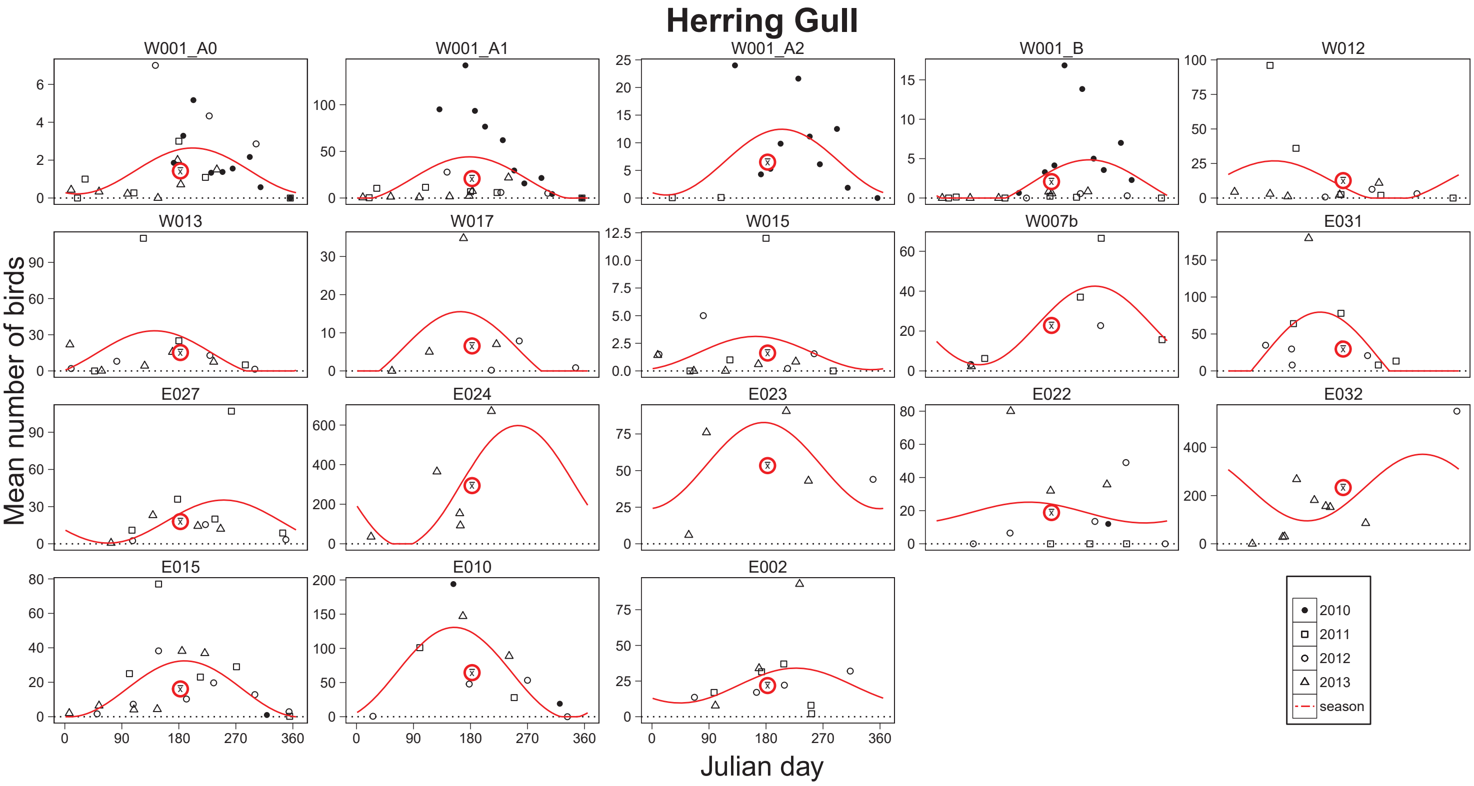


Fig. A.23: Numbers of the Herring Gull (*Larus argentatus*) on bivalve beds.

