The Ecology of Poole Harbour
John Humphreys and Vincent May (editors)

© 2005 Poole Harbour Study Group. All rights reserved.

# 14. Ecological Impacts of Sika Deer on Poole Harbour Saltmarshes

Anita Diaz, Eunice Pinn and Justine Hannaford

School of Conservation Sciences, Bournemouth University, Fern Barrow, Poole, Dorset BH12 5BB

This study investigates the effect of an introduced species, Sika Deer *Cervus nippon* on saltmarsh plant and infaunal communities. Epidermal fragment analysis was used to identify the plant species eaten by Sika Deer. Vegetation communities in deer exclosures and openly grazed areas were monitored over 4 years to investigate the effect of grazing on plant community composition and structure. The infaunal communities were assessed by extracting sediment cores. Deer were found to graze preferentially on *Spartina anglica* as intensive grazing led to swards dominated by *Salicornia ramosissima* even in upper marsh areas. Highest plant diversity was related to intermediate levels of grazing. Overall, higher levels of grazing led to higher abundance of three species of infauna detected in this study: *Hydrobia ulvae*, *Gammarus* sp. and *Nereis diversicolor*. Detailed examination revealed that the high abundance of *H. ulvae* was related to small quantities of above ground vegetation volume and that the abundance of *Gammarus* was related to small quantities of below ground vegetation biomass. The possible direct and indirect effects of Sika Deer grazing on bird populations are discussed.

## Introduction

Sika Deer *Cervus nippon* are native to Japan and East Asia and were first brought to British deer parks and private collections during the 1800s (Putman, 2000; Whitehead, 1964). The first introductions of Sika Deer to Dorset appear to have occurred in 1896 at Brownsea Island and during the early twentieth century, when they were brought to Hyde House, north of Wareham (Mitchell-Jones and Kirby, 1997; Whitehead, 1964). Animals brought to Brownsea Island are reported to have escaped by swimming ashore during their first night on the island (Whitehead, 1964) and animals escaped from Hyde House into the surrounding countryside throughout the early twentieth century and, in particular, during the Second World War (Horwood and Masters, 1981). It is not certain how many deer were originally brought to Purbeck nor where they were brought from, but it seems most likely that they originated from stock bred at Powerscourt in County Wicklow (Horwood and Masters, 1981). Sika Deer were brought to Powerscourt directly from Japan in 1861 and it is likely that these deer bred with other species of *Cervus* held at Powerscourt during the late 1800s, including Red Deer *Cervus elephus* and Sambar *C. unicolor* (Ratcliffe, 1987). Consequently the Sika Deer now feral in Purbeck are likely to exhibit a degree of hybridization (Ratcliffe, 1987).

The Isle of Purbeck currently has the largest group of feral Sika Deer in England (Putman, 2000) and deer from Purbeck are spreading further round Poole Harbour. The total number of Sika Deer in Purbeck was estimated as several hundred over a decade ago (Mann and Putman, 1989), approximately 2000 animals a few years ago (Putman, 2000) and perhaps as many as 3000 at present (Hann, pers. comm.). Poole Harbour and its surrounding countryside contain a rich mosaic of internationally important wildlife habitats and so it is crucial to be able to determine the impact of Sika Deer on these habitats and to have an effective deer management strategy.

One of the most important habitats in the Poole Basin is the intertidal flats and saltmarshes. The international importance of these in providing feeding and roosting grounds for large numbers of wintering wildfowl and waders have contributed to the harbour being designated a Special Protection Area (SPA) under the European Birds Directive and a RAMSAR Site. The saltmarshes are also important during the spring and summer as breeding sites for waders, gulls and terns. The saltmarshes in Poole Harbour are composed largely of *Spartina anglica*, a species of grass that evolved following an initial hybridization event between a native species S. *maritima* and an American introduction *S. alternifolia*. As commonly occurs in evolution of a new, fertile species by chromosome doubling (polyploidy), *S. anglica* was more vigorous than its parental species and so *S. anglica* is now the most abundant species of *Spartina* in Poole Harbour. It is an interesting coincidence that at the turn of the last century, two species arrived in Poole Harbour with enormous potential for impact on ecosystem function; a competitive plant *S. anglica* and a large herbivore, *C. nippon.* One hundred years on, both species are abundant around the harbour and this raises challenging questions on the future for nature conservation grazing management of the Poole Harbour saltmarshes.

