Chapter **2**

Reflections of a specialist: patterns in food provisioning and foraging conditions in Sandwich Terns *Sterna sandvicensis*

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ASTRACT

Highly specialised piscivorous seabirds, like Sandwich Terns *Sterna sandvicensis* have limited capacity to switch to alternative prey species when the availability of a particular prey species is low. Therefore, variations in the diet of such species are likely to reflect fluctuations in food availability. We studied food provisioning of Sandwich Tern chicks on Griend in 1992-98. The chicks were predominantly fed with Clupeidae and Ammodytidae. About 75% of the fish brought to the colony were eaten by the chicks. The rest was lost, mainly to robbing Black-headed Gulls *Larus ridibundus*. Parents met the increasing energy demands of the growing chicks by adjusting prey size, rather than increasing the rate of prey transport to the chicks. Distinct patterns in food transport rate, diet composition and prey size were associated with weather conditions and diurnal or tidal rhythms. Food transport to the colony was severely curtailed by strong winds, but was also relatively low at low wind speeds. Wind speed also had a large impact on prey size and diet composition, with a decreasing proportion of Clupeidae brought to the chicks as foraging conditions became worse. Distinct diurnal rhythms in food transport coincided with diel vertical migration patterns in Clupeidae and Ammodytidae. Clupeidae were mostly brought to the colony early in the morning and late in the evening, while the transport of Ammodytidae was highest around noon. Tidal patterns in food delivery rate were probably related to tide-specific foraging areas used by the terns. A fish-monitoring programme showed considerable variation in food abundance within the foraging area of the terns. Especially Clupeidae had a patchy distribution and most clupeids were caught in the coastal areas around Vlieland. In accordance to the pattern found in the colony, Clupeidae caught in 1996 and 1997 towards fledging of the chicks and in 1998 just after hatching of the chicks in 1998 were relatively small.

INTRODUCTION

Seabirds are highly susceptible to changes in food availability, in particular during the breeding season, when they are confined to feeding areas relatively close to the colony, and perhaps work close to the limits of their capacity. They have evolved several life history strategies that may help to overcome difficulties in foraging. Compared to other birds, seabirds lay smaller clutches, have a delayed maturation and are long-lived (Lack 1968). Moreover, they often breed in dense colonies, which may enhance their chances of finding sufficient food for their offspring when food is irregularly distributed (Evans 1982; Waltz 1987; Götmark 1990). Despite these adaptations several well-documented cases describe marked changes in breeding performance and population size of seabirds due to the collapse of components of their food stock (e.g. Heubeck 1988; Monaghan *et al*. 1989; Vader *et al*. 1990; Bailey 1991; Suddaby & Ratcliffe 1997). Generalists among seabirds may be able to buffer fluctuations in the availability of a particular prey species by switching to alternative prey. Highly specialised piscivorous seabirds like Sandwich Terns *Sterna sandvicensis*, however, face the disadvantage of restricted choice, which makes them particularly vulnerable to temporal and spatial variation in one of their food components. During the breeding season, Sandwich Terns predominantly feed on a few high quality prey species (e.g. Isenmann 1975; Campredon 1978; Shealer 1998); in the southern North Sea these prey are mainly *Clupeidae* and *Ammodytidae* (Pearson 1968; Veen 1977; Garthe & Kubetzki 1998).

Many marine fish exhibit a specific rhythmicity of activity (Thorpe 1978). Diurnal and tidal patterns in the behaviour of the fish may force seabirds to adjust their activities to the cyclic behaviour of their prey in order to raise successfully their chicks (Daan 1981). Short-term changes in the accessibility of one of the Sandwich Tern's prey species must be tackled with proper switching to other foraging areas or alternative prey. Because Sandwich Terns are single prey loaders, such shifts, if noticeable, will almost instantly be noticed in the diet of the chicks. Food provisioning to a tern colony is not only dictated by the energy requirements of the chicks (Klaassen *et al*. 1992), but as shown by various studies is also influenced by environmental conditions. Distinct diel and tidal rhythms in food transport to the colony have been described, and both food intake rate and growth of the chicks have been related to adverse weather conditions that influence fishing success of the parents (Pearson 1968; Dunn 1972, 1973; Veen 1977; Campredon 1978; Taylor 1983). However, nearly all these studies covered only a small part of the chick-rearing period. Only Veen (1977) compared the presence of different prey species in the chick diet over a period of 3 years. Our 7-year study on Sandwich Terns breeding on Griend, Dutch Wadden Sea, allows a detailed analysis of parameters affecting prey size and food delivery rate, and patterns in food transport will here be discussed in relation to changes in the availability of the prey fish.