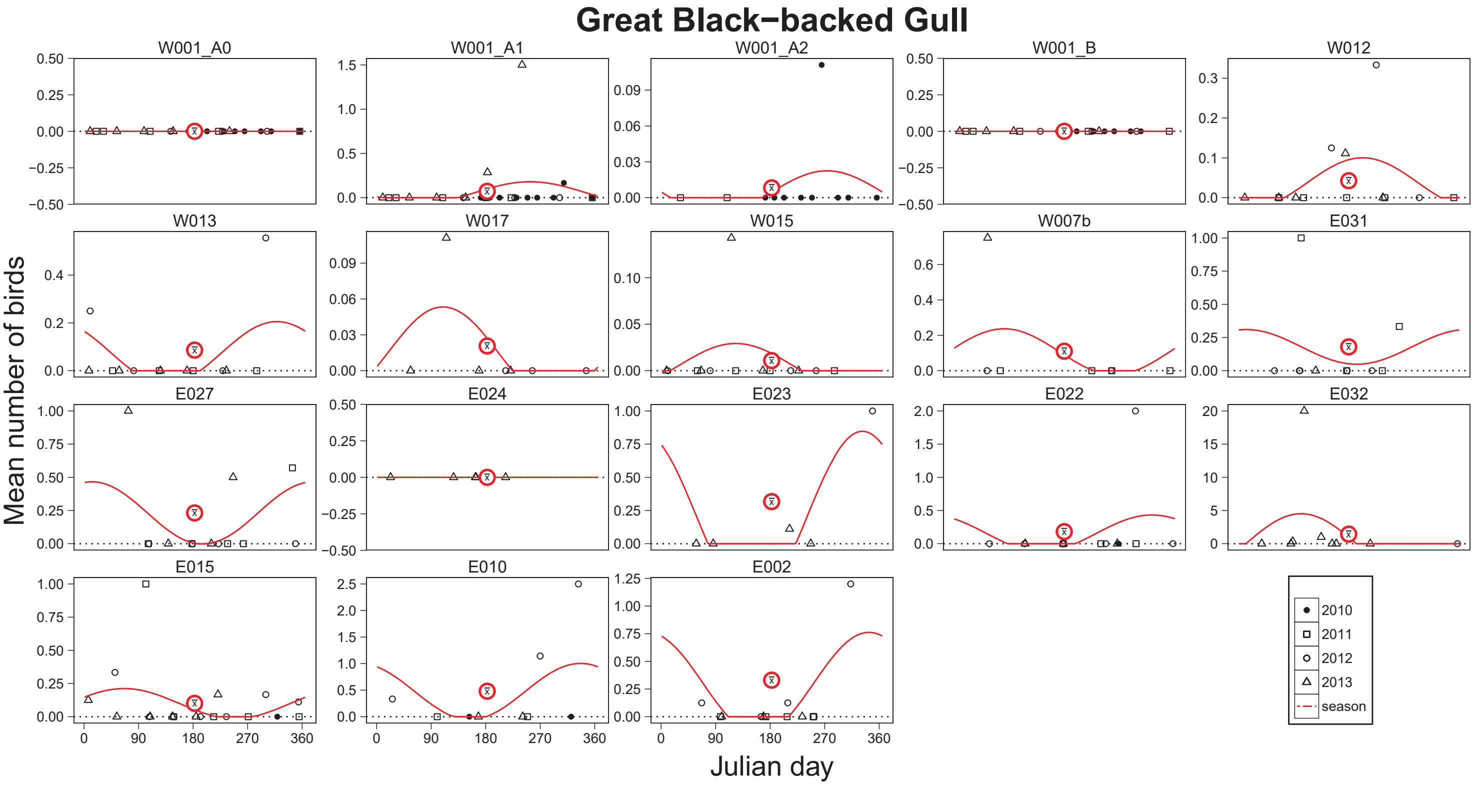


Fig. A.24: Numbers of the Great Black-backed Gull (*Larus marinus*) on bivalve beds.

