Chapter 9

Echoes from the field:
towards a causal nexus explaining population fluctuations in European Sandwich Terns

LIVING WITH GULLS

It was long believed that Black-headed Gulls *Larus ridibundus* were a threat to breeding Sandwich Terns *Sterna sandvicensis* because they prey upon tern eggs and small chicks, and rob the fish meant for the tern chicks. Therefore Black-headed Gulls were controlled at major tern colonies in The Netherlands and for many years their numbers were kept at a minimum to protect the terns (*e.g.* Brouwer *et al.* 1950). Midway the twentieth century there was a vivid discussion in Dutch ornithological literature on the impact Black-headed Gulls had on terns (Brouwer *et al.* 1950, Van den Assem 1954, Rooth 1958, 1960, 1965). Veen (1977) dedicated an extensive study to the question why Sandwich Terns often choose to breed together with Black-headed Gulls, which is hard to explain if these gulls have such a negative impact on reproductive success in the terns. From 1966-1972, he studied the predation behaviour of the gulls on Griend, Dutch Wadden Sea. Consistent with earlier studies, Veen found that a significant proportion of Sandwich Tern eggs (14 % of all eggs) and chicks (12%) were lost to predating gulls. He argued that predation had, however, no overall impact on the reproductive output of the terns because the gulls mainly took non-viable eggs and chicks. He concluded that the anti-predator function of neighbouring Black-headed Gulls (the gulls form a buffer against intruders and chase away predators) outweigh the disadvantages of the losses of eggs and chicks. The study of Veen led to a change in the attitude towards Black-headed Gulls, resulting in a halt in the management programme to control them in Dutch colonies.

My work was designed to carry on these studies at the same colony with a focus on events throughout the chick phase. Especially during brooding and during the onset of chick rearing, Black-headed Gulls offer protection to the non-aggressive terns, but as the tern chicks grow and become less prone to be caught by predators the need for protection decreases. At the same time, Sandwich Terns experience increasing disadvantages of the breeding association with Black-headed Gulls. With the aging of the tern chicks, a number of gulls develop into specialised robbers of fish meant for the tern chicks. They exert a growing pressure on prey-carrying adults causing prey delivery time to increase (chapter 5) and resulting in an increasing rate of food loss (chapter 3). Two weeks after hatching, about 25% of all prey offered to Sandwich Tern chicks on Griend was robbed and another 9% was lost outside the observer's view mainly when Black-headed Gulls were chasing after a prey-carrying tern parent. During the first two weeks post-hatching, food piracy by Black-headed Gulls is still relatively low and potential negative effects can largely be overcome. Afterwards negative effects on chick growth and survival become obvious, in particular during longer periods of strong winds (chapter 3).

The present study on the feeding ecology of Sandwich Tern was mainly performed on chicks held within enclosures made of wire netting. Enclosing chicks makes it possible to follow them from hatching to fledging as they are forced to stay within the vicinity of the nest. Sandwich Tern chicks are semi-precocial and in natural situations often leave the nest soon after hatching. In non-enclosed situations, nest departure normally occurs

3-6 days after hatching of the first egg in a nest (Veen 1977). The first days after leaving are spent hiding in the vegetation or in nest scrapes in the direct surroundings of the original nest. About two weeks after hatching, however, many laying sites have been deserted. Most chicks have then spread and are found in the vegetation surrounding the colonies. During the following weeks, the chicks further disperse and are found scattered over the entire island. In chapter 5 we argue that leaving the nest site is a behavioural trait to avoid the heavy attacks from the kleptoparasitising gulls. The timing for leaving the nest vicinity critically depends on the trade-off between a decreasing need for protection from the gulls and an increasing robbing pressure. By leaving the original laying site the chicks are led away from the robbing gulls and by spreading over the island aggregations of food input are avoided and thus the conditions for kleptoparasitism to occur are minimised. Although moving chicks probably still encounter gulls, most of these gulls have not yet learned to steal food from terns. We argue that when the chicks keep moving around, gulls can not develop into specialised kleptoparasites (chapter 5). Yet, on Griend exceptionally high robbing pressures were measured in free-living chicks as well, especially in chicks that had become trapped in natural fykes formed by the vegetation (Geschiere 1993, own observations). Similar high attack rates were observed in Sandwich Tern colonies that were surrounded by dense vegetation from which the tern chicks could hardly escape. It is not clear to what extent and when free-living chicks do leave the nest site in natural situations. It also remains unstudied if and how chicks move over breeding sites and how this relates to the spatial distribution of vegetation, and the probability of meeting conspecifics and potential kleptoparasites. It further is uncertain if and to what extent our frequent visits in some colonies have contributed to the departure from the nesting site. Around fledging Sandwich Tern chicks sometimes gather in flocks along the beach. In those flocks piracy by the gulls seems to revive, although the success rate of gulls has never been studied in these circumstances. Future studies could make use of radio transmitters to monitor Sandwich Tern chicks from hatching until fledging and to further examine the evasive behaviour of the terns.

The high incidence of food loss to Black-headed Gulls recorded in this study (19% of all food items were robbed by the gulls) is, however, not restricted to enclosed or trapped chicks only but is typical in Sandwich Terns. During the period 1966-1970, Veen (1977) found that on average 18-38% of the fish brought to non-enclosed chicks on Griend was stolen by Black-headed Gulls. At the former Dutch colony “De Beer”, Hoek of Holland, up to 25% of the fish meant for the tern chicks was robbed (Rooth 1965) and Garthe & Kubetzki (1998) report that in 1997 11% of the food brought to Sandwich Tern chicks on Juist, German Wadden Sea, was lost to kleptoparasitising gulls. At the Hompelvoet colony in the Dutch Delta area losses of 20-50% were not uncommon in the 1970s (Beijersbergen 1976). Fuchs (1977) recorded lower rates of kleptoparasitism (~ 6%) at the Sands of Forvie, Scotland, in 1973-1974 and Dies & Dies (2005) report similar low rates (5%) in Eastern Spain. Several authors mention that exceptionally high rates of kleptoparasitism (> 50%) occur during spells of bad weather (Rooth 1965, Smith 1975, Veen 1977, Glutz von Blotzheim & Bauer 1982, own observations).

The rate of food loss strongly depends on the size of the prey brought to the chicks (Dunn1972, Ratcliffe *et al.* 1997, this study chapter 2, 3). Of the two main prey types that were brought to the chicks on Griend (clupeids and sandeel; chapter 2) the gulls preferred to rob the longer sandeel. Thus, the composition of the diet of Sandwich Tern chicks on Griend greatly influenced the probability of losing the prey to kleptoparasitising gulls. Consequently, we found a strong negative relationship between the average yearly proportion of clupeids in the chicks' diet and the proportion of the food that was robbed by the gulls (chapter 4). Figures on robbing incidence and diet composition extracted from Veen (1977) suggest a very similar relationship (Fig. 9.1). In Veen's dataset lower proportions of the food were robbed, probably because that author followed younger chicks (in chapter 4 chicks > 15 days were selected) and because in the present study prey-consumption probabilities (including other causes of prey loss) were used rather than losses to robbing gulls. Veen ascribed the increased piracy on Griend in the period 1966-70 to a relative increase of the Black-headed Gull population compared to that of Sandwich Terns, but in retrospect this can also be explained by dietary changes as his data fit the expected effect of changes in diet composition very well (Fig. 9.1).