STUDY AREA AND METHODS

The isle of Griend, The Netherlands (53°15'N, 5°15'W), is situated in the centre of the western Dutch Wadden Sea (Fig. 2.1). The small island (about 57 ha during normal high tide) is inhabited by several species of colonial nesting terns and gulls. The Sandwich Tern's feeding ecology was studied during the breeding season of 1992-98. During the study period the population of Sandwich Terns fluctuated between 5600 (1996) and 8300 (1994) pairs, consisting of several subcolonies. In each year part of a subcolony, containing 50-100 nests, was fenced (further referred to as 'enclosure') to prevent the chicks from walking away from the nest site.

Chicks hatched in the enclosures were ringed and aged immediately after hatching. Each year, about 20 chicks were colour-marked for individual recognition. Data on chicks' diet were collected from an elevated blind, placed at a few metres from the colony. Continuous observations on food provisioning were made from 4:30 a.m. to 10:30 p.m. In most years chicks were followed from hatching until fledging. Only in 1992, chicks were followed until 21 days and in 1995 the age of the chicks ranged from 15-26 days. Prey size was estimated in quarters of the parent's bill size (BL = 5.43 ± 0.25 cm, N = 679). Estimating prey size was calibrated per observer by holding fishes of

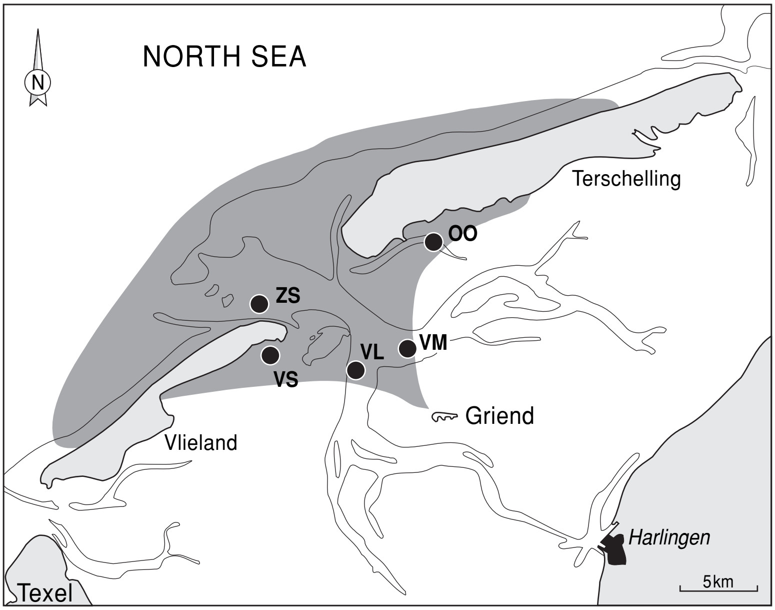

Figure 2.1. Map of the western Wadden Sea, indicating the location of Griend and the fish sampling points (dots). The grey area roughly indicates the foraging area of the Sandwich Terns breeding on Griend. ZS = Zuider Stortemelk, VS = Vliesloot, VL = Vliestroom, WM = West Meep and OO = Oosterom.

different species and various lengths in front of a stuffed tern's bill at distances comparable to the situation in the colony. Calibration greatly increased the accuracy of the estimates, and the largest error an experienced observer ultimately made was 0.25 BL. Both for *Clupeidae* and *Ammodytidae* an allometric equation relating fish length to fresh mass was obtained, using least square analysis on fish found in the colony and fish sampled in the Wadden Sea in 1993 and in 1994 (Fig. 2.2). We use the term 'delivery rate' when referring to the number of food items brought to the chicks and the term 'mass provisioning' when referring to the amount of mass brought to the chicks. Throughout the experimental work we recorded wind speed with a calibrated cup anemometer at standard meteorological level (10 m).