Arne RSPB reserve is located on the western edge of Poole Harbour and covers approximately 535 ha of saltmarsh, heathland, woodland and farmland. Arne appears to have a fluctuating but large population of Sika Deer (numbers for 2003 estimated at 500–700; Gartshore, pers. comm.) and deer can commonly be seen grazing on the saltmarshes. The saltmarshes provide winter feeding and roosting for large numbers of waders and wildfowl and breeding grounds for Redshank *Tringa totanus* (Price, 1997). The aim of the study reported here is to investigate the effect of Sika Deer on aspects of the saltmarsh ecosystem that may impact on its ability to support wildfowl populations. Four specific questions are asked:

(i) What saltmarsh plants do Sika Deer eat?

(ii) What effect do deer have on the plant species composition of the saltmarshes?

(iii) What effect do deer have on the vegetation volume of the saltmarshes?

(iv) What effect do deer have on the infauna abundance of the saltmarshes?

# Methods

## Saltmarsh plant species eaten by Sika Deer

Plants eaten by Sika Deer were identified by examination of epidermal fragments remaining in faecal pellets. Forty fresh faecal pellets were collected from the saltmarshes alongside Crichton's Heath North and South (Figure 1) in each of four weeks during July 2000. Pellets were collected at random with the restriction that only one pellet was taken from each pile of pellets to avoid pseudo-replication. Pellets were frozen on the day of collection to prevent decomposition of the epidermal fragments.

The epidermal fragments in each pellet were analysed by comparison against plant species held in an epidermal library at Bournemouth University. Species were scored as either present/absent in each of the 160 pellets to obtain a frequency of occurrence. The abundance of each species within a pellet was not measured as this can be greatly influenced by the relative digestibility of different plant species (Mitchell *et al.*, 1977). Pellets were prepared for analysis as described in Mack (2001).

A calculation was made of mean frequency of occurrence across weeks in July of each saltmarsh plant species in the epidermal fragments and this was related to the availability

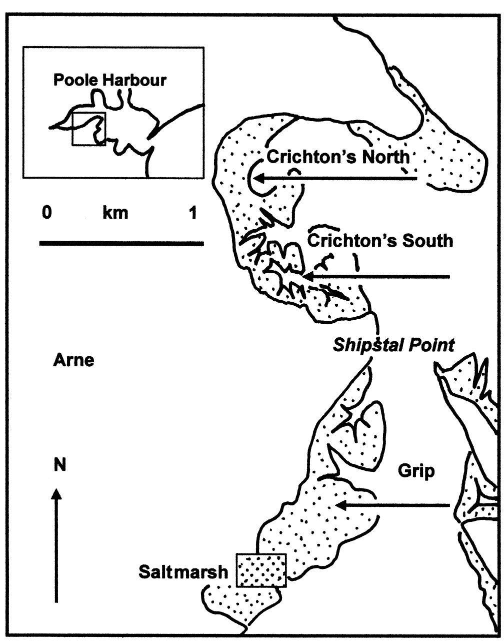


**Figure 1 Locations of the three areas of saltmarsh studied.**

of each species on the saltmarsh. The abundance of each plant species on these areas of saltmarsh was assessed by recording the vegetation in 20 randomly located 2 m x 2 m quadrats.

## Effect of deer on the plant species composition of the saltmarshes

In May 1999, 10 deer exclosures were set up in random positions on heavily grazed areas of saltmarsh at Arne (five on the saltmarsh alongside Crichton's Heath North and five on the saltmarsh alongside Crichton's Heath South (Figure 1). Each exclosure measured 2.5 m x 2.5 m and was constructed using 2 m wooden stakes inserted to a depth of 1 m at each corner. Chicken wire was then used to enclose and roof the plot. To minimize edge effects, only the central 2 m x 2 m area of each exclosure was used for data collection. Ten unexclosed plots were also set up at random on heavily deer grazed areas of saltmarsh. The vegetation community on each of the 20 plots was assessed in early July of 1999, 2000, 2001, 2002 and 2003 by recording the percentage cover of each plant species present.

During the summer of 2002, a survey of Arne saltmarsh was undertaken to assess the general extent of deer grazing at Arne. From this survey, areas that were lightly or ungrazed between 1999 and 2002 were identified, and 20 lightly or ungrazed 2 m x 2 m plots (hereafter referred to as ungrazed) were set up and their plant community composition measured as above. Five of these plots were located at Crichton's Heath North and five at Crichton's Heath South.

Detrended Correspondence Analysis was used to ordinate the differences in plant communities. Similarities and relative dissimilarities between plant assemblages were calculated using Similarity Percentages (SIMPER) and cluster analysis within the package PRIMER (Plymouth Routines In Multivariate Ecological Research; Clark, 1993). The Shannon Index was used to measure differences in plant community diversity.