By evolving a close breeding association with gulls, Sandwich Terns trade-off food against predation. In chapter 4 we describe how Sandwich Terns can organise their foraging behaviour in order to maximise prey intake rates of their chicks in the presence of kleptoparasitising Black-headed Gulls. Presupposing that enough herring is available in the foraging areas and given the relationship shown in figure 9.1, parents that face high food losses could theoretically shift the diet towards more clupeids in order to reduce the losses. However, in most years parents did not bring more clupeids to the nest when food losses increased (chapter 4), suggesting that the availability of clupeids was limited. Instead, both parents left the island to forage leaving their chicks unattended at the nest more often and thus increased the food transport. Increased foraging effort in years with

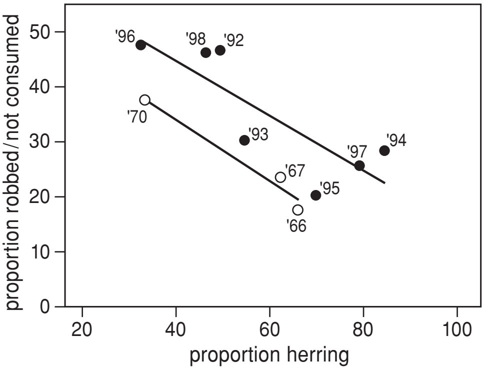

Figure 9.1. Relationship between the diet composition of Sandwich Tern chicks on Griend and the proportion of the food that is robbed or not consumed by the chicks. Black dot = non-consumed proportion in 1992-1998 extracted from chapter 4; open dot = robbed proportions in 1966-1970 extracted from Veen (1977)

low clupeid proportions in the diet enabled the parents to counterbalance an imminent food shortage. Simultaneous foraging of the parents commenced when the chicks were about 2 weeks old when they are too large to be swallowed by the major predators on Griend. Leaving the chick unprotected at the colony at that age did not result in increased predation rates. The observed variation in diet composition did not translate into differences in growth or survival of the Sandwich Tern chicks despite the differences in parasitic losses. Apparently, Sandwich Terns are well adapted to the kleptoparasitic behaviour of their associative breeding species. If they can not avoid the attacks of the gulls by moving away from them, they increase their foraging effort and compensate for these losses.

FEEDING ECOLOGY OF SANDWICH TERNS

During the breeding season, Sandwich Terns feed their chicks on a restricted number of species of marine fish. In The Netherlands, chicks are predominantly fed with herring *Clupea harengus*, sprat *Sprattus sprattus*, sandeel *Ammodytes tobianus* and greater sandeel *Hyperoplus lanceolatus* (Veen 1977, this study). Adult terns locate the fish visually and the prey is mainly caught by plunge diving, down to a maximum depth of two metres (Borodulina 1960, Dunn 1972). On Griend, the food is predominantly found within 15 km distance from the colony, but in some other colonies foraging flights > 25 km might be more common (Veen 1977, Baptist & Meininger 1984, Fasola & Bogliani 1990, Raaijmakers *et al.* 1993, own observations). Sandwich Tern parents breeding on Griend forage mainly in shallow waters and in channels around the islands of Terschelling and Vlieland (Stienen & Brenninkmeijer 1994, Fig. 9.2). Investigations in 1993 on parents equipped with radio-transmitters indicate that the foraging areas of Sandwich Terns on Griend have somewhat shifted to the southwest compared to the 1960s when the northeastern part of Terschelling was also frequently used for foraging (Veen 1977), but the foraging range is very comparable (Fig. 9.2). Parents transport the captured fish to the colony one by one (only in exceptional cases do they carry two prey items), holding it crosswise in the bill. The length of fish parents offered to the chicks on Griend ranged from 1.5 to 21.5 cm. On average, sandeel brought to the colony were somewhat longer (11 cm) than clupeids (9 cm).

The abundance of the Sandwich Terns' prey species can differ greatly from year to year (Corten 1990, 2001, Corten & van de Kamp 1979, 1996). Superimposed on this, the prey fish show distinct patterns of horizontal migration within a year (Fonds 1978, Corten 1996) causing strong changes in the species composition, distribution and length of available prey fish during the breeding season of the terns. The prey fish also move vertically in the water column with changing light conditions and tidal movements (Thorpe 1978), resulting in cyclic fluctuations in prey availability for the terns during the day. Predator fish and sea mammals cause unpredictable horizontal and vertical movements of the prey as well. This causes strong spatio-temporal variation in the availability and the quality of the Sandwich Terns' food and requires a great flexibility of these spe-

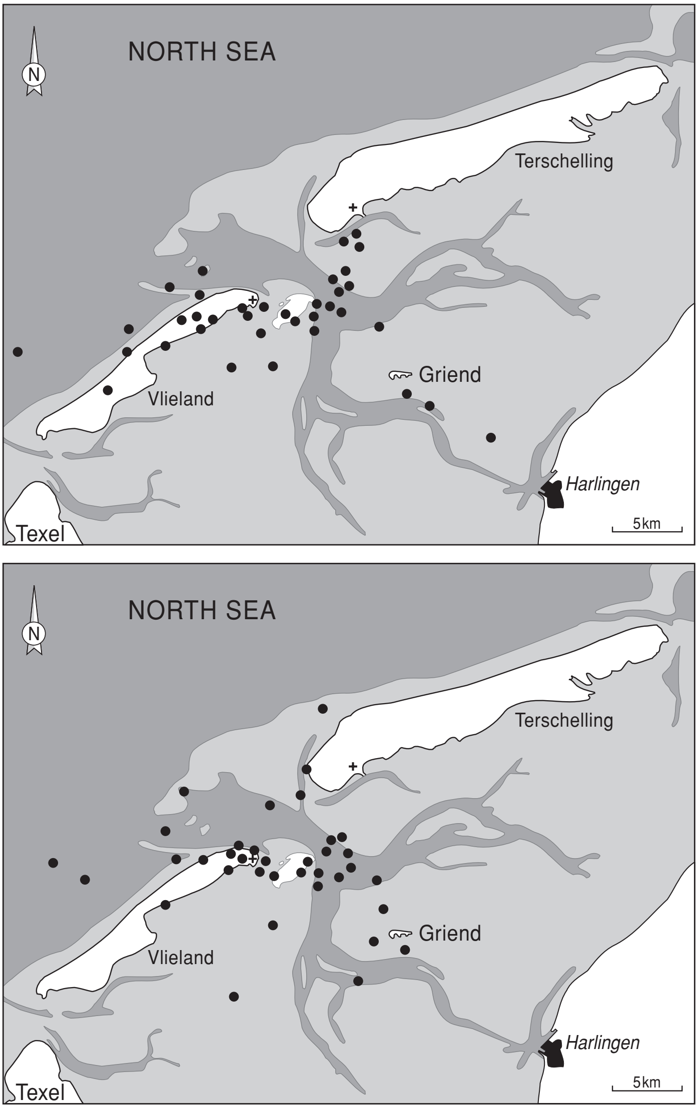

Figure 9.2. Positions (dots) of two radio tagged Sandwich Terns during chick rearing in 1993. The foraging terns were located by radio antennas placed on Griend, Terschelling and Vlieland (latter two locations indicated by +). Light shaded areas surround the mean low water coastline.

cialised foragers. Chapter 2 describes how patterns in diet composition of Sandwich Tern chicks reflect the cyclic variation in prey fish availability, for example the downward migration and shoaling of herring and sprat during the day and the dispersal and upward migration at dusk (Blaxter & Parrish 1965, Laevastu & Hayes 1981, Cardinale *et al.* 2003, Nilsson *et al.* 2003). This rhythmicity means that clupeids are typically available for the day active terns during the early morning and at dusk, matching the increased proportions of clupeids in the chicks' diet at that time.

The patterns in diet composition described in chapter 2 are the averaged results of 7 years of observation in the colony at Griend. Patterns in diet composition derived from a particular year can, however, be very deviant from this average pattern. In 1994, for example, chicks received high proportions of clupeids throughout the day. An unambiguous explanation for such an aberrant pattern can not be given. It is most likely, however, that the high availability of clupeids in 1994 (IBTS data given below) caused an increased availability of herring and sprat near the surface even during the day. A low availability of sandeel may, however, also lead to the same pattern, as terns will then be forced to feed on clupeids throughout the day. This emphasizes that it is impossible to use shifts in the diet composition of seabirds as reliable indicators for shifts in the availability of their food, even if the diet composition mirrors the underlying food composition. For predators that have an even broader choice of prey species, diet composition is without any doubt a very poor indicator of food availability, although it is often interpreted as such.