In 1995-98, a fish-sampling programme was performed at five locations in the foraging area of the terns (Vliestroom, Westmeep, Stortemelk, Vliesloot and Oosterom; Fig. 2.1). The locations covered an important part of the foraging area of the Sandwich Terns breeding on Griend. Fish sampling periods corresponded with the courtship period (end of April), the early chick stage (first week of June) and the late chick stage (end of June) of the terns. We used an Isaac's Kidd Midwater Trawl net (IKMT-net) with a mesh size of 6 mm that sampled only the upper 2 m of the water layer, in accordance with the diving depth of terns (Borodulina 1960; Dunn 1972). Each haul lasted approximately 30 minutes. The volume of water passed through the IKMT-net was measured by means of a flow meter mounted in the mouth of the net. Catches were converted to numbers per 10,000 m^3 water.

To avoid an unrealistic bias of observation duration, only when observations on fish brought to the chicks lasted more than 30 minutes (effects of time of day and wind speed) or more than 9 hours (age effects) were they used in the graphs. Unless otherwise indicated, for statistical tests all data were used, using protocol duration as offset

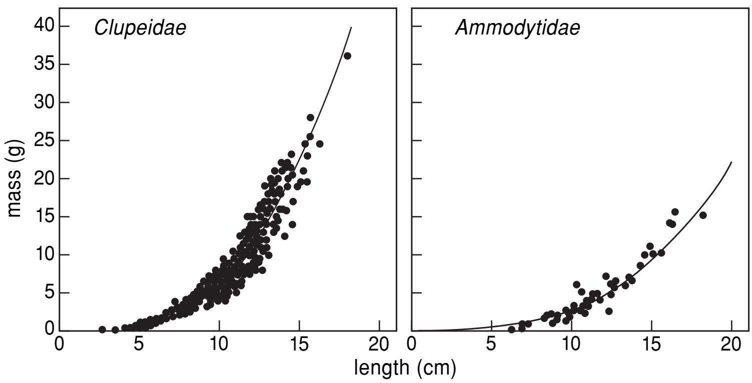

Figure 2.2. Length-mass relationship in herring and sandeel found in the colony in 1992-97 and sampled in the Wadden Sea in 1993-94. Herring: fresh weight=0.00682*length$^{2.996}$ (n = 825, r^2 = 94.0); sandeel: fresh weight=0.00296*length$^{2.982}$ (n = 73, r^2 = 97.4).

variable. For logistic regression analysis of the effects of hatching order, year, time of day, wind speed, age of the chicks and tide on delivery rate or mass provisioning rate data were separated into 1 hour periods (only periods lasting more than 30 minutes) using protocol duration as offset variable. Statistical tests were performed using the SPSS/PC+ 4.0 (Norusis 1990) and the Genstat statistical package (Genstat 5 Committee 1993).

RESULTS

Diet composition and prey size

In 1992-98, food brought to the colony mainly consisted of *Clupeidae* (herring *Clupea harengus* and sprat *Sprattus sprattus*) and *Ammodytidae* (sandeel *Ammodytes tobianus* and greater sandeel *Hyperoplus lanceolatus*). In total these prey species amounted to 99.3% of the diet (Table 2.1). Unless otherwise stated, we further use the term 'herring' when referring to *Clupeidae* and 'sandeel' when referring to *Ammodytidae*. Other prey species consisted of goby *Gobies* spp., cod *Gadus morhua*, whiting *Merlangius merlangus*, smelt *Osmerus eperlanus*, eelpout *Zoarces viviparus*, three-spined stickleback *Gasterosteus aculeatus*, pipefish *Sygnathus* spp., sea lamprey *Petromyzon marinus*, flounder *Platichthys flesus*, cephalopods *Sepia* spp. and brown shrimp *Crangon crangon*. Prey species other than herring and sandeel will only be included in this paper if relevant.

