

Spatial relations among coastal bird populations in NEW! Delta estuaries and ports

Exploration of how the metapopulation concept can provide new clues for the conservation of protected coastal bird species with the Common Tern as example



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Alterra, Wageningen
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Pieter Slim was the Alterra project leader for the NEW! Delta project and for this research on the metapopulation concept for estuaries and ports.

1 Introduction

1.1 The NEW! Delta project

Coastal and estuarine habitats are important and nowadays sensitive systems. These pure and natural systems offer robust habitats, and the species inhabiting them are adapted to high dynamics and processes of land creation and destruction. In the Rhine-Meuse-Scheldt 'delta' (estuary), human activities have influenced the natural processes, especially in recent decades. Dykes have been built to harvest land from the sea, cities and ports were developed, sea-arms were dammed and beaches and dunes 'flooded' with recreants. As a result, coastal birds that depend on temporary natural islands and sand and shell banks for their breeding colonies now suffer from a lack of breeding grounds. Harbours and port areas often include newly developed terrains which offer suitable areas for breeding and are relatively undisturbed by recreants. Coastal birds are increasingly colonizing these areas, which is a good thing, except for when these terrains are needed for the economic purposes for which they were set aside. Yet many coastal bird species are endangered and protected by law. This has led to conflicts among stakeholders, especially between environmental associations and authorities in charge of port maintenance and improvement. At the same time, there are good examples of harbour management voluntarily cooperating with nature conservationists to preserve coastal birds.

The European Commission has set out a number of policy directives and initiatives applicable to estuarine environments. Among these are the *Birds Directive* (79/409/EEC), the *Habitat Directive* (92/43/EEC), formation of the *Natura 2000* network and the *EU Water Framework Directive* (2000/60/EC). At present a major challenge is to get the various stakeholders working together to manage the estuaries, preserving both nature and economic development. The NEW! Delta project is one of the initiatives designed to help meet this challenge.

A significant number of protected areas and valuable biotopes are located in the regions covered by the NEW! Delta project and these also form part of the EU *Natura 2000* network. At many of these locations, it is vital that measures be taken to create, restore or maintain ecological values. Concerted action among a variety of actors from different countries would benefit such efforts, especially as most conservation areas derive their significance not only from their own intrinsic value but also in relation to each other; in many respects they may be regarded as a single ecosystem. An example of an issue that needs to be dealt with jointly is the protection of migratory bird routes, as some species are found at one point in the port area of Antwerp and then later move on to the Rotterdam area and farther north on the Dutch coast.

With these concerns in mind, partners in North-West European countries have joined in cooperation in the New! Delta project in order to find the best way to balance the port-nature relationship. The NEW! Delta project is a part of the so-called *European Community Initiative INTERREG III, Strand B*, which promotes interregional cooperation among the countries of North-West Europe. Its overall aim is to promote sustainable development in North-West Europe's coastal, estuary and port areas in such a way as to preserve both nature and continuance of economic-oriented port activities. The larger programme will be implemented from the French region of Haute-Normandie up the French coast to the coastal areas of neighbouring Belgium and the Netherlands through the Dutch provinces of South and North Holland right across the North Sea and the Channel to the eastern and southern coasts of the United Kingdom.

The NEW! Delta project marries environmental and economic objectives. It seeks to foster the protection of the *Natura 2000* sites as an integral part of economic port and estuary development, while enabling opportunities for social, economic and maritime benefits. From this perspective, the network of parties involved in the NEW! Delta project could act as the ideal network to develop an innovative 'port biotope management' concept which combines economic and ecological values. This new concept could provide a worthwhile alternative to current conservation practices. Use of the port biotope management concept should facilitate integration of the management plans of several neighbouring port areas and of the coastal biotopes (estuaries) that are located between them. The ecological basis for such a regional coastal management approach is found in 'metapopulation theory' (Levins 1970, Harrison 1991, Hanski & Gilpin 1991, Opdam 1991, Newton 1998).

1.2 Metapopulation theory

Opdam (1991) described metapopulations as spatially structured populations of plants or animals consisting of distinct units (subpopulations), separated by space or barriers and connected via dispersal movements. Metapopulations characteristically demonstrate a turnover, with local populations going extinct and becoming re-established, resulting in a distribution pattern that shifts over time. The metapopulation theory is used to analyse the effects of habitat fragmentation on plants and animals in the temperate zone, integrating various explanations for the paucity of species in isolated biotopes.

Figures 1 through 4 illustrate some aspects of the metapopulation theory using the example of coastal bird populations and their habitat.

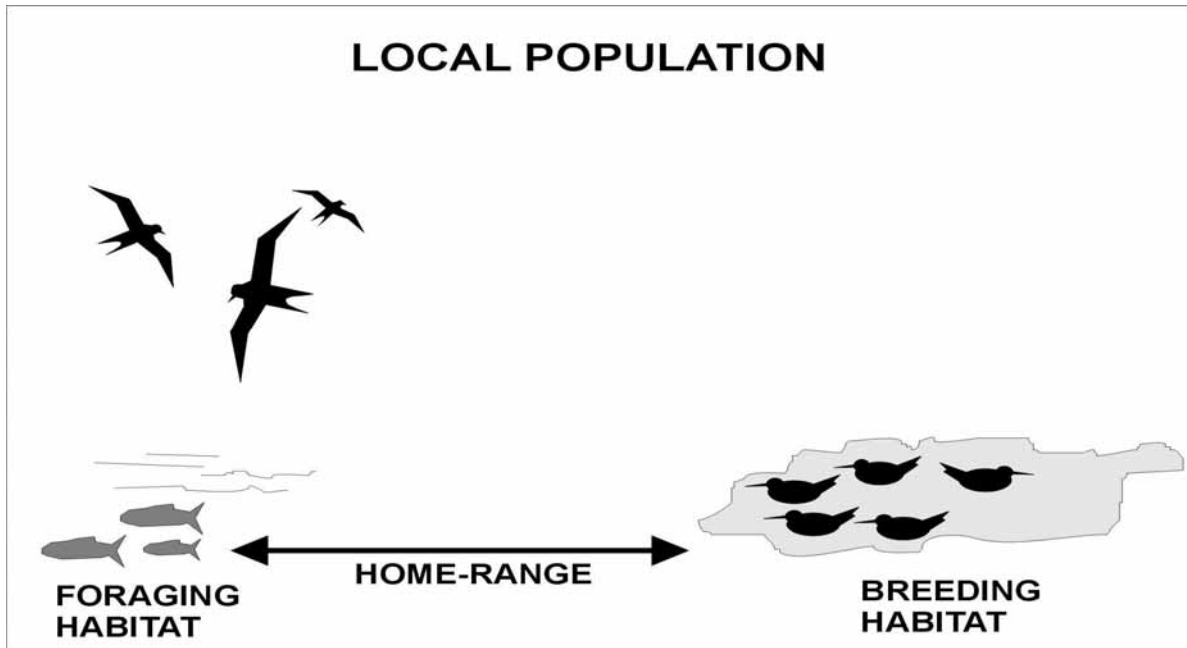


Figure 1. Coastal birds need different habitats within a certain area: breeding habitat for reproduction, foraging habitat and resting habitat. All individuals that nest at the same location belong to one 'local population'. Their home-range is defined as the area covered by their daily movements (like hunting for fish and resting on sandbars).

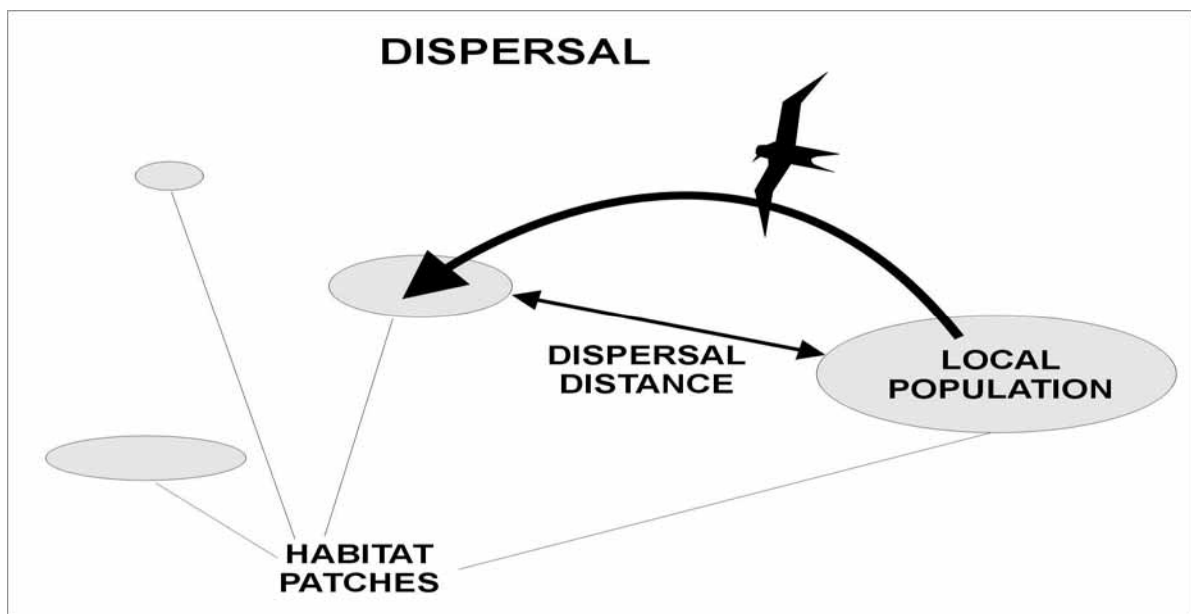


Figure 2. Birds sometimes leave their own habitat patch (occupied by a local population of coastal birds) to explore new habitat patches. This behaviour is called 'dispersal' and is observed, for example, when young birds become adult or if disaster strikes at the original habitat patch (e.g. flooding of the sandbar that acted as breeding site) and the whole breeding colony begins searching for alternative sites. In the latter case, the adult birds often join other existing colonies in the region.