In order to link patterns in the diet of seabirds to spatio-temporal changes of their prey one must concurrently study food availability locally in the foraging areas as well as the seabird's biology (*e.g.* Litzow *et al.* 2000, Mous 2000). It is, however, not easy to measure food availability of Sandwich Terns because their fish prey occur in shallow water, are patchily distributed and perform species-specific diel vertical migration, schooling and feeding behaviour (Cardinale *et al.* 2003). The fish-sampling programme conducted in the terns' foraging area in 1995-1998 by The Netherlands Institute of Fishery Research (RIVO) suggests particularly strong effects of water clarity on prey fish availability (Fig. 9.3). Especially clupeids, but also sandeel were caught more frequently in turbid water. Since we sampled fish in the upper water layer (0-2 m), this indicates that the fish move to the surface when water transparency decreases. This implies that turbid waters might offer better foraging conditions to the terns. In the present study, it could not be excluded that more fish were caught in turbid waters simply because the fish saw the approaching fishing gear less well and therefore experienced a lower probability to escape than in clear waters. However, using acoustic recordings Mous *et al.* (2000) found very similar results in Lake IJsselmeer, where increased water transparency resulted in a decreasing availability of surface-dwelling prey fish for terns. Mous *et al.* could link the spatial distribution of foraging Black Terns *Chlidonias niger* directly to the clarity of the water. This implies that species diving for fish near the surface, like Sandwich Terns, may depend on turbid waters despite the fact that they locate their prey visually.

POPULATION LIMITATIONS IN SANDWICH TERNS

Seabird populations critically depend on the dynamics in the availability of their prey and are often limited in size by the availability of their food (reviews in Birkhead & Furness 1985 and Croxall & Rothery 1991). Several studies on seabirds linked measurements of

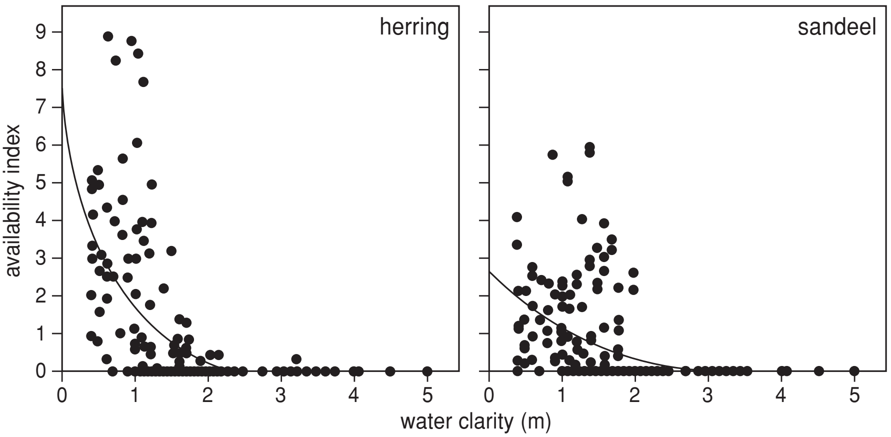

Figure 9.3. Relationship between water clarity (measured with Secchi disk) and the occurrence of herring and sandeel near the water surface. Prey fish availability was obtained by log transforming the mass of fish caught with an Isaac's Kidd Midwater Trawl net (IKMT-net) with a mesh size of 6 mm in the upper 2 m of the water layer (see Stienen & Brenninkmeijer 1998a for more details).

food abundance with the number of breeding pairs, the reproductive output, chick growth or adult survivorship of seabirds (reviews in Crawford & Shelton 1978, Cairns 1987, Furness 1989) and experimental supplementary food can increase the reproductive output of seabirds (examples in Newton 1998). Throughout the world and in many species, the population size and breeding success of seabirds has been linked with dynamics in prey stock abundance (review in Furness 1989). The most striking and best documented cases are the dramatic changes in breeding performance and population size of seabirds along the coast of central Norway in the late 1960s, in the Barents Sea in the mid-1980s and at Foula, Shetland in the mid-1980s due to the collapse of components of the seabirds' food stock (Barrett *et al.* 1987, Heubeck 1988, Monaghan *et al.* 1989, Vader *et al.* 1990, Bailey 1991, Hamer *et al.* 1991, Suddaby & Ratcliffe 1997).

The species of seabirds that tend to be the most sensitive to changes in fish abundance are small birds with restricted foraging ranges and energetically expensive foraging methods, feeding on species present near the water surface and with fast growing chicks (Furness & Ainley 1984, Furness 1989). Sandwich Terns me*et al*l criteria and are therefore ranked among the five most vulnerable seabird species to reductions in food supply in the North Sea (Furness & Tasker 2000). The unpredictable nature of their food combined with highly variable amounts of food loss to the gulls cause a high degree of food stress for Sandwich Terns during the breeding season. In particular when years of unfavourable diet composition (poor clupeid years) coincide with adverse weather conditions strong effects on the breeding performance of the terns may be expected. During the 7 years of study on Griend we found no effect of apparent changes in food availability (reflected by fluctuations in diet composition) on the reproductive output of the terns. Also growth of the chicks was not affected by changes in prey fish availability (chapter 4). In poor clupeid years, when sandeel dominated the chicks' diet, parents worked harder (sometimes at maximum levels) and were thus able to counterbalance the high proportions of food loss to the gulls. In the present study, years of poor availability of clupeids coincided with reasonable weather conditions and yet the tern parents already reached maximum buffer capacity. Therefore, strong negative effects on chick growth and survival can be expected when wind conditions are less favourable in poor clupeid years. This implies that a poor availability of clupeids has the potential to reduce chick survival but that this critically depends on the wind conditions.

Increased foraging effort of the parents in poor clupeid years might lead to reduced fecundity in the following year, as has been demonstrated in other seabirds (Wernham & Bryant 1998) as well as in a wide variety of short-living species (*e.g.* Røskaft 1985, Smith *et al.* 1987, Gustafsson & Sutherland 1988, Verhulst 1995). Being long-lived, seabirds are believed to respond most strongly to fluctuating food resources with variation in their diet, working levels and breeding success rather than adult survival rate (Drent and Daan 1980). There is, however, growing evidence that poor food availability even affects adult survival in long-lived species (Reid 1987, Jacobsen *et al.* 1995, Davis *et al.* 2005). If indeed higher working levels affect adult survival in Sandwich Terns, then a decreased clupeid availability can lead to reduced adult survival and even small reductions could have strong effects on population dynamics.

Another, more direct, link between food resources and population dynamics would be the adjustment of the non-breeding population to current food abundance. Adults that have bred the year before may decide not to breed if the conditions for breeding are not favourable in the subsequent year(s). In some seabirds, large proportions (15%-25%) of the population may not breed in unfavourable years (*e.g.* Aebischer & Wanless 1992, Bradley *et al.* 2000). Intermittent breeding would allow terns a fast response to changes in the food situation that is adaptive in highly variable environments. Non-breeding of adults explains the fast rate of decline of the Arctic Tern populations on Orkney and Shetland during 1980 and 1989 when the sandeel stock collapsed (Avery et. al. 1993). Where some other tern species exhibit a strong fidelity to their natal colony and a strong tenacity to previously used breeding areas and nesting sites within those areas (Austin 1949, Nisbet 1978, González-Solís *et al.* 1999, own observation), Sandwich Terns exhibit a highly flexible choice of nesting sites. They often change breeding sites within an established breeding area (own observations) and easily switch between breeding sites when conditions are affected by predators or other disturbances or sometimes for unidentified reasons (Courtney & Blokpoel 1983, Ratcliffe *et al.* 2000, Noble-Rollin & Redfern 2002, Ratcliffe 2004). Nomadic behaviour enables Sandwich Terns to respond to discrete events at the breeding grounds (such as disturbance, predation or competition with other species) and more importantly to adjust to the strong fluctuations of their prey fishes.