The size of the herring and sandeel provided to the chicks varied between 0.25 BL and 4.00 BL (Fig. 2.3), corresponding with 1.5-21.5 cm and 37 g as a maximum. On average sandeel were somewhat longer than herring (1.98 ± 0.42 BL and 1.59 ± 0.31 BL, respectively; two-directional Student's t-test, $t = 63.27$, $P < 0.001$), corresponding with 11 and 9 cm, respectively, and prey masses of 3.5 g and 4.5 g, respectively. Prey size significantly differed between years (Table 2.2), with relatively small herring brought to the colony in 1996 and 1998 and relatively small sandeel in 1993. Both herring and sandeel were relatively long in 1995, but this was partly an effect of the age of the chicks followed in that year. However, if effects of chick age and other effects influencing prey size were taken into account, year effects are still present (Table 2.3), but then sandeel appeared to be relatively small in 1995.

Table 2.1. The proportion of herring, sandeel and other prey species in the chicks' diet on Griend in 1992-98.

	1992	1993	1994	1995	1996	1997	1998
Herring	49.5	55.0	84.0	69.7	32.7	79.0	63.3
Sandeel	49.7	44.7	14.9	29.8	66.6	20.3	36.0
Other	0.8	0.3	1.1	0.5	0.7	0.7	0.8
Total number of fish	630	3469	3279	1290	3262	2579	2520

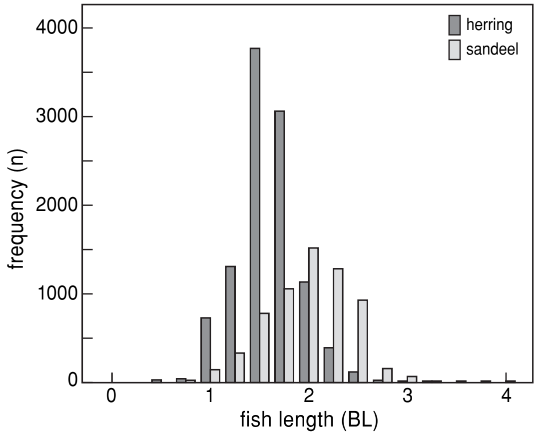

Figure 2.3. Length distribution of herring and sandeel brought to the chicks on Griend in 1992-98. BL = bill length of adult terns.

Table 2.2. Variation in prey size (BL) of Sandwich Tern chicks on Griend in 1992-98. Scheffé-test denotes significant differences (P < 0.05) with other years.

Year	Mean herring length± SD	Scheffé-test $F_{6,10373}$ = 171.39	Mean sandeel length ± SD	Scheffé-test $F_{6,6263}$ = 71.66
1992	1.63 ± 0.31	98,96	2.08 ± 0.34	93,98
1993	1.63 ± 0.30	98,96,94,97	1.83 ± 0.38	
1994	1.59 ± 0.29	98,96	2.17 ± 04.6	93
1995	1.86 ± 0.30	98,96,94,97,92,93	2.12 ± 0.32	93,98,96
1996	1.51 ± 0.30		2.02 ± 0.40	93
1997	1.59 ± 0.19	98,96	2.09 ± 0.40	93,98,96
1998	1.49 ± 0.41		1.96 ± 0.46	93

Fate of fish brought to the colony

Of all fish brought to the colony (n = 17,029) on average 69.8% were eaten by the chicks (Table 2.4). Most fish that were not eaten by the chicks was robbed by Black-headed Gulls *Larus ridibundus* (18.7%) or disappeared out of the observer's sight (7.9%). Some fish were robbed by neighbouring Sandwich Terns, but each year this was less than 2% of the total number of fish. Occasionally other species, mainly Common Gulls *L. canus* and Common Terns *S. hirundo*, succeeded in robbing fish of arriving Sandwich Terns. Some fish fell in the nest or was eaten by the parent (in total 2.9%). The latter could be divided into fish eaten by the parent under pressure of the robbing gulls (1.0%) and for