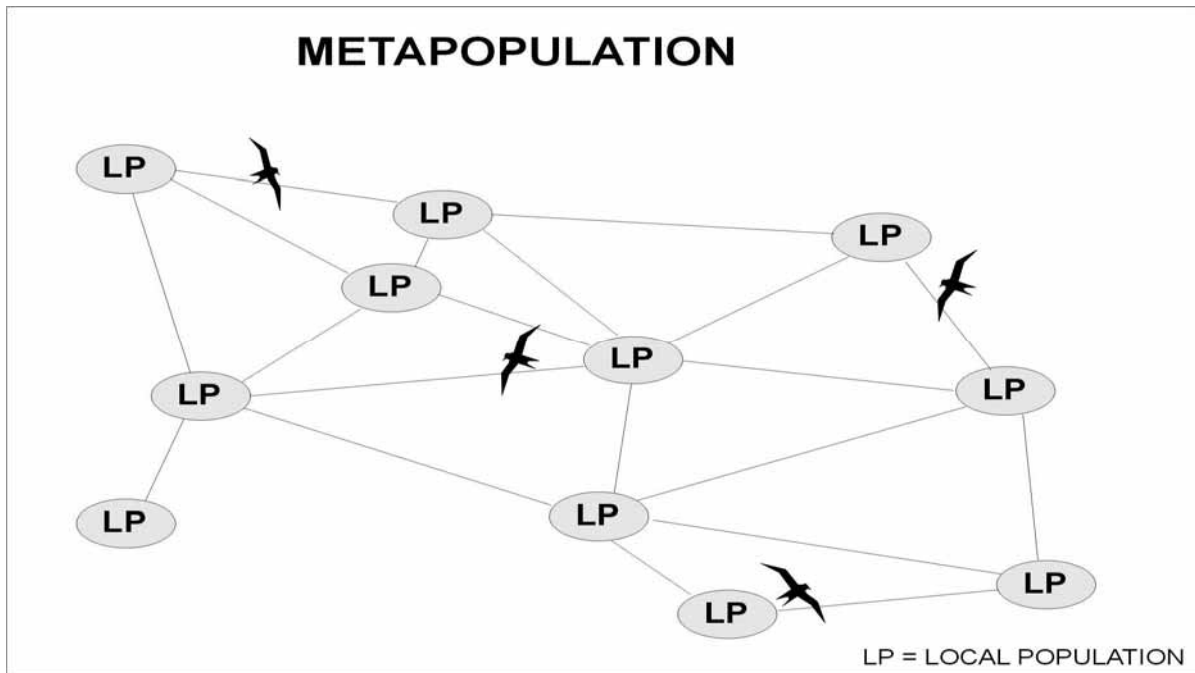


Figure 3. The network of local populations of coastal birds that are mutually linked by dispersing individuals is called a 'metapopulation'. The total number of individual birds in the whole metapopulation is often sufficient to survive in the long term (in this case we speak of a 'viable' metapopulation). By distributing this population over a network of habitat patches the bird species spreads the risk of extinction.

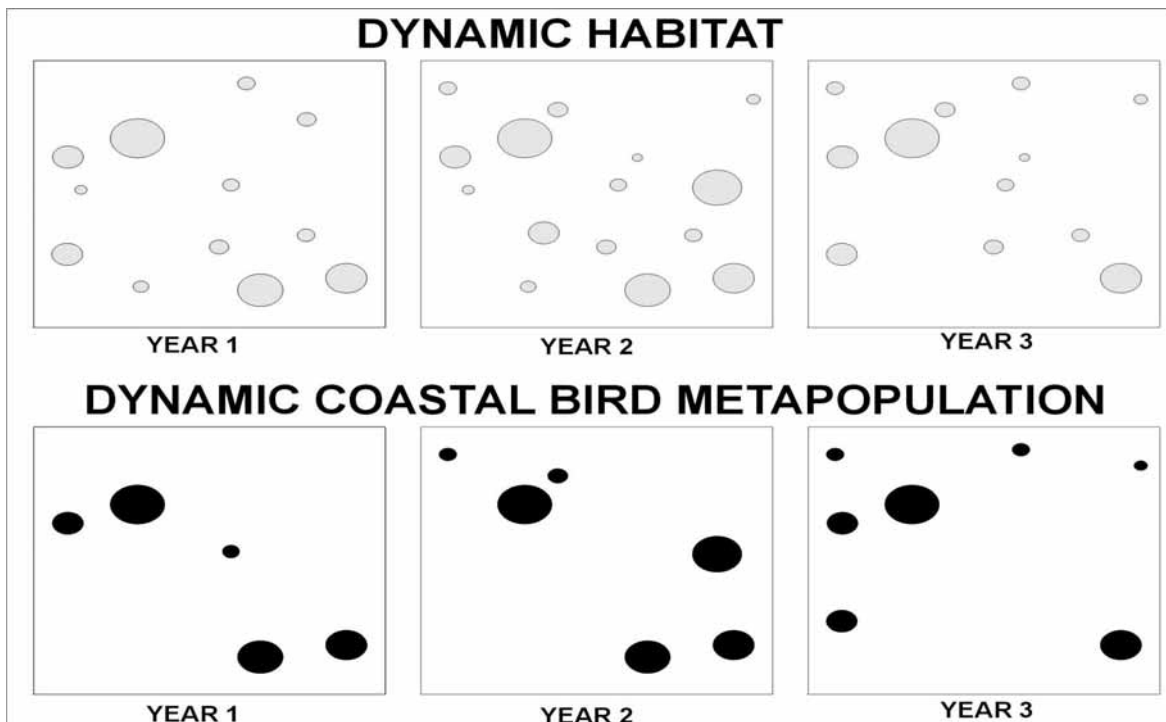


Figure 4. Coastal birds inhabit dynamic landscapes, where the availability of suitable habitat patches differs from year to year (upper row of illustrations). As a result, the distribution of local bird populations also differs year by year (lower row of illustrations), because coastal birds are real pioneer species that easily cope with habitat gain and loss.



Common Tern using port facilities for hunting (photo: Ran Schols).

So, any discontinuous spatially structured population can be described as a metapopulation (Harrison 1991). Thus, local populations of coastal birds that exist in e.g. port areas and that exchange individuals with neighbouring colonies (via dispersal) are considered to be part of a larger metapopulation that inhabits a region-wide network of habitat patches. Within such a network, particular patches change over time in the quality of habitat they offer, but the network as a whole continues to exist as a collection of suitable patches, mutually connected and able to support a (sustainable) metapopulation of the target species.

This report presents a pilot study that was carried out within the framework of NEW! Delta Theme 3: *Creation and Restoration of Coastal and Estuarine Habitats*. This theme has several objectives: to develop tools to increase ecological values of areas, to investigate and demonstrate how ports and nature can best coexist, and to set out basic principles to restore balance to the port-nature relationship.

1.3 Aim of this pilot study

Fauna and flora in dynamic habitats depend on the situation in a wider region, because the availability and distribution of suitable habitats shift over time. For example, protected birds that may be observed in the port of Antwerp in one year may move to the De Zilk dune area in the Netherlands a year later. Constructive cooperation among managers of different (port and estuary) areas is necessary in order to effectively conserve natural values in such a continuously changing context. Not all areas where nature values occur have nature conservation as their primary goal (e.g. this is true of industrial ports). As a result, implementation of the needed protection measures is not self-evident in every case. Nonetheless, EU law compels all land owners (including those in industrial and urban areas) to take conservation measures if protected species occur on their property. The current study explores how NEW! Delta ports and estuaries could, by cooperating in biotope management and nature conservation, fulfil their obligations under EU nature conservation laws without seriously hindering economic activities.

The focus of this pilot study is on coastal and estuarine birds, because this is an important group occurring in port areas and appearing on species conservation lists. Besides, coastal birds migrate on a larger scale than ground-dwelling animals and most plant species, and therefore fit better within the NEW! Delta study area.

Coastal birds naturally brood on temporary lands in tidal zones. In the past, attempts have been made to attract brooding coastal birds to specially created, human-made breeding grounds, away from ports which often – unintentionally – offer alternative breeding spaces where natural sites are lacking. These specially made breeding sites have been developed in the direct vicinity of existing port colonies and are meant to provide replacement habitats in cases where port-breeding colonies lose habitats due to industrial and commercial developments. Successful colonization of these artificial sites has proven difficult however (see Meininger & Graveland 2002). This has led to questions of whether new concepts could be found to



Courtship behaviour: starting point for reproduction (photo: Toon de Smit).

support conservation of the local coastal bird colonies occurring in port areas using knowledge about the spatial dynamics of regional populations.

Because coastal environments also tend to accommodate highly dynamic economic and ecological areas and habitats, this might be a case where rigid (European) regulations turn out to be counterproductive in terms of both economy and ecology. Here, a more flexible approach could be useful.

Our objective is to develop a practical tool with which to investigate and demonstrate the ecological values of different coastal bird areas that are all part of a larger network. The basic principle is to capture the metapopulation concept in a tool that can be used to reveal how ports and nature can coexist. This tool could then be used as part of a best practice management decision model.

We formulated a number of questions to help us explore this coastal biotope management concept:

1. Can the population dynamics of the Common Tern be satisfactorily described with the help of a metapopulation model?
2. What are the consequences for a network population of loss of all the habitats in port areas?
3. Could newly created (temporary) biotopes for coastal birds in the port area replace lost habitats in these industrial areas?
4. What would be the effect of replacing breeding sites within the port area with newly created sites in the vicinity of the port?
5. What would be the effect if we also tried to strengthen the coherence of the ecological network in the delta as a whole?
6. Does the metapopulation approach have additional value in the debate about conservation of coastal birds in the modern delta where there is strong human pressure and in dynamic harbour regions?

Scope of the pilot study

In the current study, we focus on the landscape ecological aspects of coastal bird conservation (especially of the Common Tern) along the Dutch-Belgian coast. We are particularly interested in the

role that port habitats play in the survival of coastal birds, as in recent years these sites have become – unintentionally – increasingly popular as breeding sites for terns, gulls and other coastal birds.

Some of our model scenarios are based on actual data of current coastal bird populations, but for this pilot study we have simplified the data to be useful in a model environment. Therefore, results and conclusions from this study should NOT be applied in real cases.

Furthermore, the management conditions under which new (artificial) habitats could be successful as breeding sites for coastal birds are outside the scope of this study, as are the policy aspects of coastal bird conservation, such as the legal obligation to compensate for habitat loss.



Photo: Toon de Smit.