CHANGES IN FOOD RESOURCES

Overexploitation by fisheries was long believed to be the primary factor regulating fish stocks in the North Sea after World War II. Industrial fishery for sprat and herring caused a collapse of the North Sea herring stock in the 1970s, which lead to the closure of fishery from 1977 to 1983 and fishery quota in the subsequent years (Corten 2001). The heavy exploitation by the fishing industry of predatory fish (*e.g.* cod, herring and mackerel) is thought to have relieved the predatory pressure on their prey such as sandeels and sprats, allowing the latter to become more abundant (Corten 2001). The past decades increasing attention has been directed towards environmental variability that can similarly lead to strong fluctuations in the abundance and spatial distribution of fish stocks (Bakken & Bailey 1990, Corten 2001, Ottersen *et al.* 2001, Beaugrand *et al.* 2003). During the second half of the twentieth century, the combination of fishery mortality and environmental variability led to strong fluctuations of fish stock biomass in space and time and thus strongly influenced food supply for seabirds in the North Sea.

How such changes can influence terns was illustrated in the 1980s when the collapse of the local sandeel stock around Shetland caused widespread breeding failure and population decline in terns and several other seabirds (Heubeck 1988, Bailey 1991). This led to the closure of the Shetland sandeel fishery for several years and also to intensive research on the dynamic links between sandeels and seabirds. It was finally concluded that the depletion of the Shetland sandeels and thus the seabird breeding failures were not caused by the fishery on sandeel but by natural factors acting in the early life-history of sandeels (Bailey 1991, Corten 2001). One of the most strongly affected seabird species in the Shetland crisis was the Arctic Tern *S. paradisaea* (Monaghan *et al.* 1989); a species with a very specialised diet choice similar to the case of the Sandwich Tern. Changes in food resources might therefore be important determinants of the Sandwich Tern population trend. However, long-term data on fish abundance in the southern North Sea is not available for all prey species and certainly not on a local scale. For that reason, various indices of prey fish abundance in the North Sea are used here, in the hope of finding signals that indicate changes in the availability of prey fish for Sandwich Terns. Also data on the underlying ecological processes that determine food availability for seabirds in the North Sea are used. Here I use the variation in the atmospheric pressure in the North Atlantic (the North Atlantic Oscillation or NAO) that forces the ecology of the North Atlantic Ocean and the North Sea. The NAO influences wind speed, sea temperature and salinity in the North Sea and thus strongly influences the population dynamics of marine species at different trophic levels (Stenseth *et al.* 2004). Fluctuations in the fish stocks of herring, cod and salmon are linked to the variability in the NAO (Corten 2001, Beaugrand *et al.* 2003, Stenseth *et al.* 2004). The climatic variability thus strongly influences the food availability of piscivorous seabirds and indices of NAO might be a very robust determinant that captures a package of weather conditions as well as biological variability. Data on NAO is further very useful because it spans the entire twentieth century and therefore fully overlaps with data on the Dutch Sandwich Tern population, whereas most data on fish abundance only covers the past few decades.

PAST AND FUTURE PROSPECTS OF THE SANDWICH TERN IN THE NETHERLANDS

With a total of 14 500 breeding pairs (Stienen 2002), at the end of the twentieth century The Netherlands held about one quarter of the northwest European population (53 000 – 57 000 pairs according to Delany & Scott 2002). Within The Netherlands there are currently important colonies on Griend in the Wadden Sea (7920 pairs in 2000) and on Hompelvoet (2800 pairs) and The Hooge Platen (3000 pairs) in the southern Delta area. During the past decades, smaller settlements often of a less permanent character were found at almost all other Dutch Wadden Sea islands (Texel, Terschelling, Ameland, Schiermonnikoog and Rottumerplaat) and at several localities in the Delta area. Ring recoveries indicate that the colony in the harbour of Zeebrugge in adjacent Belgium is closely connected with the colonies in the southern part of The Netherlands and for that reason the Zeebrugge colony is here included in the Delta population.

The Dutch Sandwich Tern population fluctuated strongly during the twentieth century (Fig. 9.4). During the first half of the century, it was mainly direct anthropogenic pressure that shaped the population. At the beginning of the century, large-scale egging for consumption and shooting of adult terns for use in the manufacturing industry of ladies' hats caused the population to decrease rapidly. The exact impact of these practices is not very well documented, as surveys were poor and incomplete in those years. It is, however, clear that due to this persecution by man the population reached a low around 1910. In 1908, Dutch law prohibited collecting of eggs and shooting of terns. Along with the guarding of the most important colonies during the breeding season from 1912 onwards, this resulted in a gradual increase of the Dutch population to 35 000 – 46 000 breeding pairs in the 1930s. During World War II, disturbances, shooting of terns and egg collecting caused the numbers to drop again, but the population recovered soon in the years after the war. At the end of the 1950s, numbers dropped markedly and the population was reduced to only 875 pairs in 1965. This collapse was the result of a pollution of the Dutch coastal waters with organochlorine pesticides (Koeman 1971, 1975). This heavily affected tern colonies and other waterbirds in a wide area ranging from the Delta area in the south of The Netherlands (Den Boer *et al*. 1993, Brenninkmeijer & Stienen 1992, Arts & Meininger 1994, Stienen & Brenninkmeijer 1998b) to the German Wadden Sea (Südbeck *et al*. 1998). In 1967, the spill of pesticides was stopped and from then on the numbers gradually increased. This time the population recovered much more slowly than during the previous recovery periods. In the period 1911-1940 after the population had been reduced to a level comparable to the low of 1965, the annual increase averaged more than one thousand pairs (1 336 by linear regression). Interestingly, a similar rate of increase was evident in the period 1944-1956 (annual increment 1 257 pairs) despite the

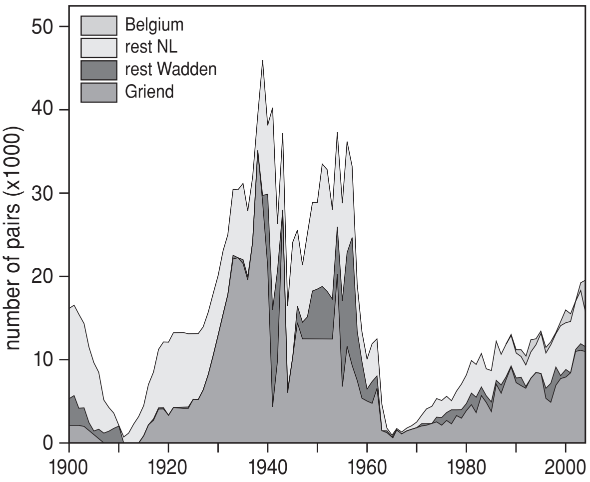

Figure 9.4. Number of breeding Sandwich Terns (pairs) in The Netherlands and Belgium during 1900-2004 (completed from Brenninkmeijer & Stienen 1992, data summarised in appendix 9.I).

fact that the low was only 16 200 pairs in 1944. In sharp contrast, in the period 1965-2004 annual growth averaged only 388 pairs, with the northern population in the Dutch Wadden Sea recovering somewhat faster than the population in the Delta area. By the end of the twentieth century, the Dutch population amounted to about 14 500 breeding pairs and in 2004 numbers had further increased to almost 19 500 pairs (including Belgium). Still this is only about half of the breeding numbers prior to the pollution incident.

The collapse of the Dutch Sandwich Tern population in the 1960s was followed by several years of a very low abundance of herring (Fig. 9.5). Yet, during this period the number of Sandwich Terns gradually increased. In the 1980s the growth of the Dutch population stagnated; first in the Delta area (period 1980-1990) and later in the Wadden Sea (1985-2001). From 1981-1998 the Dutch population slowly increased at an annual rate of 208 pairs (linear regression), but at the very end of the century numbers increased again and a maximum of 19 486 pairs was counted in 2004. During the past two decades both the Delta and Wadden Sea population showed sudden and sharp declines that can not be explained from adult mortality or poor breeding success (Delta population crashed in 1977, 1998 and 2002, and the Wadden Sea population in 1985, 1992 and 1996). Such periods of sudden population decline are most likely explained by non-breeding and/or emigration to other colonies. Apparently, these sudden population declines were not caused by the loss or degradation of the breeding grounds. Most likely they are indicative for poor feeding conditions. In the next paragraphs, the link between population changes of Sandwich Terns and food abundance will be discussed in detail using various indices of food abundance.

