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Foodwebs in intertidal ecosystems

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INTRODUCTION

FOODWEBS IN INTERTIDAL ECOSYSTEMS: TROPIC INTERACTIONS BETWEEN SHOREBIRDS AND THEIR INVERTEBRATE PREY

On the occasion of their annual congress in October 1991, organized by and held at the Netherlands Institute for Sea Research on Texel, the international Wader Study Group (WSG) brought together shorebird ecologists working on foodweb systems in intertidal areas and invertebrate biologists working on what the bird people would regard as bird food in a symposium entitled: 'Shorebirds and the availability of their benthic prey' (abstracts published in 1992 in Wader Study Group Bull. 64: 13-17). Studies of invertebrate biology and feeding of shorebirds (alternatively called waders in the Old World and Australia) are rather different realms of scientific investigation. However, acknowledging the importance of predation in shaping life-history characteristics of prey species as well as determining the distribution and abundance of their avian predators, we felt that it would be helpful to publish the proceedings of what turned out to be a stimulating workshop: reflecting the state of the art. Investigations of foodwebs in intertidal soft sediments would greatly benefit by a better integration of the separate studies of prey and predator related studies. We hope that the present special issue of the Netherlands Journal of Sea Research stimulates this.

To enhance its usefulness, we shall now try to outline the story of this issue, by putting the various contributions in a logical sequence and by pointing out the many links between the papers. DIERSCHKE (pp. 309-317) starts off with a study of an intertidal rocky shore, where the specialist shorebird predator species rarely encounters problems with the availability of its prey. Prey abundance seems to vary little in such an environment, which provides a great contrast with the intertidal-flat ecosystem of the Wadden Sea studied by BEUKEMA and colleagues (pp. 319-330). The large year-to-year fluctuations in benthic prey biomass reported by them is reflected in the diet, distribution and abundance of one predator species, the knot *Calidris canutus*, studied at another site in the Wadden Sea by PIERSMA *et al.* (pp. 331-357). The problem of the scale over which shorebirds use intertidal areas as a reflection of patterns in prey availability is followed up by VERKUIJL *et al.* (pp. 359-374) in their study of shorebirds stopping over on the wind-tidal flats in the Sivash area, Azov Sea, Ukraine. Here, the availability of prey is a function of the extent to which wind uncovers the bottoms of brackish to hypersaline lagoons, and brings together pelagic prey in shallow water layers. The theme of the numerical response of shorebirds to the abundance of their prey is more systematically studied by NEHLS & TIEDEMANN (pp. 375-384) for dunlins (*Calidris alpina*) in the northern Wadden Sea. They report the results of counts on plots with a variety of characteristics. Counting birds and invertebrates on plots has also been the approach of KALEJTA (pp. 385-393), who tried to estimate predation pressure of a dunlin-relative, the curlew sandpiper (*Calidris ferruginea*) as well as the grey plover (*Pluvialis squatarola*), feeding on polychaete worms in a rich estuary in southern Africa. Kalejta showed no depletion of the food stocks in spite of high predator pressure since these stocks were continuously renewed by fast reproducing worms. That the situation can be quite different under conditions where there is no prey renewal is shown by BEUKEMA (pp. 395-406) for a winter half year in the western Wadden Sea. Here densities of benthic invertebrates reached particularly low levels after exceptionally high death rates, probably resulting from high bird predation pressure. Beukema argues that prey switching from mussels (*Mytilus edulis*) to baltic tellins (*Macoma balthica*) and gaper clams *Mya arenaria* by oyster-catchers (*Haematopus ostralegus*) resulted in a larger-than-average mortality in the alternative prey. Food stock renewal and repercussions on predation by shorebirds is also the theme of WANINK & ZWARTS (pp. 407-418). They document differences in growth rate as a function of sediment characteristics and intertidal

level. Differences in growth rate may lead to slight morphological differences between prey at adjacent sites, in turn affecting the performance of the predators, as shown by GOSS-CUSTARD *et al.* (pp. 419-439) in a detailed study of oystercatchers feeding on mussels.

The themes of prey availability of intertidally buried invertebrate species and the effects on shorebirds' feeding performance are comprehensively summarized by ZWARTS & WANINK (pp. 441-476), a study supported by a mass of long-term empirical data from their Frisian study site in the Wadden Sea. Where Zwarts & Wanink focus on the repercussions of variation in harvestability of tidal-flat invertebrates on the feeding of shorebirds, ENS *et al.* (pp. 477-494) take the reverse view by examining the behaviour of an important shorebird prey, the fiddler crab (*Uca tangeri*) of West Africa, in the light of the crabs' own feeding and the risks of being fed upon by birds. It is likely that many solutions to contrasting fitness-related demands on prey species (eating and avoiding to be fed upon), are mediated by energetic considerations. KLAASSEN & ENS (pp. 495-502) provide a first assessment of this topic for the fiddler crab. The final paper by PIERSMA *et al.* (pp. 503-512) summarizes our knowledge about macrozoobenthic stocks of intertidal flats on a worldwide basis. To structure their story, the knot was taken as the focal predator species since knots, wherever they occur over the world, always use the mollusc-component of intertidal ecosystems. The quite limited data-base allow few generalizations, but shows a great potential for comparative studies.

It is our hope that this issue will stimulate shorebird workers to firmly establish studies of invertebrate prey animals as part of their research tradition, and benthic ecologists to take shorebirds as a scientifically profitable and often important component of the foodwebs they try to unravel.

Theunis Piersma and Jan J. Beukema