2 Methodology

We conducted this pilot study by means of a literature review, expert interviews and modelling. The literature review and expert interviews gave us good insight into the ecology of coastal birds and opportunities for habitat protection and management. We selected the Common Tern (*Sterna hirundo*, in French *Sterne pierregarin* and in Dutch *Visdief*) because for this species detailed data on life history was easily available in the literature (e.g. Stienen & Brenninkmeijer 1992, Schröder *et al.* 1996, Van der Hoorn 1997). Also, Common Tern expert E. Stienen, of the Belgian Research Institute for Nature and Forest (INBO) was willing to support the pilot study with his expertise. With a metapopulation model, called METAPHOR, we were then able to simulate population dynamics of the Common Tern in the delta region, to learn how different local populations are connected and what the impact of habitat gains and losses (especially in port areas) would be on the presence of the Common Tern in this region.

2.1 Study area

The study area is the Rhine, Meuse, Scheldt delta. For a few hundred years this 'delta' (estuary) consisted of a large number of islands divided by dynamic branches of the sea. In the course of the past three to four centuries most islands were interconnected by polders, and these larger semi-islands were connected by dams and bridges. Nowadays this delta acts as a gateway to Europe with the huge harbours of Rotterdam and Antwerp and the smaller Port of Zeebrugge. A part of the delta no longer has a tide and has been converted to a freshwater system. All of the major Common Tern colonies observed in recent years are found in the vicinity of the salt water (Figure 5).

We focused on the Dutch-Belgian delta region for metapopulation reasons (see section 2.3 below) and on practical grounds. Bijlsma *et al.* (2001: 265-266) demonstrated that the breeding distribution in this area of the Netherlands is more or less separate from the other main breeding areas (in the Wadden and IJsselmeer areas) and Dutch (mainland) coast.

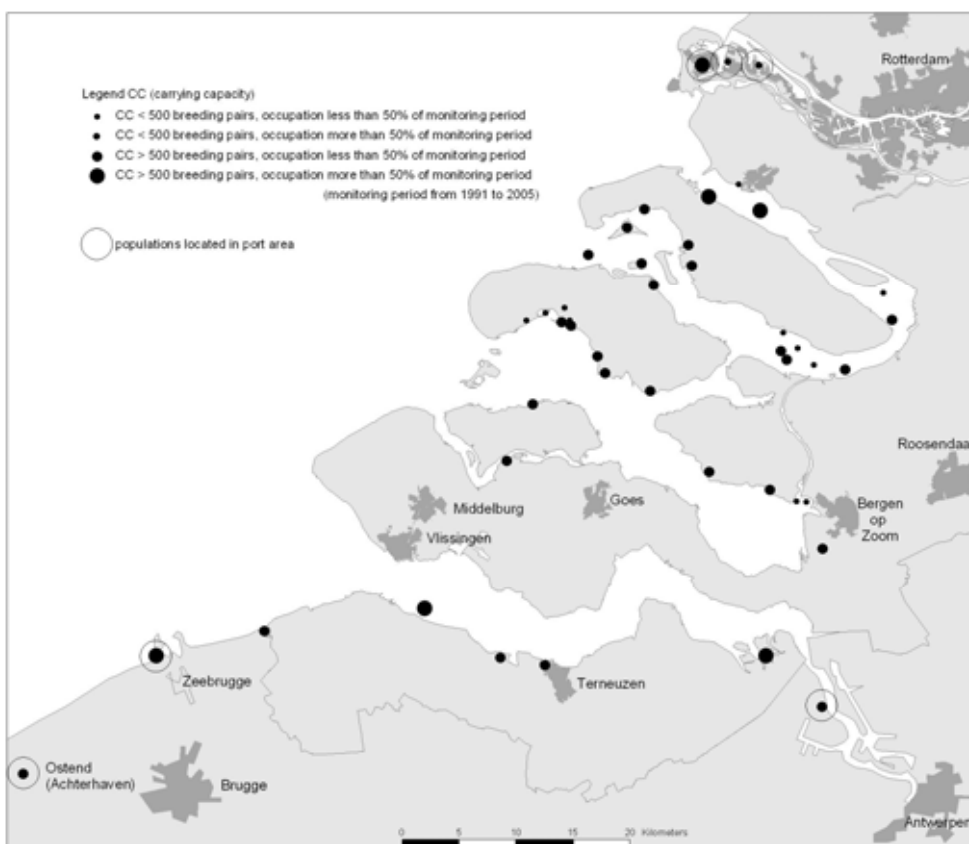


Figure 5. Distribution of Common Terns in the Dutch-Belgian delta region. Based on the size of the population and occupation in the monitoring period 1991-2005, the locations were divided in four categories. CC = carrying capacity.

2.2 Coastal birds as an indicator species

In port areas along the Dutch and Belgian coast a range of coastal bird species can be found. Gulls, terns and other coastal birds are – by nature – adapted to the highly dynamic environment of the sea, beaches, estuaries, dunes and other coastal biotopes. Human activities in those biotopes have destroyed traditional habitats but also created new habitat opportunities (Stienen *et al.* 2005). For the long-term survival of coastal birds it is important to better understand their breeding and feeding behaviour and habitat requirements, their dispersal and colonization abilities and their population dynamics on a local and regional scale. When it comes to port areas, gull and tern species are easily observed, as they usually nest in medium to large-sized colonies. These species each have their own unique ecology, with mutual differences in e.g. breeding habitat, food preferences and ability to disperse. The Common Tern is a species frequently observed in port areas, as it is quite common compared to other protected species like e.g. the Sandwich Tern.

2.3 Population dynamics of the Common Tern



One reproductive unit (photo: Bart Vannieuwenhuysse).

Data on the distribution of the Common Tern was provided by the Dutch National Institute for Coastal and Marine Management (RIKZ) and the Belgian Research Institute for Nature and Forest (INBO) (see acknowledgements). Breeding pair numbers were provided per location for the period 1991-2005 (the Netherlands) and 1960-2005 (Belgium). Data on breeding success was not available for the locations.

From the literature and expert interviews we learned that local populations of coastal birds in the Dutch-Belgian delta region can be considered as one large (meta)population (Van der Hoorn 1997, pers. comm. Stienen).

The estuaries and port areas act as a continuous dynamic habitat matrix, with large fluctuations at the local level but a relatively stable metapopulation on the regional (delta) scale, at least during the past 15 years. Apart from the intensive exchange of individuals among the delta habitats, there is also a small exchange of individuals with coastal bird populations in the Wadden Sea area and coastal regions of the United Kingdom. Because this exchange is small (less than 5% of the total population) this long-distance dispersal behaviour can be construed more as a strengthening of genetic pools than as a real contribution to other populations in terms of individuals and population size. This led us to restrict our study area to the delta region.

2.4 Modelling spatial relations in Common Tern populations

Because we wanted to improve insights into how populations of the Common Tern within port areas interact with one another and with populations in different port areas, we used a spatially explicit metapopulation model as a tool. The main processes in spatial population dynamics are reproduction, mortality and dispersal. The Wageningen UR METAPHOR model simulates these processes in order to estimate the long-term viability of a population (a metapopulation). METAPHOR calculates effects on metapopulation processes of changes in the configuration of colonies' landscape patterns induced by habitat redesign or management. METAPHOR is an individual-based, spatially explicit model. Each individual is modelled separately in space, time and individual traits. The model can be used to predict population dynamics, estimate survival probabilities and gain a deeper understanding of ecological systems.

Typical METAPHOR input consists of the following:

- i) habitat suitability map,
- ii) estimates of life-history parameters (birth rate, mortality rate, dispersal characteristics),
- iii) estimates of carrying capacity (or average potential density) of habitat units.

Habitat suitability map

Common Tern habitat consists of sites suitable for breeding colonies and water rich in fish located within a maximum of five to ten kilometres from these sites. We derived a habitat suitability map from the Common Tern distribution data, assuming that each location where the bird species was observed breeding in recent years can be considered a habitat patch. As such, the input map is more a map of the actual and former distribution of the bird species than a habitat map created from the biotope characteristics of the study area. This was done because our pilot project offered limited opportunity to gather detailed biotope maps and interpret these maps into habitat maps for the different species. However, as the maps used in this study show the locations where the bird species was actually observed breeding, they could be more accurate than habitat maps based on potential habitat opportunities. To keep the model study simple, we used only the 45 largest bird breeding locations, which together accommodated more than 95% of the Dutch-Belgian delta metapopulation, calculated over the 1991-2005 period.

As we wanted not only to model the spatial population dynamics of the current Common Tern populations, but also to gain insight into the role of port areas in offering new breeding habitats, we created several future scenario maps. Details of the scenarios are provided in section 2.5.

Life-history parameters

METAPHOR requires data and estimates on various aspects of the life history of the species:

- aging (the period in which young birds grow into adulthood),
- dispersion (the chance that birds will leave their breeding site in search of new habitat, as well as the maximum and average distances they typically travel in these cases),
- survival (the chance of the birds surviving from one year to the next),
- reproduction (number of young per pair of birds),
- age (average age as well as maximum age).

We collected these parameters from the literature and the expert interviews. Annex I illustrates how we used the life-history data for the Common Tern in the model study.

Carrying capacity

The Common Tern distribution data provided by the RIKZ (Netherlands) and INBO (Belgium) not only provided insights into the population trends in past decades, but also showed the capacity the different breeding locations could offer. We used the maximum number of birds observed at each of the 45 selected locations as an indication of the carrying capacity of these locations. Furthermore, the bird breeding data was used to indicate the presence or absence of patterns at each location, and the initial number of birds that first colonized the location. Annex II lists this data by location.

In a natural system, new breeding sites rapidly improve in quality to reach a maximum within two or three years. After the first years, without flooding or other natural disturbance, the plant succession gets under way and the quality of the terrain for breeding declines. With vegetation development, populations of mice, insects and predators grow. As a consequence, within five to ten years breeding success drops and the birds abandon the site to establish a new colony at a fresh location, if possible, in the vicinity of the same feeding grounds. In highly dynamic saltwater systems this process goes slowly and is often stopped by flooding or erosion and then started anew. In freshwater systems with little influence of such dynamics, succession is rapid. While nature management can slow this speed and mimic natural processes, it can never replace the natural system. In every system breeding sites appear and disappear. This is represented by the data on the chance of a site losing or gaining carrying capacity (Annex II).