## Effect of deer on the vegetation volume of the saltmarshes

In July 2002, above ground vegetation volume was assessed in each of the above 30 plots by visually recording the percentage occupancy of slices of the plot cuboid at 10 cm height intervals. Above ground volume was also assessed in 20 new 2 m x 2 m plots located on Grip Heath saltmarsh. Ten of these plots were located at random in heavily grazed areas of Grip Heath and 10 were located at random in lightly or ungrazed areas. To assess the possible impact of deer grazing below ground, root biomass was also investigated in each of the 50 plots. A 20 cm diameter augur drill was used to obtain three core samples to a depth of 10 cm. These samples were sieved using a 0.5 mm mesh to retain the root biomass. Where necessary, i.e. when the core contained large amounts of root biomass, cores were sub-sampled. The root biomass obtained was washed clean and transferred to an oven at 70 ºC to dry for 48 hours, after which the samples were weighed. All data were analysed using a Kruskal-Wallis test comparing grazed, ungrazed and fenced sites. The relationship between above ground vegetation cover and below ground root biomass was assessed using a Spearman's Rank Correlation.

### Effect of deer on the infauna abundance of the saltmarshes

The abundance of the macro-infauna of the saltmarsh was also assessed using the augur drill. The cores collected from the 50 plots described above were sieved through a 0.5 mm sieve and retained invertebrate fauna were identified to species level. These data were analysed using Analysis of Similarities (ANOSIM) in PRIMER.

## Results

### Saltmarsh plant species eaten by Sika Deer

Table 1 shows the mean percentage frequency of occurrence of each saltmarsh species in the deer pellets examined and the relationship of this to the abundance of each species on the saltmarsh. The most abundant species on the marsh were *Spartina anglica*, *Puccinella maritima* and *Salicornia ramosissima*. The species most frequently recorded in the pellets was *S. anglica*. The occurrence in the diet as a ratio of occurrence on the marsh is larger for *S. anglica* than for *P. maritima* while *Salicornia ramosissima* was seldom found in the faecal pellets despite its ready availability on the marsh. The amount of *Atriplex portulacoides* found in pellets as a ratio of that available on the marsh was intermediate to that for the above species.

**Table 1 Frequency of occurrence of saltmarsh plant species on the marsh (mean ± SE from 20 2 m x 2 m quadrats) and in Sika Deer faecal pellets***

| Species | Frequency of occurrence | | | | Ratio of mean occurrence pellet/marsh |
|---|---|---|---|---|---|
| | Species on marsh | | Species in pellets | | |
| | mean | SE | mean | SE | |
| *Aster tripolium* | 0.1 | 0.1 | 0.0 | 0.0 | 0.00 |
| *Atriplex portulacoides* | 11.6 | 3.2 | 16.875 | 8.4375 | 1.46 |
| *Limonium* spp. | 0.4 | 0.3 | 0.0 | 0.0 | 0.00 |
| *Plantago coronopus* | 0.1 | 0.1 | 0.0 | 0.0 | 0.00 |
| *Plantago maritima* | 0.2 | 0.1 | 0.0 | 0.0 | 0.00 |
| *Puccinella maritima* | 30.8 | 5.4 | 52.5 | 8.9 | 1.71 |
| *Salicornia ramosissima* | 19.4 | 5.9 | 7.5 | 1.5 | 0.39 |
| *Spartina anglica* | 40.6 | 8.5 | 89.4 | 2.6 | 2.20 |
| *Suaeda maritima* | 0.4 | 0.3 | 0.0 | 0.0 | 0.00 |
| *Triglochin maritima* | 0.3 | 0.3 | 0.0 | 0.0 | 0.00 |

* From a total of 160 pellets collected on four occasions.

**Table 2 Analysis (SIMPER) of the factors accounting for the differences in the floral community of fenced and unfenced plots in heavily grazed areas in 2002**

| Variable | Percentage abundance | | Cumulative percentage |
|---|---|---|---|
| | grazed | fenced | |
| *Spartina anglica* | 10.85 | 85.5 | 40.57 |
| Bare mud | 38.25 | 5.0 | 59.56 |
| *Salicornia ramosissima* | 34.65 | 4.0 | 76.33 |
| *Puccinella maritima* | 26.4 | 18.5 | 88.92 |
| *Atriplex portulacoides* | 2.25 | 17.0 | 97.44 |

## Effect of deer on the plant species composition of the saltmarshes

The areas fenced for 4 years showed a gradual shift in vegetation communities over time from *Salicornia ramosissima* dominated swards to *Spartina anglica* dominated swards (Figure 2). SIMPER analysis showed that almost half of the difference between the fenced and grazed swards was accounted for by the much lower abundance of *S. anglica* in the grazed swards (Table 2). Comparison of fenced, grazed and ungrazed plots in 2002 showed that, 3 years after being fenced, plots in previously heavily grazed areas had developed a vegetation that was not significantly different from the ungrazed plots (Figure 3). Plant species diversity was found to be greatest in plots where the level of vegetation volume (hence grazing pressure) was intermediate (Figure 4).