In the first place ICES data on the North Sea spawning stock biomass of herring were used to explain the population changes in sandwich Terns (Fig. 9.5). These surveys show

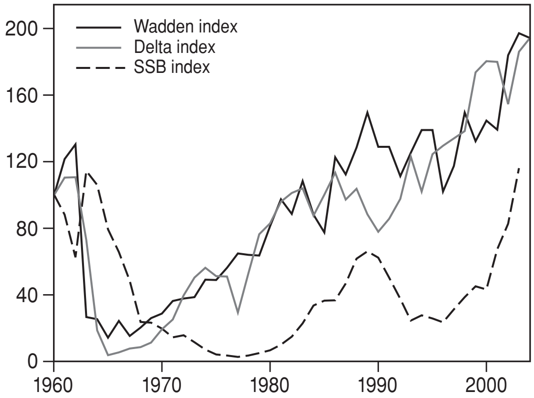

Figure 9.5. Index of the development of the Sandwich Tern populations breeding in the Wadden Sea and the Delta area (including Belgium) compared with the index of the spawning stock biomass of North Sea herring (SSB index). The population sizes in 1960 were arbitrarily set at 100%.

that at the time that the Dutch Sandwich Tern population crashed in the early 1960s, the North Sea herring stock size peaked. The herring stock did not collapse until 1965, suggesting that the poisoning of the coastal waters in the years before was the primary cause of the crash in the Sandwich Tern population and that poor food availability did not play a role. The recovery of the Dutch tern population after the crash, however, might very well have been hampered by the poor herring stock during the 1970s and early 1980s. Remarkably, the stagnating growth of the Dutch population during the 1980s was apparent long before the decrease in the herring stock in 1991. Also the peak in Wadden population in 1989 precedes the peak in the herring stock in 1990. This suggests that although herring is an important part of the diet of Sandwich Terns a link between the Dutch Sandwich Tern population and the North Sea herring stock is not a simple one. Yet, some parallels between the herring stock and the Wadden Sea population (peak at the end of the 1980s followed by a decade of low numbers and finally a strong increase in population size around 2000) invite for a further examination of the data, and for this reason a subset of another dataset has been examined.

When the more detailed ICES-data of the International Bottom Trawl Surveys (IBTS) on clupeid abundance (*i.e.* data on herring and sprat combined) in the southeastern North Sea from 1977-2004 are employed, again some striking parallels with the development of the Dutch Sandwich Tern populations appear. Peaks in clupeid abundance in 1981, 1989, 1994 and 1998, for example, coincided with peaks in the number of Sandwich Terns breeding in the Wadden Sea. Also lows in the Wadden Sea population in 1992 and 1996 correlated with a low abundance of clupeids in the southeastern North Sea. There was, however, no relationship between the breeding performance (either clutch size or reproductive output) of Dutch Sandwich Terns and the clupeid abundance

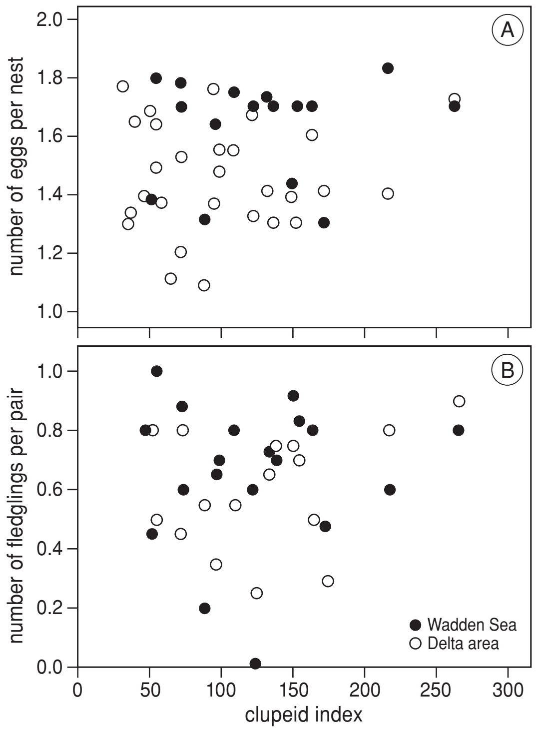

Figure 9.6. Relationship between IBTS clupeid abundance in the southeastern North Sea (population size in 1977 was set at 100%) and clutch size (averaged annual number of eggs per nest; A) and breeding success (averaged annual number of fledglings per pair; B) in the colonies on Griend in the Wadden Sea (1986-2004) and Hompelvoet/Markenje in the Delta area (1977-2004 and 1989-2004, respectively for clutch size and breeding success). Note that clutch size and breeding success are generally lower in the Delta area than in the Wadden Sea.

in the southeastern North Sea (Fig. 9.6). We conclude that if the changes in the Sandwich Tern populations are related to fish availability it will probably be an immediate response of the adult population to changes in food abundance rather than a delayed response through the reproductive output of the terns.

The reproductive output of the Sandwich Tern populations on Griend (recorded in 1986-2004) and on Hompelvoet/Markenje (1977-2004) yield a prediction of the number of recruits that may enter the populations a few years later (assuming that fledglings recruit to the natal colony 3 years later and using a recruitment rate of 0,3[1]). Assuming that breeding adults of the previous year return to the same colony (using an adult mortality rate of 0,18[1]) generates a prediction of the size of the respective populations. The relative difference between the predicted population size and the actual population size is then a measurement of the changes in the population caused by processes of immigra-

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[1] Adult mortality and recruitment rate are derived from Green *et al.* (1990) and are very similar to values for the Dutch population given by Brenninkmeijer & Stienen (1992).

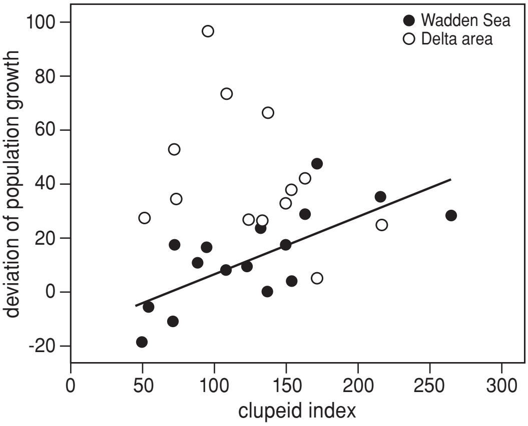

Figure 9.7. Relationship between IBTS clupeid abundance in the southeastern North Sea and the Δ – population growth of the Wadden Sea and Delta populations of Sandwich Tern (see text for more details).

tion/emigration and/or intermittent breeding (further called Δ–population growth). A strong positive relationship (linear regression, $r^2 = 0{,}52$, $P < 0.01$) between the IBTS clupeid abundance in the southeastern North Sea and the Δ–population growth of the Wadden Sea population was found (Fig. 9.7). This result is in accordance with the hypothesis that the recent changes in the Dutch Sandwich Tern population are linked to fluctuations in prey fish stocks, although the relationship seems not to hold for the Delta population. As was supposed earlier in this chapter there seems to be a direct link between the amount of food available in determining how many terns decide to breed or not to breed in the Wadden Sea, but so far as we know, there is no simple relationship to the terns' subsequent reproductive successs (confirming chapter 4). It remains puzzling what caused the population changes in the Delta area. This population might more critically depend on the stock size of Downs herring that spawns in the English Channel or other local prey stocks that are not very well represented in the IBTS surveys. Alternatively, the southern population might be driven more by other ecological processes (*e.g.* wind, predation, habitat changes etc.). It must also be mentioned that the restricted data used here (*e.g.* no reliable data on sandeel availability and clupeid abundance may differ locally) may be insufficient to explain all patterns in detail.