Results

The main result of analysis with METAPHOR is the viability of a metapopulation, as a probability of surviving for a certain period of time (e.g. 100 years). More interesting results are obtained by comparing outcomes of several METAPHOR simulations. Sensitivity analysis is performed by varying life-history parameters, and can reveal the most important parameters for managing population

processes. In scenario studies the landscape is changed. Scenario studies can show the effects of enlarging and connecting habitat patches or enhancing habitat quality.

2.5 Spatial scenarios for current and future habitat patterns



Natural breeding site in salt marsh vegetation (photo: P. Steerenberg).

The case of *Sterneneiland* ('Tern Island') in the Port of Zeebrugge (Belgium) shows that the creation of artificial breeding habitats near existing populations can be successful. In 2004, 1,832 Common Terns, 138 Little Terns (*Sterna albifrons*, in French *Sterne naine* and in Dutch *Dwergstern*) and 4,067 Sandwich Terns (*Sterna sandvicensis*, French *Sterne caugek*, Dutch *Grote Stern*) were observed breeding on this island. Part of this population presumably originated from an existing location in the Port of Zeebrugge. This experiment provided new insights into the role that human-made habitats could play in the protection of endangered coastal birds, especially in areas like ports, where the Common Tern's nesting behaviour might conflict with e.g. port development.

Although we know from other cases that offering alternative breeding sites for the Common Tern is not always successful, in this pilot study we explored how the location and size of extra habitat could affect the overall population dynamics of the Common Tern. In doing so, we looked at the metapopulation level, since colonization, extinction and the tern's overall viability act at this level. Furthermore, we assumed that other conditions, like the management of the site, were optimal (as they are outside the scope of this study). On this basis, we defined a series of spatial scenarios that enabled us to explore future opportunities to deal with Common Tern populations in port areas.

The scenarios were designed as follows:

- 0) basic,
- 1) basic without ports (see question 2),
- 2) basic with local replacement of habitats in port areas (see question 3),
- 3) basic with extra habitats in the vicinity instead of replacement within the port area (see question 4),
- 4) basic with extra habitats at the centre of the metapopulation network instead of replacement within port areas (see question 5 earlier).

We selected seven port area breeding locations to explore the role of ports as breeding habitats for Common Terns (Table 1). These locations represent areas of major economic activity in the port as well as key breeding locations for the Common Tern.

Table 1. Selected port area breeding locations and their carrying capacity in the scenarios. Carrying capacity of the current situation was derived from the numbers of breeding pairs observed in the 1991-2005 period. For the other scenarios, numbers were ESTIMATED based on expert knowledge (e.g. outside port areas there could be more breeding place).

Port Area	Carrying Capacities of Port Breeding Areas, Scenarios 0-4				
	Nr. 0	Nr. 1	Nr. 2	Nr. 3	Nr. 4
Ostend, Achterhaven	68	0	68	2000	2000
Antwerp	208	0	208	500	500
Oostvoorne, Europoort	930	0	930	0	0
Oostvoorne, Shell-grounds	775	0	775	1000	1000
Oostvoorne, Maasvlakte	1150	0	1150	2000	2000
Zeebrugge, Sterneneiland	3100	0	1500	2000	2000
Zeebrugge, Westdam		0	1600	2000	2000

We ran the five scenarios, with 100 runs for each to obtain insight into variations in the model outcome per scenario. For the scenario based on the present situation (0) we used the actual data as collected by the RIKZ and INBO (see acknowledgements and Annex II). For the alternative scenarios we varied only the carrying capacity and location of the seven selected port locations, as indicated in Table 1. The situation at the other 38 locations was taken as the same for all scenarios.

Scenario 0

The baseline scenario (0) is based on the present situation (only the larger breeding sites are included in this scenario). Data is provided in Annex II.

Scenario 1

In the first alternative scenario (1) we assumed that all habitats in the ports had been lost (see zero values in Table 1). This result gives us an appreciation of the importance of the port locations for the network population.

Scenario 2

In the second alternative scenario (2), we replaced the lost habitats primarily within the port itself. This is – from an ecological point of view – not an optimal solution, but in this way the relation between habitat loss and replacement is most clear. The carrying capacity of these in-port locations was kept the same as the original port habitats. In the case of Zeebrugge the replacement of the ‘Tern Island’ habitat was divided over two locations, together having a similar carrying capacity to that of ‘Tern Island’ in the basic scenario (0). This was also done in scenarios 3 and 4.

Scenario 3

The vicinity of port areas often provides better locations for breeding sites than the port areas themselves, as space is available for larger breeding sites, and birds can reach feeding grounds more easily. To test whether the exact location of the replacement site is important we explored three versions of this scenario. Furthermore, we enlarged the carrying capacity of the replacement sites compared to the basic scenario (0). Numbers were estimated based on the more suitable locations found outside of the port areas for the Common Tern. Because the Port of Antwerp is not located near the coast (which is the optimal habitat for the Common Tern), the carrying capacity there was set lower than for the other replacement sites.

Scenario 4

For the last scenario (4) we located the replacement site for each port habitat at the centre of the study area, as this would theoretically be the best option to strengthen metapopulations (Pulliam 1988, Wiens 1989). So, whereas the carrying capacity of the sites was the same as in the previous scenario, the replacement sites were moved away from the port area to suitable places at the heart of the Common Tern metapopulation (the Dutch Province of Zeeland). This enabled us to explore the impact of the location of the replacement site.



Reproductive success (photo: P. Steerenberg).

3 Results

3.1 The dynamics of Common Tern populations

According to the RIKZ and INBO data, Common Terns were observed breeding at 162 locations in the Dutch-Belgian delta region during the 1991-2005 period. Most of those locations show large fluctuations in the number of breeding pairs over the years, as illustrated in Figure 6.

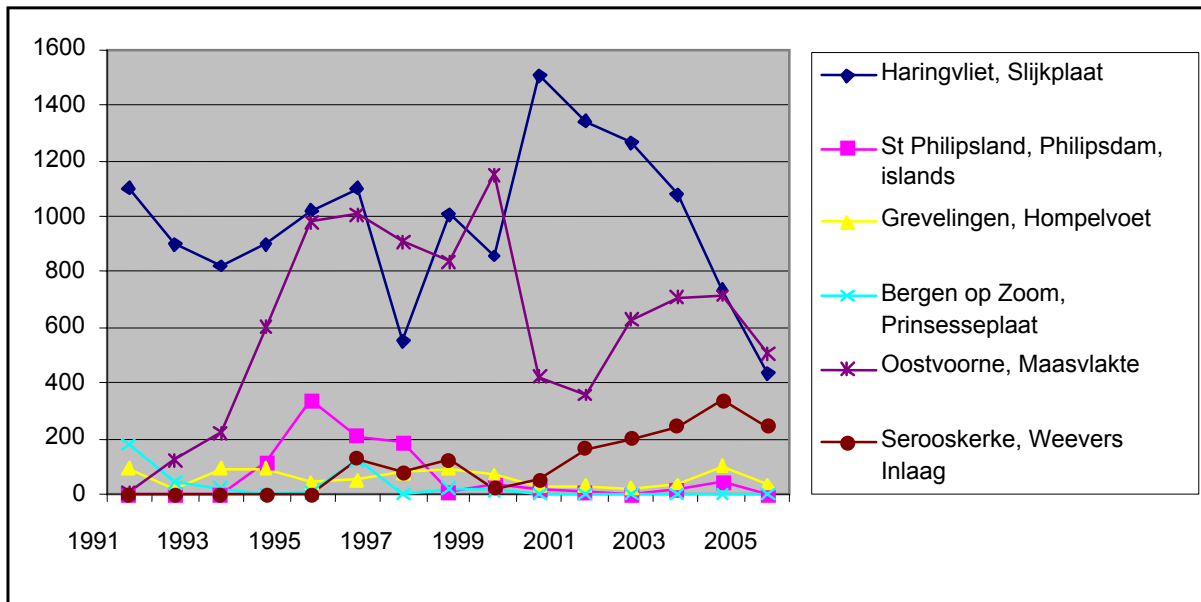


Figure 6. Some examples of local common tern populations. Note the large fluctuations in many of the 162 (former) populations within the delta region. The y-axis shows breeding pair numbers per location.

In some cases, local populations of Common Terns appeared to have moved among different neighbouring locations, as was the case in the mid-1990s in the Port of Rotterdam (Figure 7).

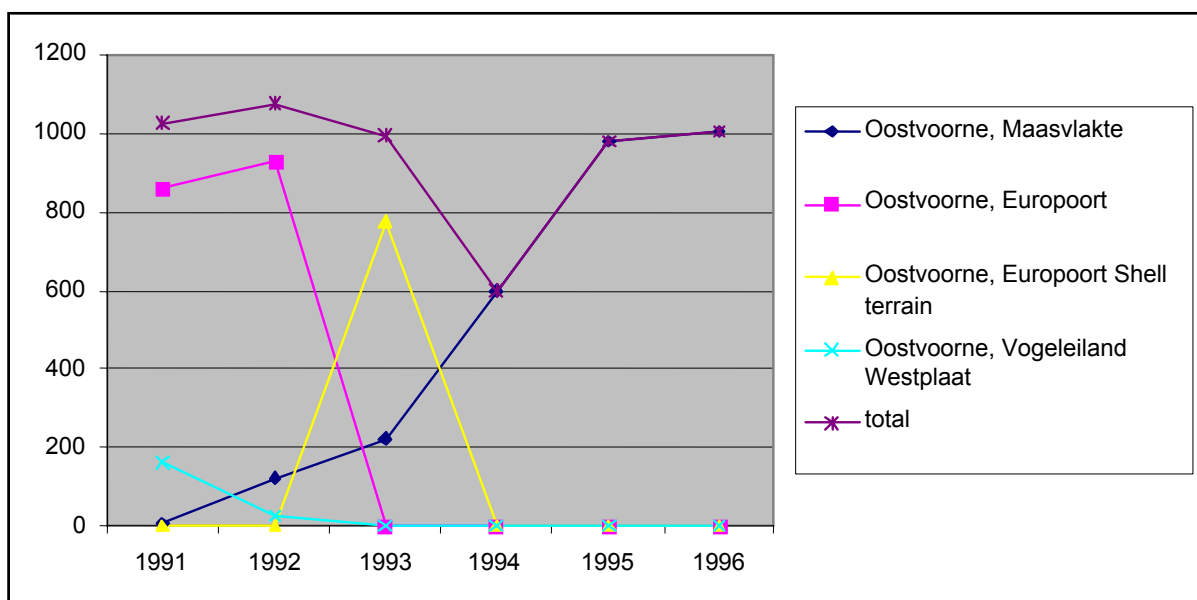


Figure 7. Breeding pair numbers of Common Terns nesting at different locations in the Port of Rotterdam. Common Terns appear to have shifted their breeding habitat location over the years.

