

INTERFERENCE COMPETITION AMONG FORAGING WADERS

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Competition is among the most studied topics in ecology, both theoretically and empirically. Nevertheless, understanding of competition is still wanting; ecologists are not quite able to tell why or to predict how much competing animals suffer from mutual interactions. This thesis strives to contribute to understanding of competition by studying the mechanisms of interference competition among waders (*Charadrii*), foraging in intertidal areas. It attempts to extend previous work by applying an experimental approach to the empirical study of interference competition and an evolutionary approach to its theoretical study.

The experiments presented in this thesis yielded the following results:

1. Chapter 2 reveals that (1) interference effects on intake rate are different for red knots (*Calidris canutus*) and ruddy turnstones (*Arenaria interpres*), (2) that the mechanistic basis of interference effects differed between these two species, but (3) that in neither of the two species interference effects resulted from kleptoparasitism (i.e. the stealing of food items), which is the most widely discussed interference mechanism.
2. Chapter 3 shows that the extent to which captive turnstones suffer from interference competition depends on both the spatial distribution of food and the relative social dominance status of focal individuals. When food is spatially clumped, interference competition may arise from the monopolisation of food clumps, and interference effects may be unrelated to the amount of agonistic behaviour. Chapter 4 shows that the spatial distribution of food affects the amount of agonistic behaviour and the distribution of free-living turnstones, but it does not affect the time focal individuals spent digging for food, which is taken as an approximation of intake rate.
3. Chapter 5 shows that the extent to which captive turnstones suffer from interference competition depends on the distribution of food and on the foragers' social dominance status (as before), but also on the divisibility of food, which is one of the differences between food items (indivisible) and food clumps (divisible).

Thus, interference competition among foraging waders need not result from the stealing of food items, but may also result from interactions over food clumps, and these two mechanisms may differ in a way that is essential to the interference process. The theoretical chapter of this thesis (chapter 6) reveals that models of interference competition have not yet reached consensus about the kinds of interference behaviour that can be expected to evolve. Although evolutionary models of interference competition appear to be similar, they yield strikingly different predictions regarding the evolutionary stability of various interference strategies. To unify previous approaches, a systematic event-based description of the foraging process is presented and the use of techniques from Adaptive Dynamics theory is promoted. Through a critical discussion of the setup, the assumptions and the way of analysis of some evolutionary models of

interference competition, crucial assumptions and potential pitfalls in modelling the evolution of interference behaviour are identified.

Together, these experimental and theoretical results contribute to a mechanistic and evolutionary understanding of interference competition. At the same time, they make it clear that we cannot claim having reached such an understanding yet. This implies that it still is premature to base models of population dynamics on presumed knowledge of the interference process.

SPATIO-TEMPORAL VARIABILITY WITHIN THE MACROBENTHIC *ABRA ALBA* COMMUNITY, WITH EMPHASIS ON THE STRUCTURING ROLE OF *LANICE CONCHILEGA*

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The Belgian Continental Shelf (BCS) is situated in the southernmost part of the North Sea and is characterized by a high geomorphological and sedimentological diversity in soft-bottom habitats. The combinations of the ecological and the socio-economic values of the BCS cause conflicts between both interests. Initiatives are being taken by the scientific community to optimize the integration of the ecological value of the BCS with those of the different user functions, like shipping, dredging, sand and gravel extraction, fishing and tourism. The government has made a start with the implementation of Marine Protected Areas into the law (framework law of 20/01/1999): proposals for such areas have been made and are under investigation. In the mean time, it is important to provide the policy makers with a scientific basis for the development of a sustainable management plan for the natural resources of the BCS. One of the most important components of the marine ecosystem is the macrobenthic fauna. This component is considered to be suitable to characterize and monitor the marine ecosystem because of its size (macroscopic), its relative immobility and its direct link with the sediment and with the processes that occur immediately above the seabed.

This study delivers information on the structure and functioning of the macrobenthos in the marine ecosystem of the BCS. More specified, it aimed to investigate the macrobenthic community structure on the BCS, the spatial and temporal variability within the ecologically most important macrobenthic community (*Abra alba* community) and the importance and population dynamics of an ecologically important species (the sand mason, *Lanice conchilega*) within this community. Based on the information of a part of the marine ecosystem (macrobenthos), some remarks on the conservation of ecologically important areas or species on the BCS can be formulated.