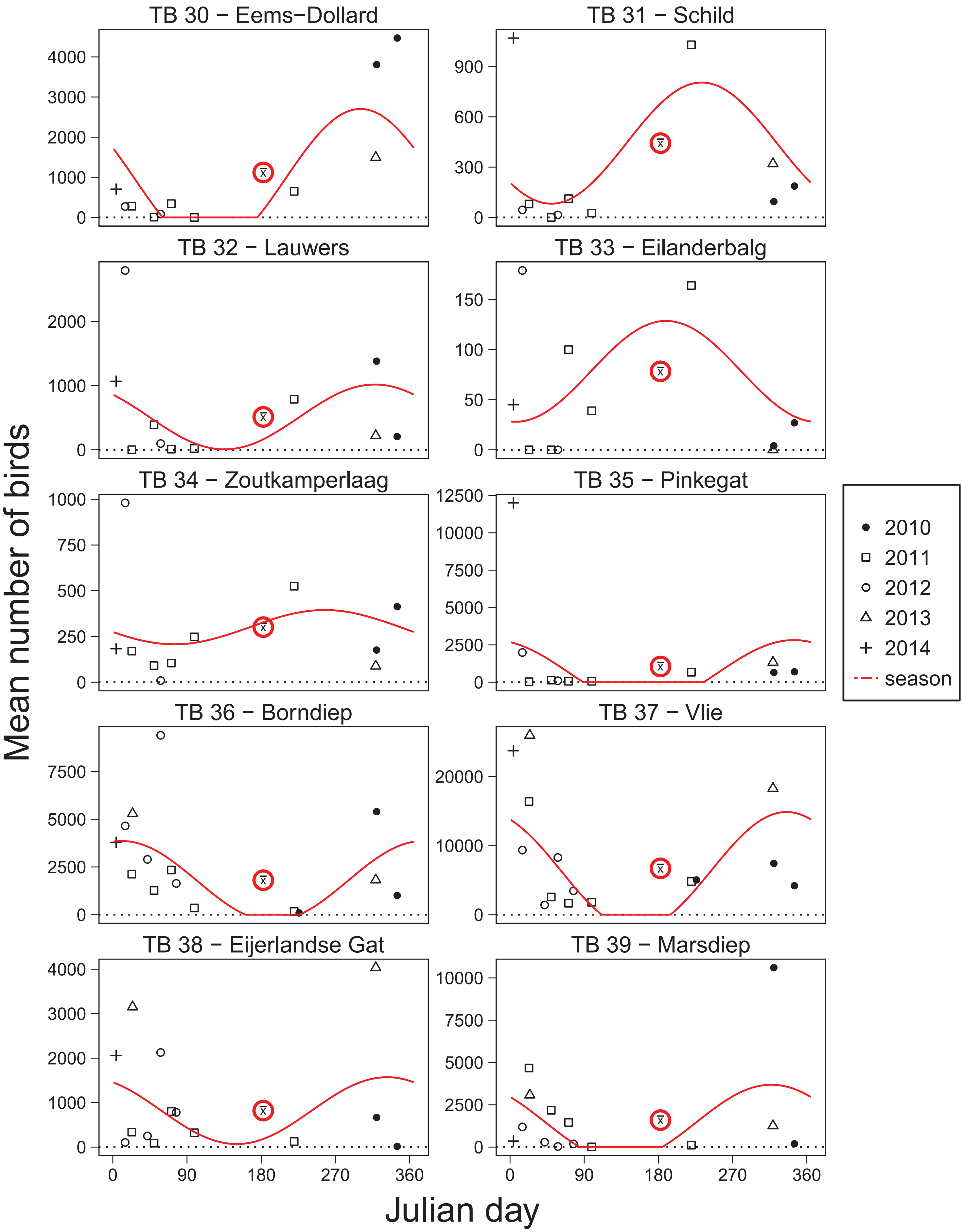


Fig. A.25: Numbers of Common Eider (*Somateria molissima*) above the intertidal.