Overall, despite the large fluctuations in local populations, the total delta metapopulation can be considered quite stable, with the total number of Common Terns varying between 5,000 and 10,000 breeding pairs between 1991 and 2005 (Figure 8).

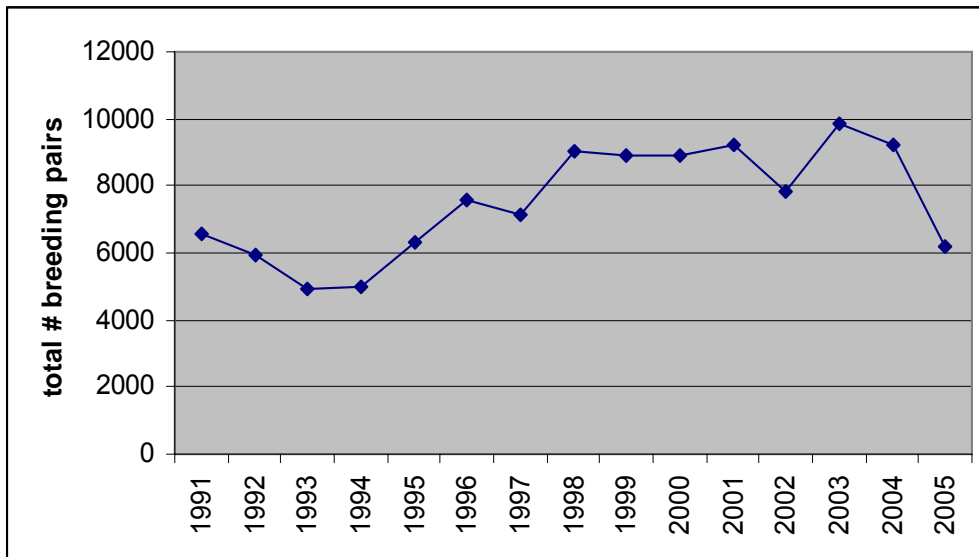


Figure 8. Total number of Common Tern breeding pairs in the delta region (Netherlands and Belgium).

It is worth mentioning that a small set of just 10 locations (see Annex II) accommodated more than 72% of the total Dutch-Belgian delta population (with 544 individuals per location on average), whereas 100 other locations accommodated less than 10 individuals per year. The metapopulation can therefore be described as a network of a few large and stable populations surrounded by many small and unstable populations.



Hunting fish for the youngsters in the colony (photo: Bart Vannieuwenhuyse).

3.2 The role of port areas as Common Tern breeding habitat

From the RIKZ and INBO data we learned that in the 1991-2005 period the proportion of the delta metapopulation of Common Terns nesting in port areas increased from 25% to 40% (Figure 9). This is explained largely by the fact that natural sites are rare in the delta at present, and birds depend mainly on semi-natural sites created by human activities like waterworks and the development of new port areas. Most remaining natural sites, such as beaches, are too disturbed by recreation to provide homes to bird colonies. Port areas have therefore become increasingly important breeding sites for the Common Tern.

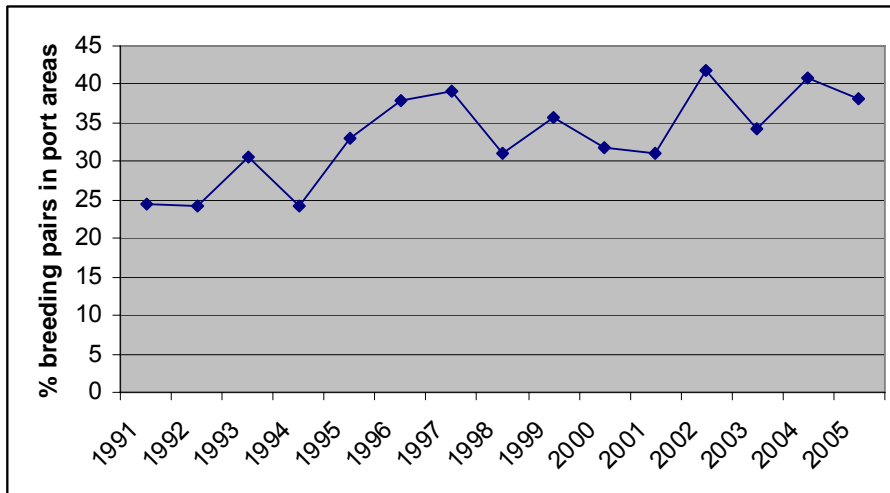


Figure 9. Proportion of Common Tern breeding pairs nesting in port areas.



An almost full-grown member of the colony (photo: Bart Vannieuwenhuysse).

3.3 Simulation of the current population dynamics of the Common Tern

The METAPHOR model and the inputs described in Annexes I and II enabled us to simulate the current population dynamics of the Common Tern in the delta region. Results of model runs with scenario 0 (basic) showed trends similar to the actual situation observed in the 1991-2005 period (Figure 10).

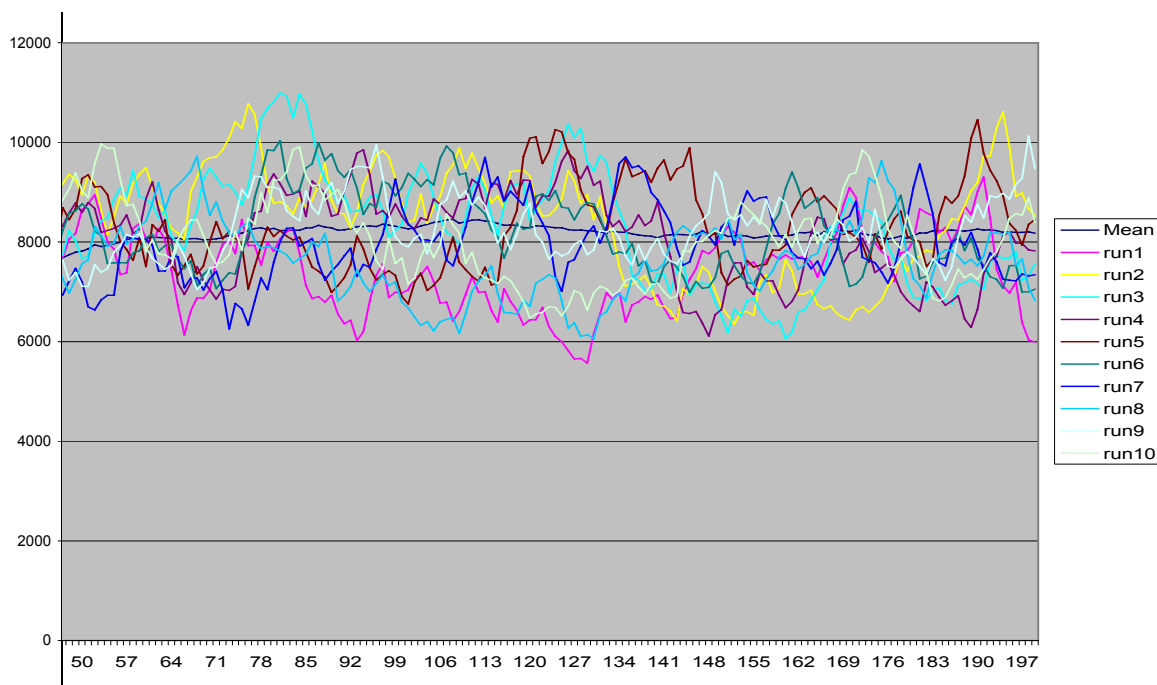


Figure 10. METAPHOR model results for scenario 0 (basic), illustrating the number of Common Tern breeding pairs for different runs. Numbers for the total metapopulation increased from the initial 4,223 (see Annex II) to an average of 8,000 breeding pairs, with fluctuations between 6,000 and 10,000, similar to the real situation.

At the level of individual local populations the model results also show fluctuations similar to those observed in real colonies.

3.4 Exploration of future developments in Common Tern populations

Using the model adjustments made for the current situation, we ran the model for the four alternative scenarios.

Scenario 1: delta metapopulation without port habitats

The network without port colonies appeared to be sustainable. It never went extinct, although the population size reached a minimum level of as few as 2,500 pairs. The overall population fluctuated between some 3,000 and 8,000 pairs, with an average level of some 5,000 pairs. The drop in the average size – compared to scenario 0, the current situation – is as large as the maximum number of pairs in all of the port habitats together, which is relatively high. If we had left out all of the non-natural breeding sites (including e.g. the habitats in the Port of Terneuzen) the situation would have been even worse with extinction possible.

Scenario 2: port habitats replaced within the same port area

Replacement sites for lost port habitats that were located within the port itself provided about the same metapopulation level as in the present network (scenario 0). This is what we expected, as for the network as a whole it does not matter where exactly in the vicinity of lost habitats the replacement becomes available.

Scenario 3: port habitats replaced in the vicinity of the port area

This scenario tested the impact on the Common Tern metapopulation of suitable replacement sites being provided outside of the port areas. It appeared that in the METAPHOR model the exact location of the replacement sites had no influence on the metapopulation, as for each port habitat three alternative external port-replacement sites were used in the model and this resulted in no differences. But of course when a new location is planned, research is needed on the local (abiotic and biotic) situation.

However, in contrast with the other scenarios, this scenario did not result in a stable metapopulation size after an initial period (Figure 11). A probable explanation could be that we assumed that dispersing birds prefer moving to existing colonies. This raises questions about how fast sites directly outside of a port area could function as replacements for inner-port losses.