Table 2.3. *P*-values of multiple or logistic regression analyses examining the effects of hatching order (single chick, first hatchling, second hatchling), year (1992-98), time of day (hour 4-22), wind speed (in m s^{-1}), chick age (in days) and tide (hours before and after high tide) on the length of herring and sandeel (multiple regression, n = 9957 and 5901, respectively), the number of herring and sandeel and the total number of fish (poisson distributed logistic regression, n = 35983, 35004 and 35004, respectively) and mass (multiple regression, n = 35004) provisioned to Sandwich Tern chicks on Griend. For the analysis of the provisioning rate of herring and total prey hour 4 was omitted because of the deviate pattern (see text). Similarly hour 4-5 were omitted from the analysis examining the patterns in mass provisioning.

		Prey length		Number of prey			
Parameter	df	Herring	Sandeel	Herring	Sandeel	Total	Prey mass
Hatching order	2	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Year	6	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Time of day	1	< 0.001	< 0.001	NS	< 0.001	< 0.001	NS
Time of day2	1	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Wind speed	1	NS	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Wind speed2	1	< 0.001	< 0.001	< 0.01	< 0.001	< 0.001	< 0.001
Age	1	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Age2	1	< 0.001	< 0.001				
Tide	11	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Table 2.4. Fate (%) of fish brought to Griend by Sandwich Terns in 1992-98.

	1992	1993	1994	1995	1996	1997	1998
Eaten by chick	81.0	72.6	70.4	80.3	63.9	72.1	64.2
Robbed by Black-headed Gull	11.4	16.1	20.5	14.7	22.9	11.6	24.0
Robbed by Sandwich Tern	1.0[1]	1.6	0.8	0.2	0.5	0.1	0.1
Robbed by other species		0.1	0.2	0.0	0.1	0.1	0.0
Disappeared out of sight	5.1	6.9	5.4	4.1	11.5	8.6	9.4
Left in nest			0.4	0.1	0.2	0.6	0.4
Eaten by parent (gull pressure)	1.6[2]	2.7[2]	1.6	0.4	0.5	0.5	1.7
Eaten by parent (other reason)			0.7	0.2	0.6	6.4	0.2
Total number of fish	630	3469	3279	1290	3262	2579	2520

[1]no distinction made between ‘robbed by Sandwich terns’ and ‘robbed by other species’
[2]no distinction made between ‘eaten by parent under gull pressure’ and ‘eaten by parent because of other reasons’.

other reasons (1.6%). Prey size differed between the various categories of fate (Fig. 2.4). Fish robbed by Black-headed Gulls were significantly larger than fish eaten by the chicks, and fish lost from view were larger than fish eaten by the parents (Scheffé-test, herring and sandeel F = 66.6 and 84.7, respectively, P < 0.05).