## Effect of deer on the vegetation volume of the saltmarshes

Across all sites, above ground vegetation volume was found to be significantly lower in the grazed plots than in the ungrazed or fenced plots (Figure 5, $K = 37.60$, $P < 0.001$). Mean root biomass was found to be significantly lower in the grazed plots and greater in the ungrazed and fenced plots (Figure 6, $K = 23.69$, $P < 0.001$). As above ground vegetation increased so did the below ground root biomass (Figure 7) ($r = 0.68$, $P < 0.001$).

## Effect of deer on the infauna abundance of the saltmarshes

Only three infaunal species were observed in the current study: a snail *Hydrobia ulvae*, a crustacean *Gammarus* sp. and the ragworm *Nereis diversicolor*. All species were found to be most abundant in the grazed plots and least abundant in the fenced plots (Figure 8). ANOSIM found the differences in invertebrate abundance in relation to grazing regime to be significant (Global $R = 0.126$, $P < 0.01$). Reasons for this relationship were explored by comparing invertebrate abundance to abundance of above and below ground vegetation using partial correlation analysis to hold one factor constant whilst the relationship of invertebrates with the other factor is quantified. This revealed that *Hydrobia ulvae* was

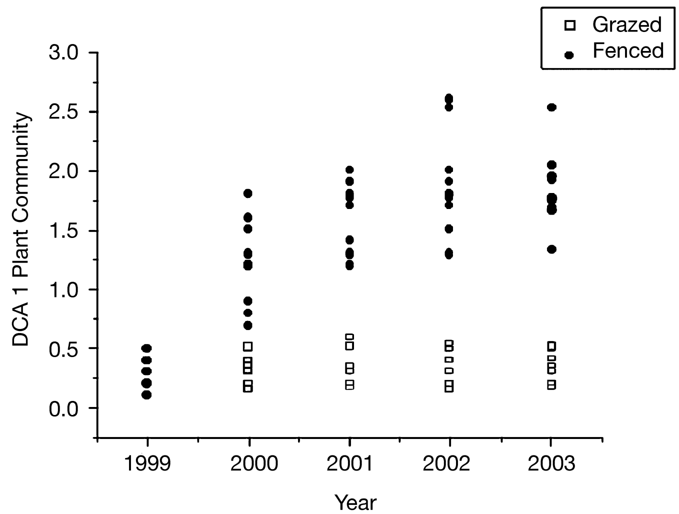


**Figure 2** **Changes in plant community composition (DCA 1) over time (1999–2003) for fenced and unfenced plots in heavily grazed areas. DCA 1 represents a gradient of communities where communities with low DCA values are dominated by *Salicornia ramosissima* and those with high values for DCA 1 are dominated by *Spartina anglica*.**

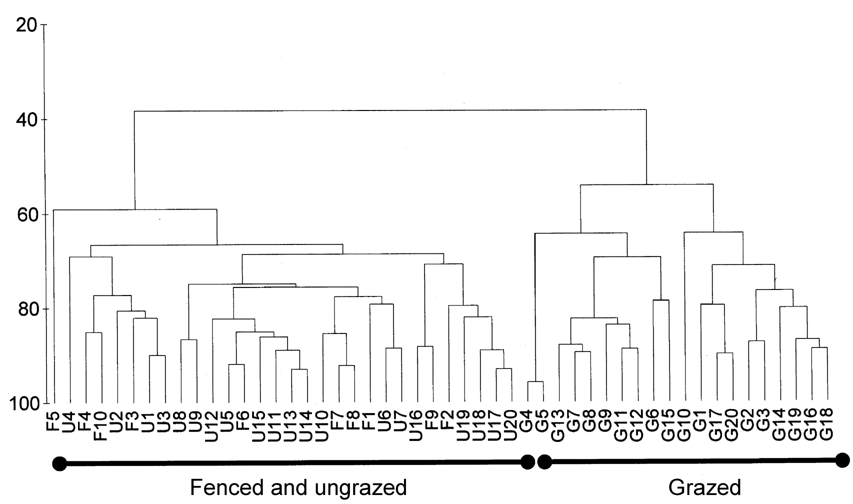


**Figure 3** **Degree of similarity of plant community composition between fenced plots (F), unfenced plots in grazed areas (G) and unfenced plots in ungrazed areas (U) in 2002. Plots fenced for 4 years have a vegetation similar to those of plots in ungrazed areas.**