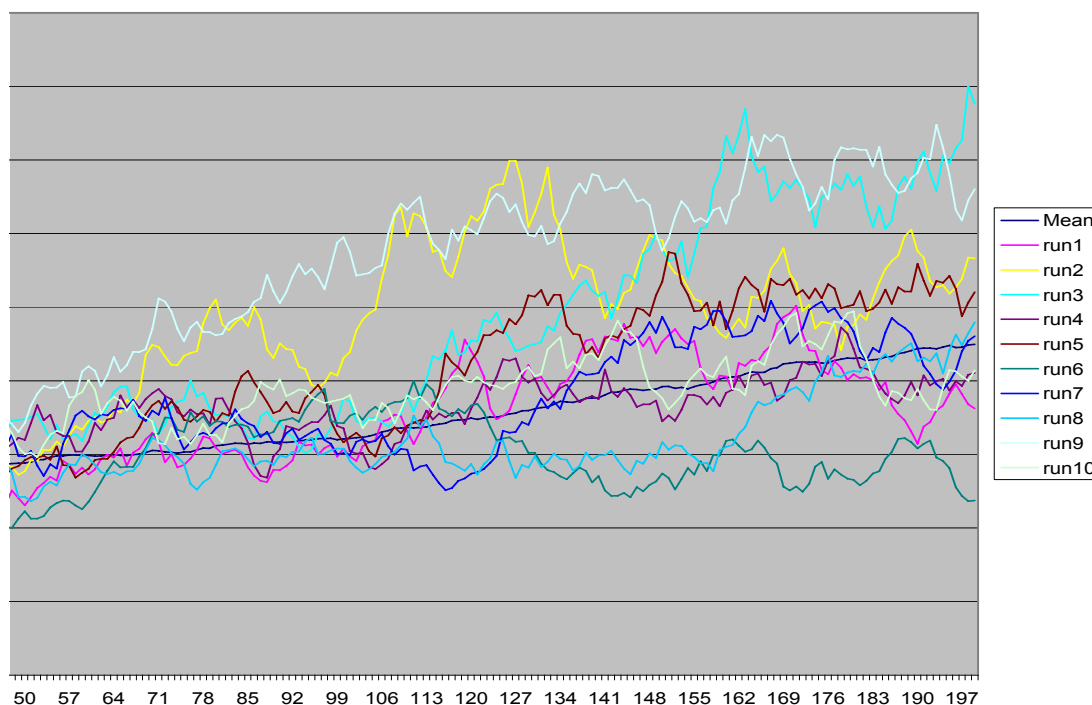


Figure 11. METAPHOR model results for scenario 3, illustrating the number of Common Tern breeding pairs for different runs. Numbers for the total metapopulation appeared to remain unstable after an initial period.

Scenario 4: port habitats replaced at the centre of the Common Tern metapopulation

When replacement sites were located at the centre of the Common Tern metapopulation, the overall population fluctuated between some 6,000 and 16,000 pairs, with an average level of some 10,000 pairs. This is better than the basic situation (scenario 0) and also provided a relatively stable metapopulation level. Such a measure would thus appear to be effective at the metapopulation level, but would also imply that habitat sites outside the centre would be less frequently used by Common Terns.

We calculated the trends for the different scenarios as the average model results (Table 2).

Table 2. Trends for the different scenarios, calculated for each scenario as the average of the model results.

Scenario	Average	Minimum	Maximum
0 – basic	8200	5300	11500
1 – basic without ports	5200	2400	8300
2 – basic with local replacement of habitats in port areas	7900	4750	11400
3 – basic with extra habitats in the vicinity (instead of replacement in the ports)	7500	5000	16000
4 – basic with extra habitats at centre of network (instead of replacement in the ports)	9800	6200	15900

4 Discussion and conclusion

From our pilot study, it appears plausible that for a coastal bird species like the Common Tern the dynamics of the delta population can be adequately described by a spatially explicit metapopulation model (like METAPHOR). Processes simulated in the model, like reproduction, mortality, colonization and extinction, resulted in population fluctuations at the local and metapopulation level similar to those observed in the wild. Nevertheless, more data on life history and habitat suitability is needed to make the model sufficiently accurate that its results can be directly applied to real cases.

Although our model study was a pilot study, it nonetheless provides initial insights on the potential impacts of local habitat losses and habitat replacements on the size and distribution of the Common Tern metapopulation. We explored this idea for port areas in particular, because – derelict land and flat roofs within these areas have unintentionally become more and more popular as breeding sites for coastal birds.

Model results indicate that if the breeding sites located in port areas were lost, the size of the delta metapopulation of Common Terns would decline to a low level, however, without leading to overall extinction. If, to replace the lost habitats, additional habitat patches were created within the port area as alternative breeding sites, loss of the current sites would lead to only a small decrease of the delta metapopulation. However, if those additional habitats were developed outside of the port area, where there is more space for nesting birds, the end-result might be positive instead of neutral or negative with respect to the size of the metapopulation.

Furthermore, our model results suggest that the exact location of the replacement site is unimportant, as long as the sites are located in or near the port area. If replacement sites, however, were situated at the centre of the metapopulation, we found an increased impact on metapopulation size. This suggests that a ‘coastal bird-friendly’ arrangement and management of nesting sites at the centre of the metapopulation would make the best contribution to the sustainability of the Common Tern populations in the delta region.

How reliable is the model?

A good model is a simplified mathematical representation of current knowledge in which relations are established at a lower level to explain dynamics at a higher level. With this model, we integrate ecological knowledge of the Common Tern to explain dynamics at the metapopulation level.

Although this a preliminary study, we based our model on the RIKZ report by Schröder *et al.* (1996) which describes a non-spatially explicit model for the Common Tern. Our model takes into account the fact that the bird favours proximity to other nests (Dittmann *et al.* 2005). Furthermore, we included environmental and demographic stochastic processes. As mentioned in the literature (e.g. Van der Hoorn 1997) the dispersal between patches was parameterized in a conservative way, with animals always returning to their old population unless it is seriously overcrowded. This means that the simulated animal behaviour in the model will at least roughly mimic the actual behaviour of the Common Tern.

Another way to judge the value of the model is to evaluate whether the model’s output is realistic given the fact that the input is realistic. Figure 10 shows an average level of 8,000 animals in scenario 0 (basic), which matches the actual levels measured, as depicted in Figure 8, indicating that our model performs well in the realism test. Furthermore, our model was previously used to evaluate the effects of landscape configuration on bird metapopulation dynamics, in a study that resulted in papers published in highly respected scientific journals (e.g. Vos *et al.* 2001, Verboom *et al.* 2001).

In conclusion, our model represents a widely accepted scientific approach that was parameterized at least close to the Common Tern’s ecology, giving realistic results in the scenario that we can test, meaning that our results should be taken seriously. Altogether we think that this pilot study illustrates the added value that a metapopulation approach can have in discussions about the presence of protected coastal bird species in and around port areas. In the near future we will carry out research to further develop this approach, to support the quest for sustainable ways to achieve the dual objectives of bird conservation and economic development in coastal areas. Concerning our model, it was developed to explore opportunities to simulate the population dynamics of coastal bird species,

especially the Common Tern. Although the results concerning scenario 0 are comparable to the real situation as observed in the 1991-2005 period, further adjustments are needed if the model is to be used as a tool for more detailed analysis. Sensitivity analysis should reveal which input values and standards require further investigation as well as the reliability of the model results at a lower scale level.

Finally, we would like to underline the fact that this pilot study (only) provides an instrument for (political) debate on responsibilities for maintaining favourable conservation conditions for the Common Tern, but as such does not interfere in this debate.

Annex I – METAPHOR Common Tern parameterization

Survival (from Schröder et al. 1996)

Adult survival $S_a = 0.84$ (range 0.8-0.9) First year survival $S_j = 0.61$ (is included in the recruitment, R_e).

Juvenile to adult transition (aging) (from Schröder et al. 1996)

- 1) first year juvenile -> adult: probability ($P_{ja} = 0$)
- 2) second year juvenile -> adult: probability ($P_{ja} = 0$)
- 3) third year juvenile -> adult: probability ($P_{ja} = 0.5$)
- 4) fourth year juvenile -> adult: probability ($P_{ja} = 0.5$)
- 5) fifth year juvenile -> adult: probability ($P_{ja} = 1.0$)

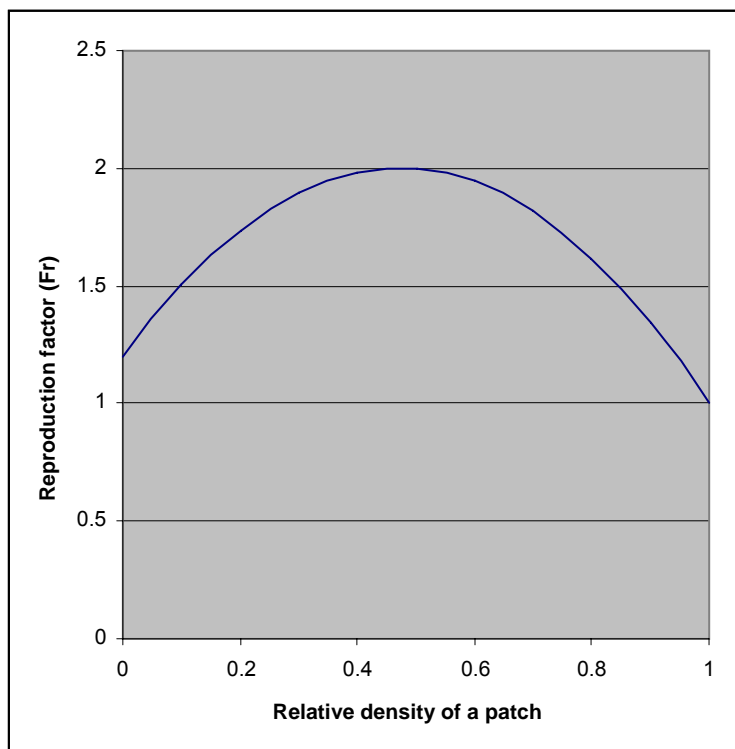
Density-dependent reproduction

The reproductive success of this species appears to be best at intermediate density since birds prefer company for nesting. Furthermore, we assume zero growth at carrying capacity. Density dependence seems to be the main factor affecting recruitment because large differences in nesting success were reported in the literature. We therefore expect density-dependent reproduction to be the main factor in density regulation. To obtain maximum population growth at intermediate densities we introduced a factor affecting recruitment (F_r) that is dependent on the proportional density.

$$R_d = R_e F_r$$

$$F_r = (-3.6D^2 + 3.4D + 1.2)$$

$R_e = 0.18$ juvenile females per female is the recruitment at carrying capacity at which the growth is about zero. This value is of the same order as the value 0.14 used by Schröder *et al.* (1996). D is the proportional density = number of females/carrying capacity of females. F_r is a parabolic function having a value of 1.2 at $D = 0$, having a maximum of 2 at $D = 0.5$ and having a value of 1 at $D = 1 =$ carrying capacity.