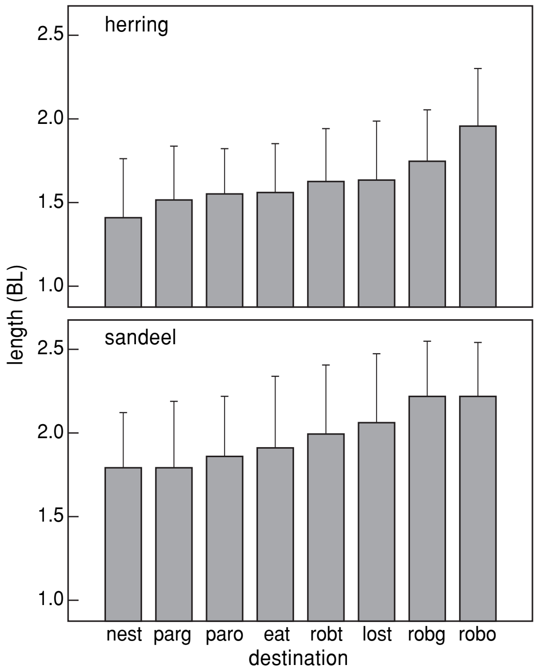

Figure 2.4. Length of herring and sandeel (mean ± SD) brought to the chicks on Griend in 1992-98 according to the fate of the fish. Nest = fallen in nest, parg = eaten by parent as a result of gull pressure, paro = eaten by parent for other reasons, eat = eaten by chick, robt = robbed by Sandwich Tern, lost = disappeared of the observer's sight, robg = robbed by Black-headed Gull and robo = robbed by other species.

Food provisioning in relation to the age of the chicks

In 1994 and 1996, prey delivery rate significantly increased towards the end of the chick-rearing period (Pearson regression, $r^2 = 0.03$, $P = 0.003$ and $r^2 = 0.45$, $P < 0.001$, respectively). In 1994, however, the increase was small. In all other years, there was no general trend or delivery rate slightly decreased (1998) with ongoing age of the chicks (Pearson regression, $r^2 = 0.05$, $P = 0.001$ in 1998). A logistic regression analysis also accounting for effects other than chick age showed a slight but significant increase in the delivery rate of herring, sandeel and total fish with age (Table 2.3). Instead of bringing in more fish, in all years parents brought in longer fishes to keep pace with the growing energy demands of their growing chicks (Fig. 2.5, Table 2.3). On average the daily prey mass brought to the colony amounted less than 15 g at hatching to about 55 g near fledging (Fig. 2.5). Prey other than herring and sandeel were mainly supplied during the first days after hatching, but on average never amounted more than 0.25 prey chick^{-1} day^{-1} (Fig. 2.5).