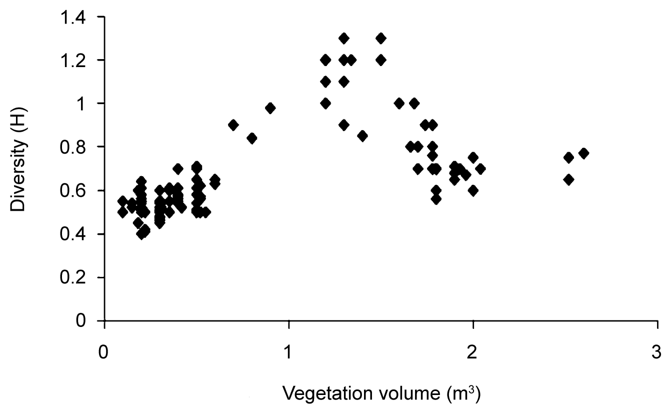


**Figure 4 Relationship between grazing level (measured in terms of remaining vegetation above ground volume) and plant species diversity (measured by Shannon Index (H)).**

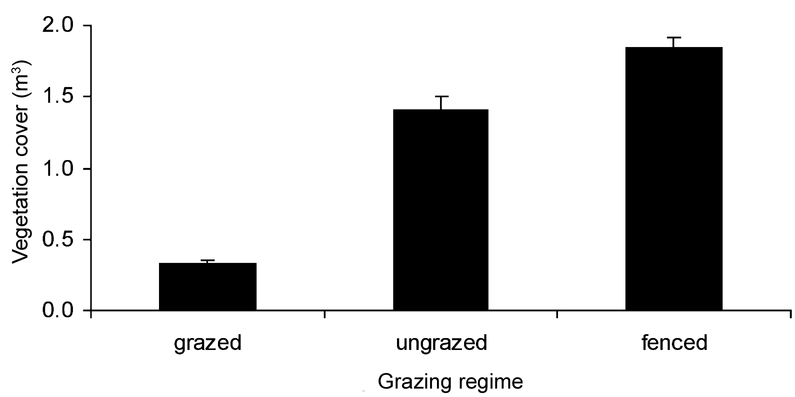


**Figure 5 Above ground vegetation volume (mean ± SE) in grazed, ungrazed and fenced plots in 2002.**

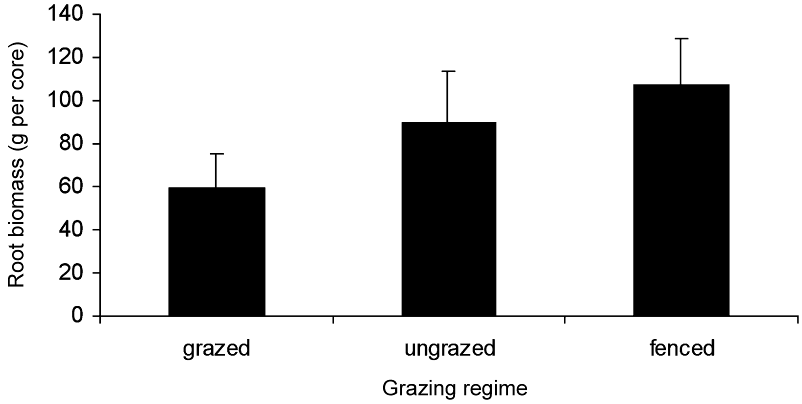


**Figure 6 Below ground vegetation (roots) volume (mean ± SE) in grazed, ungrazed and fenced plots in 2002.**

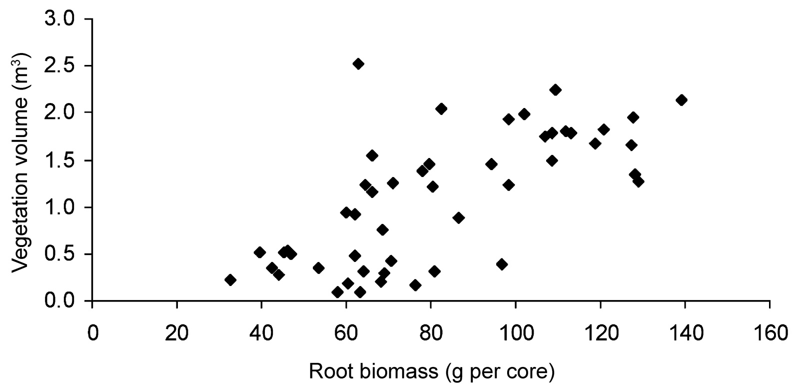


**Figure 7 Relationship between above ground and below ground vegetation volume in 2002.**

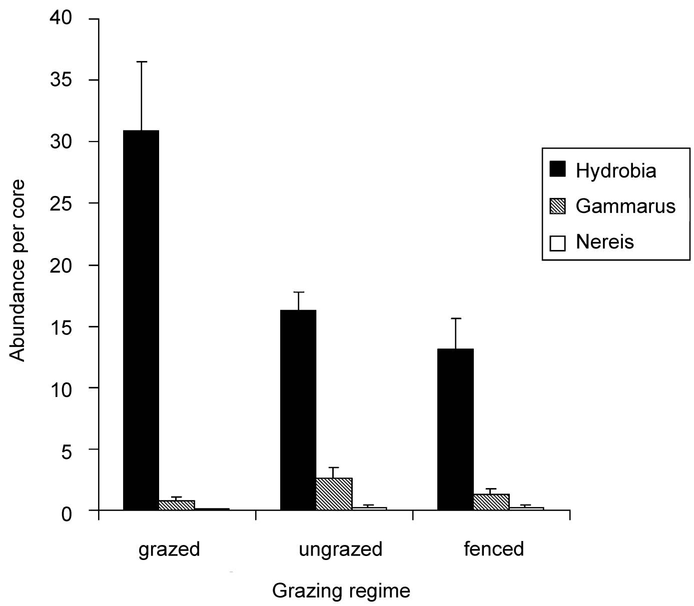


**Figure 8 Abundance of infauna (mean ± SE) in grazed, ungrazed and fenced plots.**

most abundant where there was least above ground biomass, irrespective of the amount of below ground biomass (Table 3). By contrast, *Gammarus* sp. numbers appeared unaffected by the amount of above ground biomass but abundance was greatest in areas of relatively low below ground biomass (Table 3). *Nereis* abundance showed no relationship with either above or below ground biomass. However, this result may be caused by low statistical power due to the small numbers of *Nereis* in our samples.

# Discussion

Sika Deer were found to have a significant impact on the saltmarsh flora and fauna at Arne. Where grazing was severe, there was an almost total loss of vegetation cover. Species that respond best to grazing are those such as *Salicornia ramosissima* that are quickly able to colonize the gaps created (Bertness, 1991; Pehrsson, 1988) and appear to be unpalatable to grazers. The creation of bare patches in saltmarshes can lead to the development of hypersaline conditions due to increased surface evaporation in the absence of vegetation cover (Bertness, 1991). This may have contributed to the development of lower saltmarsh communities, able to tolerate high levels of salinity during the summer, dominated by *Salicornia ramosissima*, in the intensively grazed areas of the higher marsh positions at Arne.

**Table 3 Partial correlation coefficients showing relationship between infauna abundance and (i) vegetation volume and (ii) root biomass**

| | Partial correlations | |
|---|---|---|
| | **For above ground vegetation volume** | **For below ground root biomass** |