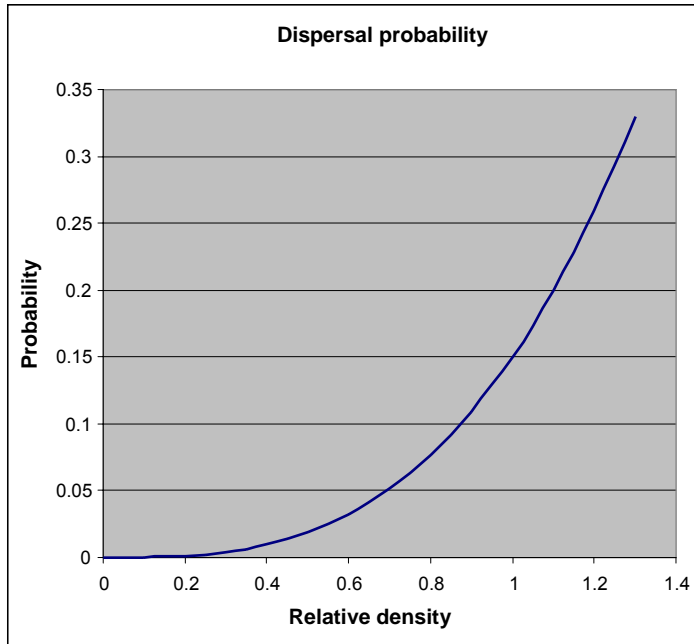


Dispersal: probability to disperse

The probability to reproduce per individual approaches zero at close to carrying capacity. This means that it is profitable for an individual to leave the patch in search of a patch with a lower density. We indicate this in the model with a density-dependent dispersal function, in which the probability to leave a patch (P_{leave}) increases with the density:

$$P_{leave} = 0.15 \cdot D^3$$

Here D = density (number of females older than one year/carrying capacity).



Dispersal: interpatch relations

Both juveniles and adults appeared to be attached to their old habitat patch (Van der Hoorn 1997), meaning that they move only when necessary; for instance, when a patch is full or is flooded. In such cases we assume that an individual disperses according to the following probability function:

$$P_{i \rightarrow j} = \frac{F_{dj} \cdot C \cdot \exp(-\alpha \cdot d_{ij})}{\sum_{j=1}^n F_{dj} \cdot C \cdot \exp(-\alpha \cdot d_{ij})}$$

Here F_d is a factor that determines the quality of the receiving population j . C is carrying capacity (females/population), d_{ij} is the distance between patch i and j , α = a parameter that determines the decrease in connectivity over the distance.

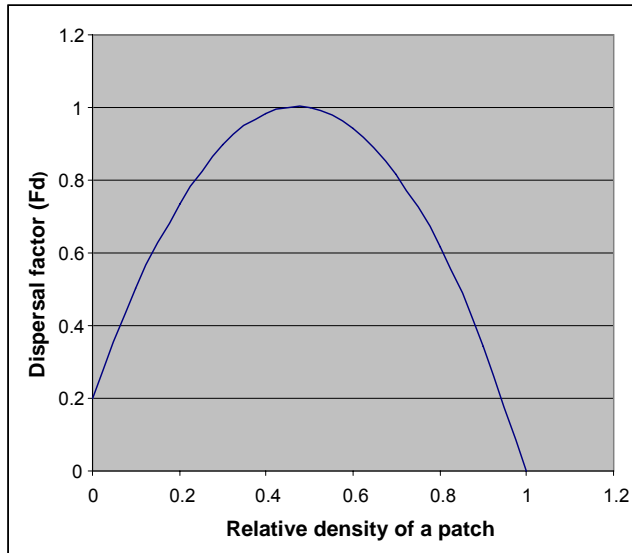
F_d is defined analogously to F_r , which means that species have a lower probability of going to a population that is lower in quality. We assumed that the attraction of a population is a function of its proportional density.

$$F_r = (-3.6D^2 + 3.4D + 0.2)$$

F_d is a parabolic function having a value of 0.2 at $D = 0$, making it possible for a population to start, having a maximum of 1 at $D = 0.5$ and having a value of 0 at $D = 1$ = carrying capacity. Note that populations reaching carrying capacity do not receive dispersing animals.

The parameter $\alpha = 0.6931 \cdot 10^{-4}$ and (d_{ij} in m) means that the same population at 20 km receives half the number of animals compared to a population at 10 km distance and a population at 30 km receives half the number of a population at 20 km, so a quarter compared to 10 and so on.

Three dispersal rounds are allowed; and before every dispersal round the dispersal matrix is recalculated.



Dispersal: probability to settle

When an individual arrives at a new patch it must decide whether to settle or continue to search for a new patch. It appears that these birds like to have some company before they settle. Therefore, we introduced a start-up threshold of 30 animals. This means that after each dispersal event (three per year) the number of arriving individuals is counted. If the sum is larger than a critical value (30 females) the birds all settle. If the number is lower the birds continue their search in the next dispersal event. After three events, however, the birds stay and breed in the new patch, even if means that the same population at 20 km receives half the number of animals compared to a population at 10 km distance and a population at 30 km receives half the number of a population at 20 km, so a quarter compared to 10 and so on.

Three dispersal rounds are allowed; and before every the number is lower than the critical value. Next year these animals will stay, even if their number is below the critical value.

Patch suitability

The birds like to breed in patches which offer them a good overview of their surroundings. To accomplish this, most patches need a disturbance event to reset the vegetation succession (e.g. flooding). Yet such an event makes the patch temporarily unsuitable, meaning the resident birds must settle in other patches.

The probability of a suitable patch being transformed into an unsuitable patch ($P_{s \rightarrow u}$) is shown in the (pres \rightarrow abs) column (ON_OFF) of Annex II. The probability that a certain patch recovers ($P_{u \rightarrow s}$) is shown in Annex II the abs \rightarrow pres column (OFF_ON).

Annex II – Carrying capacity of Common Tern breeding locations

PATCH_ID	LOCATION	X	Y	CC	ON_OFF	OFF_ON	INIT_NR	INIT_ON
1	Bergen op Zoom, Prinsesseplaat	74755	391537	176	0.43	0.29	176	1
2	Den Bommel, Ventjagersplaten	83329	415000	193	0.10	0.13	0	0
3	Dinteloord, Dintelse Gorzen, islands	79090	406425	133	0.17	0.40	0	0
4	Grevelingen, Hompelvoet	54647	422424	100	0.01	0.99	90	1
5	Grevelingen, Kabbelaarsbank	50314	419384	201	0.10	0.50	1	1
6	Grevelingen, Markenje	56620	424451	233	0.08	0.99	55	1
7	Grevelingen, Stampersplaten	56305	418385	173	0.08	0.99	25	1
8	Haamstede, Koudekerkse Inlagen	43368	411882	163	0.40	0.40	130	1
9	Haringvliet, Slijkplaat	69555	424317	1504	0.05	0.99	1100	1
10	Hellevoetsluis, Quackgors, islands	67145	427264	287	0.25	0.10	0	0
11	Markiezaat, Spuitkop	76574	386342	150	0.25	0.33	110	1
12	Melissant, Slikken van Flakkee Zanddepot	61545	420463	154	0.17	0.50	57	1
13	Melissant, Slikken van Flakkee Zuid	61930	418153	88	0.20	0.50	23	1
14	Ooltgensplaat, Hellegatsplaten, islands	84354	412006	247	0.22	0.60	0	0
15	Oude-Tonge, Krammersche Slikken Oost, islands	73772	408829	293	0.25	0.05	10	1
16	Oude-Tonge, Nieuwkoopers islands	72146	410543	408	0.40	0.22	0	0
17	Oud-Sabbinge, Middelpaten	41175	396177	176	0.01	0.99	176	1
18	Ouwerkerk, Ouwerkerkse Inlagen	57221	403974	110	0.57	0.43	64	1
19	Serooskerke, Flaauwers Inlaag	48400	411300	226	0.10	0.14	0	0
20	Serooskerke, Flaauwers-Weevers Inlagen/Prunje	48245	411892	157	0.20	0.10	50	1
21	Serooskerke, Prunje Noord	47645	413333	387	0.10	0.10	0	0
22	Serooskerke, Schelphoek, outside the dykes	45507	412741	128	0.10	0.13	0	0
23	Serooskerke, Weevers Inlaag	47361	411702	339	0.10	0.11	0	0
24	St Maartensdijk, De Pluimpot	63861	394919	143	0.08	0.99	140	1
25	St Philipsland, Philipsdam, islands	72528	407493	338	0.20	0.50	0	0
26	St Philipsland, Plaat van de Vliet, islands	71873	408506	105	0.22	0.60	0	0
27	Stellendam, Scheelhoek, islands	63770	425870	1621	0.10	0.17	0	0
28	Terneuzen, DOW Nieuw Neuzenpolder II	40468	373992	90	0.33	0.40	90	1
29	Terneuzen, locks	45470	373143	289	0.01	0.99	146	1
30	Tholen, Karrevelden Schakerloopolder	70633	392904	133	0.09	0.33	2	1
31	Verdronken land van Saeftinge	70205	374212	869	0.01	0.99	522	1
32	Volkerakmeer, Noordplaat	75581	406918	341	0.50	0.05	250	1
33	Westerschelde, Hooge Platen	31963	379529	1350	0.01	0.99	775	1
34	Wissenkerke, Inlaag 's-Gravenhoek	44071	402522	307	0.01	0.99	80	1
35	Zierikzee, Cauwers Inlaag en Karrevelden	51364	407895	326	0.20	0.75	0	0
36	Zierikzee, Zuidhoekinlaag West	52171	405990	79	0.25	0.50	2	1
37	Zonnemaire, Slikken van Bommenede	57640	415907	57	0.01	0.99	14	1
38	Zoommeer, Boereplaat	73664	391655	278	0.50	0.08	0	0
39	Zwin (BE)	14000	377000	135	0.18	0.33	135	1
Port areas								
340	zzOstend, Achterhaven (BE)	-13000	361000	68	0.17	0.50	55	1
341	zzAntwerpen linkeroever (BE)	76500	368500	208	0.08	0.25	30	1
342	zzOostvoorne, Europoort	65993	441001	930	0.50	0.05	859	1
343	zzOostvoorne, Europoort Shell-terrein	69486	440597	775	0.95	0.08	0	0
344	zzOostvoorne, Maasvlakte	63087	440627	1150	0.07	0.93	4	1
345	zzZeebrugge incl. Sterneneiland (BE)	1900	374200	3100	0.05	0.99	650	1
				18718			5821	
	45 patches							

Explanation of column headings:

X and Y	Coordinates expressed in the Dutch Amersfoort-coordinate standards.
CC	Carrying capacity of the location for breeding pairs of the Common Tern, calculated from the maximum number of breeding pairs observed in the 1991-2005 period.
ON/OFF	The chance that an occupied habitat location will be left empty by Common Terns a year later, calculated from the presence and absence of Common Terns at each location in the 1991-2005 period.
OFF/ON	The chance that an empty habitat location will be occupied by Common Terns a year later, calculated from the presence and absence of Common Terns at each location in the 1991-2005 period.
INIT.NR	The initial number of breeding pairs that can be found at each location, similar to the number of breeding pairs in 1991.
INIT.ON	Indication of whether the location was occupied in the first year, derived from the presence of Common Terns at each location in the year 1991.