In Chapter 2, the different macrobenthic communities and their distribution on the BCS were characterized based on a large number of samples gathered between 1994 and 2000. These samples cover a diverse range of habitats: from the sandy beaches to the open sea, from the gullies between the sandbanks to the tops of the sandbanks, and from clay to coarse sandy sediments. To investigate the large-scale spatial distribution of the macrobenthos of the BCS, the data of 728 samples were combined and analysed. By means of several multivariate techniques, ten sample groups with similar macrobenthic assemblage structure were distinguished. Each sample group is found in a particular physico-chemical environment and has a specific species composition. Four sample groups are differing drastically, both in habitat and species composition, and are considered to represent four macrobenthic communities: (1) the muddy fine sand *Abra alba* – *Mysella bidentata* community is characterized by high densities and

diversity, (2) the *Nephtys cirrosa* community occurs in well-sorted sandy sediments and is characterized by low densities and diversity, (3) very low densities and diversity typify the *Ophelia limacina* – *Glycera lapidum* community, which is found in coarse sandy sediments and (4) the *Eurydice pulchra* – *Scolelepis squamata* community is typical for the upper intertidal zone of sandy beaches. Of course these macrobenthic communities are not isolated from each other, but are linked through six transitional species assemblages. The transition between the *A. alba* – *M. bidentata* community and the *N. cirrosa* community, is characterized by a reduction in the mud content and is dominated by *Magelona johnstoni*. The transition between the *N. cirrosa* and the *O. limacina* – *G. lapidum* community is distinctive by decreasing densities and coincides with a gradual transition between medium to coarse sandy sediments. From the *N. cirrosa* to the *E. pulchra* – *S. squamata* community, transitional species assemblages related to the transition from the subtidal to the intertidal environment, were found. Each community or transitional species assemblages was found over a specific range along the onshore-offshore gradient, four types can be discerned: (1) almost restricted to the near-shore area, but possible further distribution, (2) distributed over the full onshore-offshore gradient, (3) restricted to the near-shore area, and (4) restricted to the sandy beach environment. The diversity pattern on the BCS follows this division, with species rich and poor assemblages in the near shore area to only species poor assemblages more offshore. The distribution and diversity patterns are linked to the habitat type, discerned by median grain size and mud content.

The small- to large scale geographical pattern within the ecologically most important macrobenthic community (*A. alba* community) of the BCS was investigated in Chapter 3. The *A. alba* community is widely spread in the coastal zone of the English Channel and the Southern Bight of the North Sea. The community is located in shallow, fine muddy sands. Its spatial distribution is characterized by a number of isolated patches (Atlantic French, British and German coast) and one large continuous distribution area (northern France up to the Netherlands). The aim of this study was to investigate the geographical patterns within the macrobenthic *A. alba* community at different scales: the community's full distribution range (i.e. large scale) and a selected area with a continuous distribution of the *A. alba* community (i.e. small scale) in relation to structuring environmental variables. Therefore, an analysis of newly collected samples along the Belgian coastal zone was combined with available information on the *A. alba* community throughout its distribution range. Although the community structure shows a high similarity across the full distribution range of the *A. alba* community, large- as well as small-scale changes in community composition were observed: the BCS should be considered as a major transition from the rich southern to the relatively poorer northern distribution area of the *A. alba* community. At a large scale (i.e. full distribution range), the differences in community structure are expected to result from (1) the specific hydrodynamic conditions in the English Channel (Atlantic ocean waters) and the Southern Bight of the North Sea, with a consequent differential connectivity between the different areas and (2) the climatological and related faunal shift from temperate (English Channel) to boreal conditions (German Bight). At a small scale (i.e. within the continuous distribution area), structural and functional community aspects may result from geographic differences in (1) detrital food availability, related to riverine input and pelagic productivity, along and across the coastline and (2) the amount of suspended matter, impoverishing the *A. alba* community when excessively available.

The study in Chapter 4 outlines the seasonal and year-to-year variations in the *A. alba* community. This variation is typical for macrobenthic communities in temperate, shallow coastal waters and is investigated in the *A. alba* community on the BCS during nine years (1995-2003). During the investigated period, the community did not show a cyclic pattern, but a shift between the years 1995-1997 and 1999-2003, possibly triggered by changes in the hydroclimatic state of the North Sea and reflected by a small shift of the dominant species in the *A. alba* community.