During the twentieth century, three periods of positive population growth can be distinguished during which the Dutch Sandwich Tern population grew faster than was expected from survival parameters (Fig. 9.8). A first positive phase can be seen around 1920, resulting from the wardening of colonies and protection against egging and shooting. The increase was apparent in the Delta area and not in the Wadden Sea because at the Dutch Wadden Sea was not very important as a breeding station for Sandwich Terns at that time. The strong growth of the Wadden population between 1920 and 1940 was most probably the result of an influx of immigrants into the Wadden Sea (partly but not

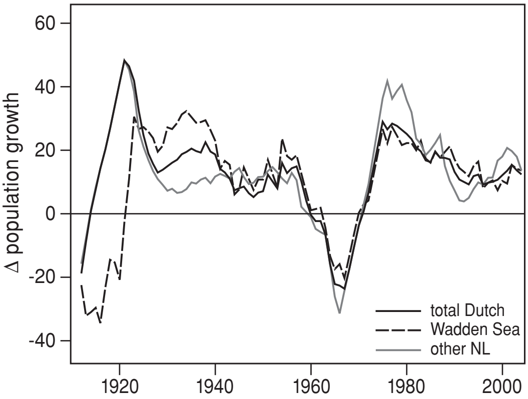

Figure 9.8. Outline of the development of the total Dutch population as well as the populations in the Wadden Sea and other parts in The Netherlands during 1910-2004. The lines represent the 10-year running means of the Δ – population growth (assuming a breeding success of 0.7 fledglings per pair).

entirely originating from the Delta area). In 1959, both the Delta and Wadden Sea populations entered a period of strong negative population growth caused by the poisoning of adults and chicks. This period was followed by a strong population increase that presumes a strong net influx of terns. Again the influx was more apparent in the Delta area than in the Dutch Wadden Sea. Figure 9.8 further suggests that by the end of the twentieth century, the processes of emigration/mortality and immigration/recruitment were more in balance with each other. The strong growth of the Delta population during 1999-2004, however, again suggests a net influx of individuals originating from other colonies. So the Delta population seems to depend more on processes of immi- and emigration than the Wadden Sea population.

A BIOGEOGRAPHICAL PERSPECTIVE

The longer periods of positive population growth (*e.g.* in the Wadden Sea from 1920-1940 and in the Delta area after the recovery of the crash in 1965) may point towards periods of increased reproductive output or may result from immigration from other colonies, whereas shorter periods of strong population changes may reflect intermittent breeding. Ring recoveries indeed confirm that there is considerable interchange between colonies throughout large parts of NW-Europe (Møller 1981, Brenninkmeijer & Stienen 1997, Noble-Rollin & Redfern 2002). Recoveries of foreign ringed terns on Griend come from pulli ringed in colonies in Great Britain & Ireland, Belgium, Germany, Denmark, Sweden and Estonia (Fig. 9.9). There is also considerable exchange with other Dutch colonies. On the other hand, pulli ringed on Griend have been reported breeding in the

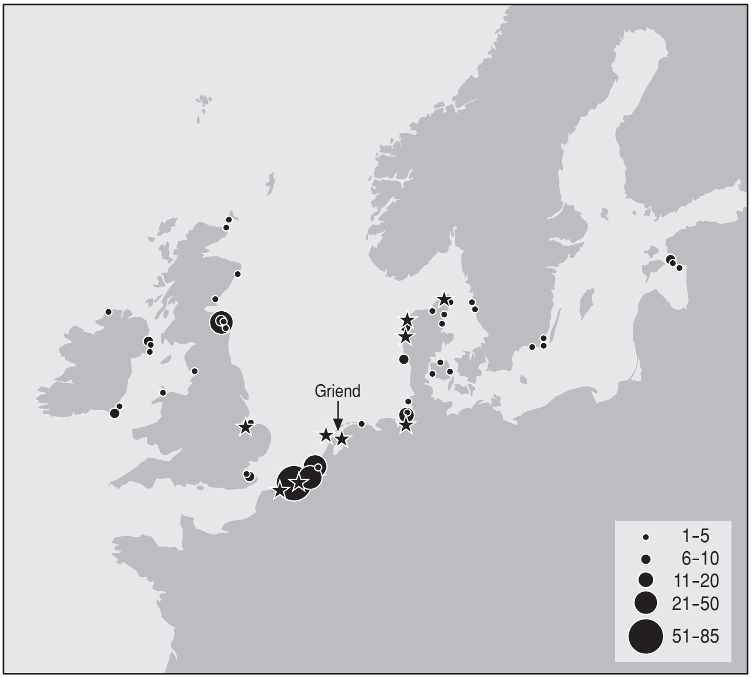

Figure 9.9. Ringing locations of 349 Sandwich Terns recovered on Griend during the breeding season (May-June) and ringed as pulli elsewhere (dots). The asterisks show recovery locations of 32 Sandwich Terns ringed as pulli on Griend and recovered elsewhere in a subsequent breeding season when of breeding age (> 2 cy). Hatched circle = Griend. Data Vogeltrekstation Arnhem.

UK, France, Belgium, Dutch colonies other than Griend, Germany, and Denmark. According to the recoveries analysed by Brenninkmeijer & Stienen (1997) about 23% of the Sandwich Terns nesting on Griend in the 1990s originated from colonies other than Griend, with Griend having strong connections with colonies in the Dutch Delta area, and to a lesser extent with colonies in the UK and Denmark (and probably from Germany where not so many birds have been ringed as in the other countries).

Sandwich Terns have ample opportunities to mix with terns from other colonies. Sandwich Terns from The Netherlands share common wintering quarters with Irish, British, Belgian, German and Danish colonies. When migrating northwards from the African wintering areas to the breeding areas European terns visit various colony sites located to the south of their natal colony. At each breeding location they can decide to stay if conditions for breeding are good or alternatively to continue their flight northwards. After breeding, parents and fledglings from Dutch colonies first move northwards (up to Denmark) before starting their southward migration to the African wintering areas. There is post-fledging dispersal of British and Belgian birds to The Netherlands and Denmark as well (Møller 1981, Noble-Rollin & Redfern 2002, own data). By visiting non-natal breeding sites individuals can sample the food situation in large parts of the Atlantic and the North Sea, and they can monitor the number of fledglings in various other colonies (which may be indicative for feeding conditions). The connectivity with other colonies and the high rates of interchange between colonies imply that population dynamics in Sandwich Terns must be dealt with on a European scale. Most studies, however, only consider fluctuations in the breeding numbers at the colony, region or county level and often link local changes in breeding numbers to discrete events (*e.g.* Südbeck & Hälterlein 1997, Lloyd *et al.* 1991, Merne 1997, Ratcliffe *et al.* 2000, Ratcliffe 2004) and have not considered exchange of birds between European colonies.

Before the crash of the Dutch population in the 1960s, the European Sandwich Tern population amounted to about 50 000 pairs. At that time, The Netherlands supported about 70% of the total European population. For that reason, the collapse of the Dutch population caused a temporary decrease of the European population to a low of about 15 000 pairs in 1965. After the Dutch population crash, numbers gradually increased and in the early 1990s Europe again supported about 50 000 pairs. However, the distribution over the various countries had drastically changed. The Netherlands only supported less than 25% of the European population, while other European colonies had gained in importance (Brenninkmeijer & Stienen 1997). A comparison of the population trends in the Dutch populations (Wadden Sea and southern North Sea) with those in the adjacent populations of the United Kingdom, Ireland and Germany (data available from 1969 onwards) shows that after the crash of the Dutch population a strong increase was apparent in all northwest European populations, except for those in Great Britain and Ireland (Fig. 9.10). Particularly high rates of population growth were found in the North Sea/Channel, Dutch Wadden Sea and Germany, whereas numbers increased much less rapidly in eastern UK waters. After 1980, growth stagnated in many regions or even became negative; first in the German North Sea population (1981-1986), followed by the eastern UK colonies (1983-1998), the southern North Sea (1986-1994), the Dutch Wadden populations (1990-2000) and again in Germany (1997-2001). Remarkably, in all parts of Europe those periods of recessions were followed by a revival of the population growth at about the same rate as prior to the stagnation. In contrast to the population changes prior to the 1970s that were all related to human impact (egging, shooting of adults, pollution), this time the changes were probably not directly anthropogenic and most probably related to food availability. The stepwise pattern of the Sandwich Terns' population growth in various parts of Europe may point towards sudden shifts within the North Sea ecosystem. During the past decades similar shifts, so-called regime shifts, were noted at different levels of the North Sea ecosystem, spanning the lower trophic levels, via fish to birds and marine mammals (*e.g.* Edwards et. al. 1999, 2001, Corten 2001, Reid *et al.* 2001, Ottersen *et al.* 2001, Weijerman *et al.* 2005). In the North Sea and Wadden Sea sudden and stepwise ecosystem changes occurred in 1988 and 1998 imposed on more gradual trends as a result of an increased inflow of oceanic water (Reid *et al.* 2001), so largely coinciding with the shifts in the Sandwich Tern populations in many parts of Europe.