References

- Bijlsma, R.G., F. Hustings & C.J. Camphuysen. 2001. Avifauna van Nederland 2; Algemene en schaarse vogels van Nederland. GMB Uitgeverij/KNNV Uitgeverij, Haarlem/Utrecht.
- Dittmann, T., D. Zinsmeister & P. H. Becker. 2005. Dispersal decisions: common terns, *Sterna hirundo*, choose between colonies during prospecting. *Animal Behaviour* 70: 13-20.
- Hanski, I. & M. Gilpin. 1991. Metapopulation dynamics - brief history and conceptual domain. *Biological Journal of the Linnean Society* 42: 3-16.
- Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* 42: 73-88.
- Hoorn, B. van der. 1997. A contribution to the population dynamics of the Common Tern (*Sterna hirundo*) in the Netherlands. RIKZ/OS-97.815X. RIKZ & Vakgroep Systematiek, Evolutie & Paleobiologie, Universiteit van Amsterdam. Middelburg/Amsterdam.
- Levins, R. 1970. Extinction. In: M. Gerstenhauber (ed.). Some mathematical questions in biology (Vol. 2). American Mathematical Society, Providence: 77-107.
- Meininger, P.L. & J. Graveland. 2002. Leidraad ecologische herstelwerkzaamheden voor kustbroedvogels; Balanceren tussen natuurlijke processen en ingrijpen. RIKZ-rapport 2001. Rijksinstituut voor Kust en Zee, Middelburg. 51 p.
- Newton, I. 1998. Population limitation in birds. Academic Press Limited, London.
- Opdam, P. 1991. Metapopulation theory and habitat fragmentation: a review of holartic breeding bird studies. *Landscape Ecology* 5: 93-106.
- Pulliam, H.R. 1988. Sources, sinks and population regulation. *The American Naturalist* 132: 652-661.
- Schröder, S.E., J.H.M. Schobben & P.L. Meininger. 1996. Een populatiemodel voor de Visdief *Sterna hirundo*, RIKZ -96.021. RIKZ, Den Haag.
- Stienen, E.W.M. & A. Brenninkmeijer. 1992. Ecologisch profiel van de visdief (*Sterna hirundo*). RIN-rapport 92/18. DLO-Instituut voor Bos-en Natuuronderzoek, Arnhem.
- Stienen, E.W.M., W. Courtens, M. van de Walle, J. van Waeyenberge & E. Kuijken. 2005. Harboured nature: port development and dynamic birds provide clues for conservation. In: Herrier J.-L., J. Mees, A. Salman, J. Seys, H. Van Nieuwenhuysse & I. Dobbelaere (eds). Proceedings 'Dunes and Estuaries 2005' – International Conference on Nature Restoration Practices in European Coastal Habitats, Koksijde, Belgium, 19-23 September 2005, p. 381-392.
- Vos, C.C., J. Verboom, P.F.M. Opdam & C.J.F. ter Braak. 2001. Toward ecologically scaled landscape indices. *American Naturalist* 157(1): 24-41.
- Verboom, J., R.P.B. Foppen, J.P. Chardon, P.F.M. Opdam & P. Luttikhuisen. 2001. Introducing the key patch approach for habitat networks with persistent populations: an example for marshland birds. *Biological Conservation* 100(1): 89-101.
- Wiens, J.A. 1989. The Ecology of Bird Communities. Volume 1 Foundations and patterns. Cambridge University Press, Cambridge.

Other literature

Beijersbergen, R.B. & P.L. Meininger. 1980. De functie van het Deltagebied als broedplaats voor sterns. *Sterna* 24: 79-99.

Brenninkmeijer, A. & E.W.M. Stienen. 1992. Ecologisch profiel van de Grote Stern (*Sterna sandvicensis*). IBN-DLO, Arnhem.

Catry, T., J.A. Ramos, I. Catry, M. Allen-Revez & N. Grade. 2004. Are salinas a suitable alternative breeding habitat for Little Terns *Sterna albifrons*? *Ibis* 146, 247–257.

Dijk, A.J. van, L. Dijkse, F. Hustings, K. Koffijberg, J. Schoppers, W. Teunissen, C. van Turnhout, M.J.T. van der Weide, D. Zoetebier & C. Plate. 2003. Broedvogels in Nederland in 2003. SOVON-monitoringrapport 2005/01. SOVON, Beek-Ubbergen.

Foppen, R.P.B., J.P. Chardon & W. Liefveld 2000. Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. *Conservation Biology* 14: 1881-1892.

Godfried, W.N.M., S. Bouma, M.J.M. Meijer, R.H. Witte, R. Lensink, M.J.M. Poot, J.M. Reitsma & G.C.W. van Beek. 2002. Het belang van de ruimtelijke rangschikking van gebieden voor het voorkomen van soorten in de Noordzee en kustwateren, implicaties voor locatiekeuze en succes van herstelmaatregelen. Bureau Waardenburg, Culemborg.

Hagemeijer, J.M.W. & M.J. Blair. 1997. The EBCC Atlas of European Breeding Birds, their distribution and abundance. T&AD Poyser, London.

Hustings, F., C. Borggreve, C. van Turnhout & J. Thissen. 2004. Basisrapport voor de Rode Lijst Vogels volgens Nederlandse en IUCN-criteria, SOVON onderzoeksrapport 2004/13. SOVON, Beek-Ubbergen.

Kubetzki U. & S. Garthe. 2004. Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. In: *Marine Biology* 143 (1) / July, 2003, Springer, Berlin, Heidelberg.

Lindeboom, H., J.G. van Kessel & L. Berkenbosch. 2005. Gebieden met bijzondere ecologische waarden op het Nederlands Continentaal Plat, Rapport RIKZ/2005.008 / Alterra-rapport nr. 1109.

Marion, L. & J. Le Gentil. 2006 Ecological segregation and population structuring of the Cormorant *Phalacrocorax carbo* in Europe, in relation to the recent introgression of continental and marine subspecies. *Evolutionary Ecology* 20: 193–216, Springer.

Meijninger, P.L. 1987. Samenvatting van ornithologisch onderzoek in het Deltagebied in 1972 t/m 1986 aan de hand van rapportages. Rijkswaterstaat, Middelburg.

Meijninger, P.L. 1989. Populaties van enkele soorten broedvogels in het Deltagebied in 1988 met een samenvatting van tien jaar monitoring 1979-1988. Nota GWAO-89.1007 Rijkswaterstaat, Dienst Getijdewateren, Middelburg.

Meininger, P. L., M. S.J. Hoekstein, S. J. Lilipaly & P. A. Wolf. 2006. Broedsucces van kustbroedvogels in het Deltagebied in 2005. Rapport RIKZ/2006.006, Den Haag.

Meininger P. L. & A.D. Vethaak. 2003. Kustbroedvogels in 'De Slufter': knelpunten en mogelijkheden, Rapport RIKZ/2003.047, Den Haag.

Pouwels, R., M.J.S.M. Reijnen, J.T.R. Kalkhoven & J. Dirksen. 2002. Ecoprofielen voor soortanalyses van ruimtelijke samenhang met LARCH, Alterra-rapport 493, Wageningen.

Pouwels, R. & E.A. van der Grift. 2000. Een vooronderzoek naar de inbreng van natuurmaatregelen in de planvorming en uitvoering van wegenprojecten (LARCH – SNIP/MAAT). Alterra-rapport 073, Wageningen.

Pouwels, R., R. Reijnen, H. Sierdsema, C. van Swaay & H. Houweling. 2002. Voorstel voor verbetering van de habitatmodellering in het kennisstelsel LARCH: van een vaste begroeiingstypenkaart naar een kaartlagensysteem. Alterra-rapport 704, Wageningen.

Rattiste, R. & U. Tartes. 2005. Long-term studies of common gulls (*Larus canus*) in Estonia; Responses to environmental conditions. In: Acta Zoologica Lituanica 15 (2). Institute of Zoology and Botany of the Estonian Agricultural University, Riia 181, Tartu, Estonia.

Schotman, A.G.M. 2002. Onderbouwing en uitbreiding van het kennisstelsel LARCH: dispersievermogen, lokale populatie afstand en duurzaamheid van lokale populaties. Alterra-rapport 213, Wageningen.

Stikvoort E., J. Graveland & R. Eertman. 2002. Leve(n)de Noordrand, pragmatische toekomstvisie voor het ecologische herstel van het estuarium van het Rotterdamse havengebied, RIKZ-rapport RIKZ/2002.32, Den Haag.

Verboom, J., A. Schotman, P. Opdam & J.A.J. Metz. 1991. European nuthatch metapopulations in a fragmented agricultural landscape. *Oikos* 61: 149-156.

Vermeersch, G., A. Anselin & K. Devos. 2005. Bijzondere Broedvogels in Vlaanderen in de periode 1994-2005 Populatietrends en recente status van zeldzame, kolonievormende en exotische broedvogels in Vlaanderen. INBO, [Brussel].

Vos, C.C. & P.F.M. Opdam (eds). 1992. Landscape ecology of a stressed environment. IALE-studies in Landscape Ecology, Vol. 1. Chapman & Hall, London.



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