In the years 1995-1997, the temporal pattern was dominated by strong year-to-year differences, coinciding with different successive events (strong recruitment, sedimentological changes, cold winters) and therefore those years were characterized as the unstable period. All those events had an effect on the macrobenthic density, diversity and species composition. The mass recruitment of *S. subtruncata* caused a decrease in the density and diversity of the macrobenthos, whereas the increase of mud content was responsible for a crash of the species richness and macrobenthic density. After those events, the *A. alba* community needed time to recover (1996-1998), which was possibly slowed down by a slow amelioration of the habitat conditions, unsuccessful recruitment and the occurrence of a cold winter. This period was followed by some years where the seasonal dynamics in the community superimposed the lower year-to-year variability and therefore those years were characterized as the stable period. The seasonal dynamics in the study at hand were characterized by high macrobenthic densities and diversity in spring and summer, with a decline in autumn towards the end of the winter. It can be concluded that mainly local factors were responsible for the short term variations within the community, whereas some global events (hydroclimatic, cold and mild conditions) caused the long term changes.

In Chapter 5, the population dynamics, recruitment and persistence of the *L. conchilega* populations in subtidal soft-bottom sediments along the Belgian coastline are described. An intensive sampling campaign (monthly-biweekly from April until August), the discrimination of different benthic stages and cohort analysis of the adult population enabled the discrimination of trends in recruitment patterns of *L. conchilega*. Three recruitment periods were defined based on the occurrence of peaks of aulophore larvae in the water column and peaks of recently settled individuals in the benthos: (1) spring recruitment period (April-July), (2) summer recruitment period (July-September), and (3) autumn recruitment period (September-November). The spring recruitment period was the most intense and was characterized by high densities of recently settled individuals and juveniles. These high densities resulted in an adult population, which consisted of different cohorts and which was characterized by a high turn over. The summer and autumn recruitments were less intense and did not occur at every station or in every year. Spatial and temporal variations in timing and intensity of settlement and recruitment were observed and described. Results indicate that *L. conchilega* is an opportunistic species, characterized by a long pelagic phase, high settlement of larvae and a high turn over in the adult population. Due to this recruitment strategy and the preferential settling of the larvae in adult patches, the studied *L. conchilega* population was able to maintain high abundances in moderately stable patches.

The tube building polychaete *L. conchilega* has a wide distribution and can form dense aggregations. Unfortunately, the effects of *L. conchilega* on the surrounding benthic community have received little attention, especially in subtidal areas. Therefore, the

effects of the presence of *L. conchilega* on the abundance, species richness, diversity and species composition of the North Sea benthos in relation to sedimentology and depth were evaluated in Chapter 6. The results show that *L. conchilega* does have an effect on the benthic density and species richness in soft-bottom sediments. The density of the benthic species increased and was significantly (positively) correlated with the density of *L. conchilega*. Furthermore, the species richness increased with increasing density of *L. conchilega*. This trend was, however, not consistent: the number of species no longer increased or even decreased after reaching a certain density of *L. conchilega* ($>500 \text{ ind.m}^{-2}$). The same overall pattern was detected concerning the expected number of species. The N_i-diversity index showed similar or slightly higher values in *L. conchilega* patches compared to patches without *L. conchilega*. The effects on density and diversity were most pronounced in shallow fine sands, which are the preferred habitat of *L. conchilega*, and less in deep fine sands. The changes in benthic characteristics result from the alterations of the habitat by *L. conchilega* (hydrodynamics, sediment stability, improved oxygen) and the complex interactions between the benthic organisms and the biogenic structures consisting of *L. conchilega* tubes. A lot of benthic species can profit from the creation, modification and maintenance of that habitat by *L. conchilega*, which results in an increased density and species richness in *L. conchilega* patches compared to the surrounding soft-bottom sediments. Finally, the results indicated that *L. conchilega* has an effect on the benthos present in a particular habitat, rather than forming its own association.

The general conclusion, considering the macrobenthos, is that from a nature conservation viewpoint the coastal zone is of high ecological value. This is due to the high diversity of macrobenthic communities and the presence of the diverse *A. alba* community with the key-species *L. conchilega*. This high ecological value of the coastal zone is in conflict with the socio-economic interests of this zone and a focus on an integrated coastal zone management is necessary and in progress. This study delivers information on the structure and functioning of the macrobenthos on the BCS and can be used as scientific input in the nature conservation discussions.