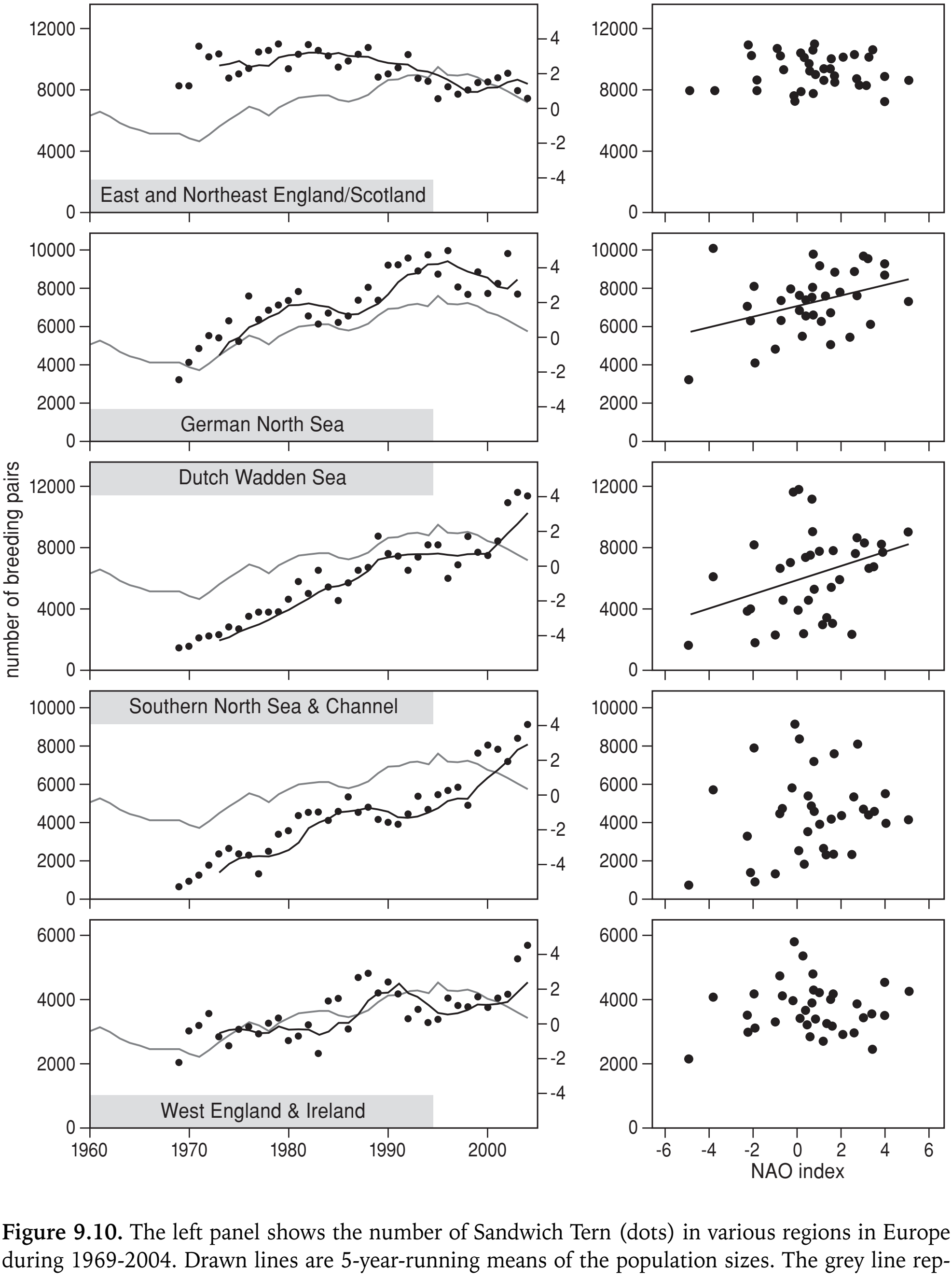

Figure 9.10. The left panel shows the number of Sandwich Tern (dots) in various regions in Europe during 1969-2004. Drawn lines are 5-year-running means of the population sizes. The grey line represents the 10-year-running mean of the index of the North Atlantic Oscillation during December-March (data from Hurrell 2005) and is plotted against the right axis. The right graphs show the relationship between the NAO-index and the number of breeding pairs in each region.

THE NORTH SEA ECOSYSTEM AND THE NAO

The functioning of the North Sea ecosystem is highly complex and not very well understood, but the major driving forces are the periodical changes of the NAO influencing sea surface temperature and the sudden inflows of nutrient rich oceanic water into the North Sea (Reid *et al.* 2003). The NAO has major impact on fish stocks in the North as well as the transport of fish larvae across the North Sea (Corten 2001, Beaugrand *et al.* 2003, Stenseth *et al.* 2004). When the NAO is in a positive phase herring larvae are transported from the spawning grounds in the eastern UK waters to the nursery areas in the Wadden Sea and the Skagerrak/Kattegat (Corten 2001). During negative phases the larvae fail to reach the nursery areas. Because herring is a very important food source for Sandwich Terns one may expect that the NAO strongly influences the feeding condition of Sandwich Terns nesting in the more eastern parts of the North Sea. With the collapse of the herring stock in the 1970s (at least in part due to the industrial fishery) the NAO was in a negative phase and herring larvae failed to reach the nursery areas in the eastern North Sea. With the failure of herring larvae to reach the eastern North Sea, the sprat stock in the western North Sea expanded enormously (Corten 2001). In other words: while the feeding conditions for Sandwich Terns deteriorated in the eastern North Sea, conditions improved in the western North Sea. In the mid 1980s, the NAO reverted to a positive phase and the transport of herring larvae returned to normal while the sprat stock in the western North Sea declined (Corten 2001). After 1985, therefore, feeding conditions for Sandwich Terns improved in the eastern and deteriorated in the western North Sea. In accordance with this, around 1985 growth resumed in the German Sandwich Tern population, while the eastern UK population started to decline (Fig. 9.10). In fact the German North Sea population closely followed fluctuations in the NAO throughout the period 1969-2004, and also in the Dutch Wadden Sea the number of breeding pairs were positively correlated with the NAO-index. Although the population development of the German North Sea population and the Dutch Wadden Sea population largely overlap, there are some interesting differences. During periods of positive NAO-indices in 1985-1995, the German North Sea population increased while at the same time growth stagnated in the Dutch Wadden Sea. When the NAO-index changed to negative values after 1996, breeding numbers decreased in Germany and strongly increased in the Dutch Wadden Sea. This suggests a link between the populations in the Dutch Wadden Sea and colonies in the German Wadden Sea and a high degree of exchange of individuals linked to fluctuations in feeding conditions in the more eastern colonies. Similarly, when feeding worsened in the eastern UK waters after 1985 birds may have migrated to German (and Dutch) colonies where feeding conditions had improved. Ring recoveries of breeding adults on Griend confirm that a disproportionately large number of immigrants from UK-colonies were ringed in the 1980s, whereas recoveries of birds ringed in Danish colonies were more evenly distributed over the past four decades (Table 9.1).

Table 9.1. Number of Sandwich Terns per decade ringed as pulli in the United Kingdom and Denmark, and recovered in a subsequent breeding season (May and June) on Griend in 1971-2003. Data derived from Vogeltrekstation Arnhem.