| *Hydrobia* | r = -0.3567<br>*P* = 0.012 | r = 0.0700<br>*P* = 0.633 |
| *Gammarus* | r = 0.2026<br>*P* = 0.045 | r = -0.2876<br>*P* = 0.045 |
| *Nereis* | r = 0.0116<br>*P* = 0.938 | r = 0.1167<br>*P* = 0.425 |

The main saltmarsh species eaten by Sika Deer was found to be *Spartina anglica* and this was consumed in preference to *Puccinella maritima*. The tolerance of *Puccinella maritima* to grazing has been reported in other studies carried out in several countries (Esselink *et al.*, 2000; Jensen, 1985; Bakker, 1978; Cadwalladr *et al.*, 1972). Consequently there is strong evidence that further intensification of grazing in the Poole Harbour saltmarshes may result in a change in the dominant plant species from *Spartina anglica* to *Puccinella maritima*. Similarly, results from this study and inference from the findings of other studies indicate that a reduction in grazing would be expected to lead to a further domination of the marsh by *Spartina anglica* except in areas around the creeks and low saltmarsh where the dominant species would likely be *Atriplex portulacoides* (Andresen *et al*., 1990; Jensen, 1985; Bakker and Ruyter, 1981).

In this study, grazed plots regained the species composition typical of ungrazed plots within 4 years. This rapid rate of recovery is encouraging at face value, but is likely to be, in part at least, fuelled by the ready availability of propagules from nearby ungrazed areas. It is clear also that a total exclusion of grazers is not beneficial in terms of plant diversity, as this was highest in areas with intermediate levels of grazing. The actual grazing pressure exerted in such areas (deer $ha^{-1}day^{-1}$) is difficult to ascertain accurately but is currently being investigated. However, the general finding agrees with other studies that show that diversity is maximized by intermediate levels of grazing (Bouchard *et al.*, 2003; de Leeuw and Bakker, 1986; Bakker, 1985; Jensen, 1985). A high alpha and beta diversity of plant species may also lead to higher diversity in other trophic levels. For example, high densities of Redshank are closely correlated with a diverse vegetation community and structure (Norris *et al.*, 1997) and the highest densities of Redshank have been associated with moderately grazed marshes (Allport *et al.*, 1986; Norris *et al.*, 1998).