Year of birth	Number of UK- immigrants (%)	Number of DK- immigrants (%)
1960-1969	10 (9.4)	11 (28.9)
1970-1979	13 (12.3)	6 (15.8)
1980-1989	62 (58.5)	8 (21.1)
1990-1999	21 (19.8)	13 (34.2)

From the above we may conclude that there is substantial evidence that the NAO is the driving force that changes the distribution and composition of fish stocks in the North Sea and ultimately determines the distribution of Sandwich Terns over Europe. It still remains puzzling how the population changes in the southern North Sea, Channel, Ireland and west England are related to this. The strong links between the European populations and the supposed link with the dynamics of their prey fish argue for a close cooperation between various countries in resolving this puzzle. As Sandwich Terns are indicators of the food situation par excellence and because reproductive parameters and the demography of the populations can be measured relatively easily, a European wide study on breeding numbers and reproductive output and a better organisation of ringing and ring recovery than was done hitherto is called for. The results of this study should then be coupled with a North Sea wide study on the dynamics of clupeids stocks as well as sandeel.

THREATS TO THE EUROPEAN SANDWICH TERN

So far we have seen that Sandwich Terns are highly vulnerable to reductions in food supply in the breeding areas and to pollutants that accumulate in the food web. Sandwich Terns have a restricted choice for breeding habitats and breed gregariously in a few very dense colonies. Northwest Europe only harbours a few large colonies (10-20 depending on the definition) of this species. If anything happens to one of these colonies, this can have major consequences for the size of the European breeding population as a whole. This happened in the 1960s in The Netherlands, when poisoning of the Dutch coastal waters caused that about two-thirds of the total European population perished. Likewise persecution by humans (large-scale egging and shooting of adults) has heavily reduced the European population in the beginning of twentieth century.

The highly gregarious behaviour of this species also poses a threat during wintering. All European Sandwich Terns share the same wintering areas and the distribution over the wintering areas does not differ between terns of various breeding origin (Møller

1981, Brenninkmeijer & Stienen 1999). The main wintering grounds are situated along the coast of West Africa, with Senegal and Ghana as strongholds (Müller 1959, Møller 1981, Urban *et al*. 1986, Brenninkmeijer & Stienen 1999). This implies that it is not likely that the distinct changes in numbers in the various European countries are caused by factors acting in the wintering areas, although at the same time changes in the wintering area can have large effects on the European population as a whole. At present, the food situation during winter is probably not limiting the size of the European population (chapter 8), but other factors such as the trapping of terns in the wintering areas may limit the growth of the population.

Local people living near the terns' main wintering grounds in Senegal and Ghana, are notorious for their habit of tern trapping (Mead 1978, Dunn 1981, Meininger 1988, Staav 1990). On an annual basis several thousands of terns are the victims of this practice, with Sandwich Tern being one of the most affected species (Stienen *et al*. 1998). However, the exact impact of this practice remains unknown, as the estimates are very imprecise and based on incomplete coverage of the wintering area. In countries where tern trapping is a common habit, the recovery rate of ringed terns will be higher than elsewhere. In Mauritania for example the density of the human population is extremely low and tern trapping is not commonly practiced, resulting in relatively low recovery rates from this country. Estimates of the number of terns wintering in Mauritania (Perennou 1991) are much higher than expected from the distribution based on ring recoveries (Brenninkmeijer & Stienen 1999). Integral counts of the number of terns wintering in Africa have never been made and counts carried out in the wintering areas are scarce and widely scattered in time and space.

In many West-African countries a strong increase in commercial fishery took place during the past decades. At present, the coastal waters along West Africa are heavily exploited by European, Russian and Asian vessels and effects on the marine ecosystem are already obvious. There is a particularly high fishing pressure on pelagic fish (Alder & Sumaila 2004) that can potentially have a large impact on piscivorous birds like Sandwich Terns. There is a strong need for a scientifically based fishery policy and regulation of commercial fishery in West African waters to avoid overexploitation and to reduce the impact on the ecosystem (Kaczynski & Fluharti 2002, Alder & Sumaila 2004).

Another recent threat to European Sandwich Terns is the growing economic interest in coastal areas by the offshore wind industry. With the first offshore power plants already in operation and many more projects under consideration, wind farms will soon be a widespread phenomenon along the Atlantic and North Sea coasts. For economical reasons shallow coastal waters will be the most interesting sites to situate offshore power plants and thus the accumulated impact of offshore wind farms (barriers and increased mortality as well as possible effects on the fish stocks) may particularly affect near-coastal migrants like Sandwich Terns.

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Appendix 9.1. Number of breeding pairs of Sandwich Tern in various parts of The Netherlands and in Belgium during the period 1900-2004. Data before 1960 are reconstructed (interpolated at the colony level accounting for known trends in adjacent colonies) from figures given in literature (see Brennikmeijer & Stienen 1992 for more details). From 1960 onwards, almost all Dutch colonies were counted annually and figures are much more reliable.

Year	Griend	rest Wadden	rest NL	Belgium
1900	2000	3085	11000	0
1901	2000	3485	11000	0
1902	2000	2085	11000	0
1903	2000	2085	10000	0
1904	1500	595	9000	0
1905	1000	185	8000	0
1906	500	1100	7000	0
1907	0	1000	4000	0
1908	0	1250	3000	0
1909	0	1500	2000	0
1910	0	1750	500	0
1911	0	0	500	0
1912	0	0	1000	0
1913	0	0	2000	0
1914	3	0	3000	0
1915	300	50	4000	0
1916	2000	50	5000	0
1917	2500	50	6000	0
1918	4100	50	7000	0
1919	4100	50	8000	0
1920	3000	0	9000	0
1921	4200	0	9000	0
1922	4200	0	9000	0
1923	4000	150	9000	0
1924	4000	50	9000	0
1925	5000	50	8000	0
1926	5000	50	8000	0
1927	6000	50	8007	0
1928	8000	25	8002	0
1929	10000	4	8381	0
1930	12500	21	8000	0
1931	15000	19	8800	0
1932	17500	4	7860	0
1933	22000	300	8082	0
1934	22000	0	8305	0
1935	21465	300	9436	0
1936	18640	450	8650	0
1937	25000	110	9500	0
1938	35000	110	10750	0
1939	27500	2010	8550	0
1940	15000	15005	10210	0
1941	4000	10000	12220	0
1942	8000	15016	10100	0
1943	25000	3035	9225	0
1944	5000	200	11000	0
1945	8000	550	15500	0
1946	15000	1153	9260	0
1947	12500	1535	7310	0
1948	12500	2800	10549	0
1949	12500	5750	10560	0
1950	12500	5875	10460	0
1951	12500	6000	15000	0
1952	12500	5500	14760	0
1953	12500	4000	11510	0
1954	22500	3292	11435	0
1955	6500	8905	13321	0
1956	12500	10332	13314	0
1957	10000	14882	7490	0
1958	7500	6622	4860	0
1959	5500	3906	4079	0
1960	5250	715	4057	0
1961	5000	2352	4514	0
1962	7000	858	4489	0
1963	1500	92	3004	0
1964	1500	15	752	0
1965	725	90	60	0
1966	1500	2	193	0
1967	900	2	298	0
1968	1200	2	364	0
1969	1600	0	436	0
1970	1700	1	717	0
1971	2100	70	1019	0
1972	2100	236	1640	0
1973	2200	53	2100	0
1974	2700	270	2354	0
1975	2250	687	2105	0
1976	2700	752	2102	0
1977	2500	1385	1200	0
1978	3300	603	2203	0
1979	2950	851	3150	0
1980	4000	616	3400	0
1981	4650	1212	3923	0
1982	4100	1150	4106	0
1983	6000	633	4100	0
1984	5050	305	3500	0
1985	3900	610	4170	0
1986	6900	500	4700	0
1987	5900	750	3985	0
1988	7600	12	4250	1
1989	9000	130	3414	250
1990	7300	300	3204	300
1991	7000	750	2524	950
1992	6600	0	2778	1100
1993	7600	0	3300	1650
1994	8300	0	3351	800
1995	8200	60	4850	250
1996	5600	496	4601	670
1997	5000	1987	4975	425
1998	7000	2050	4500	73
1999	7800	0	6350	720
2000	7918	737	5800	1550
2001	8207	17	6350	920
2002	10970	142	6200	46
2003	11260	500	6700	823
2004	11275	351	3793	4067