A reduction in above ground vegetation cover as a result of grazing is perhaps an obvious finding, and one that has been reported elsewhere (e.g. Bakker, 1978; Morris and Jensen, 1998; Esselink *et al*., 2000; Seliskar, 2003). The current study also found that grazing affected below ground biomass. Although this reduced allocation of tissue to roots concomitant with loss of above ground biomass is well documented (Morris and Jensen, 1998; Belsky, 1987), the relationship between changes in above ground primary production and root biomass required investigation as it does not exist for all species in all environments (Milchunas and Lauenroth, 1993). Trampling of the vegetation may also have considerable influence on the plant community. Chandrasekara and Frid (1996) observed that trampling by humans in saltmarshes led to distinct changes in the community similar to those recorded for grazing. In addition, compaction and trampling alters the sediment density which can affect the structure and function of the benthic community (Morris and Jensen, 1998).

At Arne, the macro-infauna were most abundant in the grazed areas and least abundant in the fenced exclosures. High levels of root biomass have been found to inhibit the development of a diverse infaunal community (Hedge and Kriwoken, 2000). However, the same authors reported higher levels of invertebrates in vegetated saltmarshes than on the adjacent mudflats so clearly root biomass is only one of a number of important variables. None of the infauna species in this study are important food sources for Redshank as it feeds largely on *Corophium* spp. (Ferns, 1992). However, the infaunal species present are important food sources for other birds. For example, *Hydrobia* are consumed by Shelduck (*Tadorna tadorna*) and other species of duck (Cadee, 1994) and *Gammarus* is an important food source for waders such as Dunlin (Verkuil *et al*., 1993), as well as for many fish that are themselves bird prey (Bartlett, 1996).

In conclusion, this study has found that deer grazing has both beneficial and detrimental effects on the saltmarsh, related to the intensity of grazing. Heavily grazed areas of the upper marsh are a concern as they lack the above ground vegetation structure to support breeding birds such as Redshank that require tussocks of tall grass. Such areas do, however, harbour a large abundance of infauna bird prey. Some grazing of the saltmarshes is clearly beneficial in terms of conservation management. Although grazing by Sika Deer is harder to manage than cattle grazing, their greater agility at crossing creeks may make them worth considering as a tool for grazing inaccessible areas of marsh.

## Acknowledgements

We thank all staff at RSPB Arne, particularly Dr John Underhill-Day, Neil Gartshore and Ian Clowes for their many contributions to this work. We would also like to acknowledge Vanessa Penny, Lisa Mack and Craig House and thank them for the valuable preliminary studies they carried out by during their time as undergraduates at Bournemouth University.

## References

Allport, G., O'Brien, M. and Cadbury, C. J. (1986) *Survey of Redshank and Other Breeding Birds on Saltmarshes in Britain 1985. CSD Report*, No. 649. Peterborough: Nature Conservancy Council.

Andresen, H., Bakker, J. P., Brongers, M., Heydeman, B. and Irmler, U. (1990) Long-term changes of salt marsh communities by cattle grazing. *Vegetatio*, **89**: 137–148.

Bakker, J. P. (1978) Changes in a salt-marsh vegetation as a result of grazing and mowing – a five year study of permanent plots. *Vegetatio*, **38**: 77–87.

Bakker, J. P. (1985) The impact of grazing on plant communities, plant populations and soil conditions on salt marshes. *Vegetatio*, **62**: 391–398.

Bakker, J. P. and Ruyter, J. C. (1981) Effects of five years of grazing on a salt-marsh vegetation. *Vegetatio*, **44**: 81–100.

Bartlett, C. M. (1996) Morphogenesis of *Contracaecum rudolphii* (Nematoda: Ascaridodea). a parasite of fish-eating birds, in its copepod precursor and fish intermediate hosts. *Parasite-Journal de la Société Française de Parasitologie,* **3** (4): 367–376.

Belsky, A. J. (1987) The effects of grazing: confounding of ecosystem, community and organism scales. *The American Naturalist*, **129**: 777–783.

Bertness, M. D. (1991) Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology*, **72**: 125–137.

Bouchard, V., Tessier, M., Digaire, F., Viver, J. P., Valery, L., Gloaguen, J.-C. and Lefeuvre, J. C. (2003) Sheep grazing as management tool in western European saltmarshes. *Comptes Rendus Biologies*, **326**: 148–157.

Cadee, G. C. (1994) Eider. Shelduck and other predators, the main producers of shell fragments in the Wadden Sea – paleoecological implications. *Palaeontology*, **37**: 181–202.

Cadwalladr, D. A., Owen, M., Morley, J. V. and Cook, R. S. (1972) Wigeon (*Anas penelope* L.) conservation and salting pasture management at Bridgwater Bay National Nature Reserve, Somerset. *Journal of Applied Ecology*, **9**: 417–425.

Chandrasekara, W. U. and Frid, C. L. J. (1996) Effects of human trampling on tidalflat infauna. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **6**: 299–311.

Clark, K. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**: 117–143.

De Leeuw, J. and Bakker, J. P. (1986) Sheep grazing with different foraging efficiencies in a Dutch mixed grassland. *Journal of Applied Ecology*, **23**: 781–793.

Esselink, P., Zijlstra, W., Dijkema, K. S. and van Diggele, R. (2000) The effects of decreased management on plant-species distribution patterns in a salt marsh nature reserve in the Wadden Sea. *Biological Conservation*, **93**: 61–76.

Ferns, P. (1992) *Bird Life of Coasts and Estuaries*. Cambridge: Cambridge University Press.

Hedge, P. and Kriwoken, L. K. (2000) Evidence for effects of *Spartina anglica* invasion on benthic macro-fauna in Little Swanport estuary, Tasmania. *Australian Ecology*, **25**: 150–159.

Horwood, M. T. and Masters, E. H. (1981) *Sika Deer*. Second (revised) Edition. Hampshire: The British Deer Society.

Jensen, A. (1985) The effect of cattle and sheep grazing on salt-marsh vegetation at Skallingen, Denmark. *Vegetatio*, **6**: 37–48.

Mack, L. (2001) An Investigation into the Effects of the Sika Deer Populations on the Vegetation of Arne. Unpublished B.Sc. dissertation, Bournemouth University.

Mann, J. C. E. and Putman, R. J. (1989) Patterns of habitat use and activity in British populations of sika deer of contrasting environments. *Acta Theriologica*, **35**: (5): 83–96.

Michell, B., Staines, B. W. and Welch, D. (1977) *Ecology of Red Deer: A Research Review Relevant to their Management in Scotland*. Banchory: Institute of Terrestrial Ecology.

Milchunas, D. G. and Lauenroth, W. K. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**: 327–366.

Mitchell-Jones, T. and Kirby, K. (1997) *Deer Management and Woodland Conservation in England*. Peterborough: English Nature.

Morris, J. T. and Jensen, A. (1998) The carbon balance of grazed and non-grazed *Spartina anglica* saltmarshes at Skallingen, Denmark. *Journal of Ecology*, **86**: 229–242.

Norris, K., Brindley, E., Cook, T., Babbs, S., Forster-Brown, C. and Yaxley, R. (1998) Is the density of redshank *Tringa totanus* nesting on saltmarshes in Great Britain declining due to changes in grazing management? *Journal of Applied Ecology*, **35**: 621–634.

Norris, K., Cook, T., O'Dowd, B. and Durdin, C. (1997) The density of redshank *Tringa totanus* breeding on the salt-marshes of the Wash in relation to habitat and its grazing management. *Journal of Applied Ecology*, **34:** 999–1013.

Pehrsson, O. (1988) Effects of grazing and inundation on pasture quality and seed production in a salt marsh. *Vegetatio*, **74**: 113–124.

Price, B. (1997) *A Survey of Saltmarsh Communities within Poole Harbour, Dorset for Breeding Waders and Gulls*. Sandy: RSPB.

Putman, R. J. (2000) *Sika Deer*. London/Fordingbridge: The Mammal Society/British Deer Society.

Ratcliffe, P. R. (1987) Distribution and current status of Sika deer, *Cervus nippon*, in Great Britain. *Mammal Review*, **17**: 39–58.

Seliskar, D. M. (2003) The response of *Ammophila breviligulata* and *Spartina patens* (Poaceae) to grazing by feral horses on a dynamic mid-Atlantic barrier island. *American Journal of Botany*, **90**: 1038–1044.

Verkuil, Y., Koolhaas, A. and Vanderwinden, J. (1993) Wind effects on prey availability – how northward migrating waders use brackish and hypersaline lagoons in the Sivash, Ukraine. *Netherlands Journal of Sea Research*, **31** (4): 359–374.

Whitehead, G. K. (1964) *The Deer of Great Britain and Ireland*. London: Routledge and Kegan Paul.