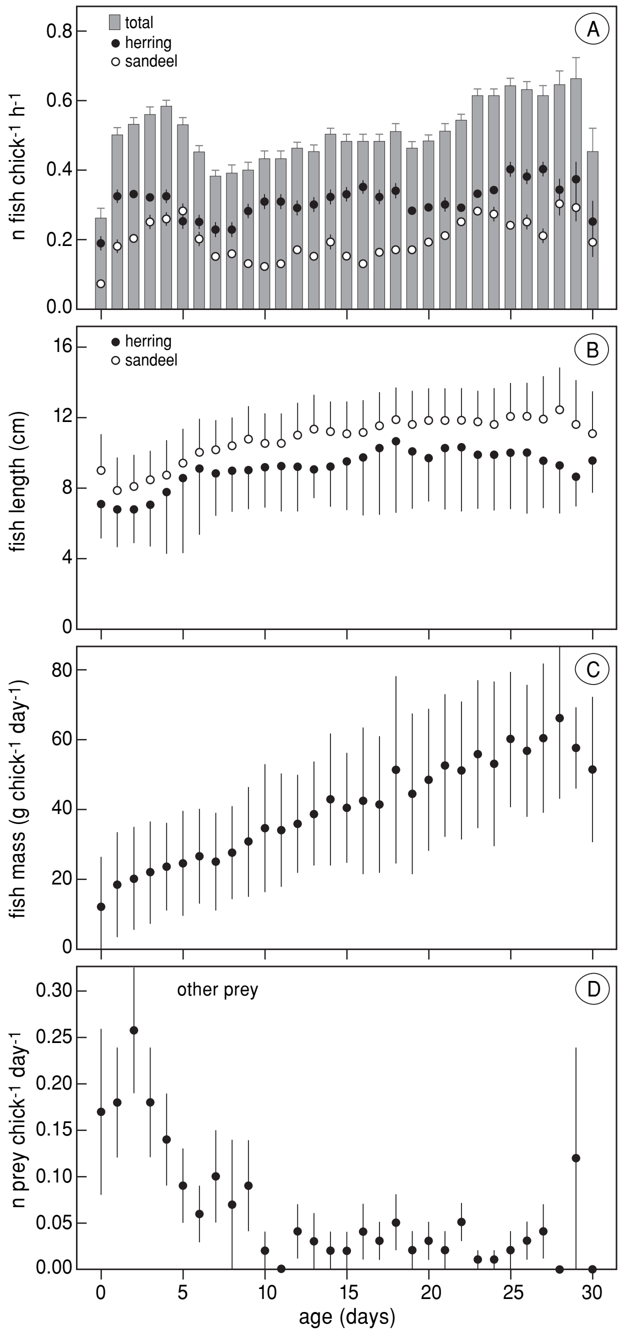

Figure 2.5. Effects of the age of Sandwich Tern chicks on Griend in 1992-98 on the provisioning rate of herring and sandeel (± SE, graph A), mean length of herring and sandeel (+/- SD, graph B), mean daily amount of mass (± SD, graph C) and mean provisioning rate of preys other than herring or sandeel (± SE, graph D).

Effects of hatching order

Hatching order had a large effect on the number of fish brought to the chicks (Table 2.3). The average daily number of fish offered to single chicks (9.56 ± 4.03, n = 1789) was slightly, but significantly lower than that offered to first hatched chicks in a brood of two (10.16 ± 5.22, n = 207). Since also the length of the herring significantly differed between those groups, there was no difference in mass provisioning rate (multiple regression, t = 0.94, n = 35004, n.s.). Second hatchlings were fed less than 3 fish per day (2.83 ± 2.80, n = 155) and although they were fed somewhat larger fish than their older sibling, there was still a large difference in mass provisioning rate between first and second hatchlings in a brood of two (multiple regression, t = 11.40, n = 35004, P < 0.001). The difference in prey length between first and second hatchling was only present in the first 12 days after hatching (Fig. 2.6). In this period, fish offered to second hatchlings was about the same size as that offered to their three days older sibling (the difference in hatching date is about 3 days, Veen 1977). In other words, parents seem to adjust prey size to the age of their first chick and as a consequence the second chick is fed with fish that is meant for its 3 days older sibling.

Food provisioning in relation to wind speed

The number of fish transported to the colony was particularly low at wind speeds less than 3 m s^{-1} and at wind speeds higher than 14 m s^{-1} (Fig. 2.7, Table 2.3). In between, food delivery to the colony was fairly stable at a rate of about 0.5 fish $chick^{-1}$ h^{-1}. Wind speed had also marked effects on the composition of the chicks' diet: the proportion of herring gradually decreased from about 65% when wind was weak to less than 50% at wind speed of 16 m s^{-1}. When wind was even stronger, the proportion of herring increased again. These changes were the result of different changes in the number of herring and sandeel brought to the colony with increasing wind speed (Fig. 2.7). The

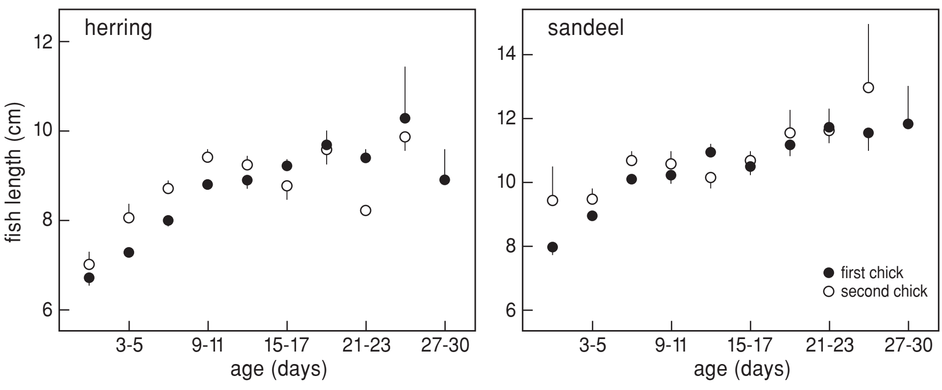

Figure 2.6. Differences in prey length in relation to hatching order and age of Sandwich Tern chicks on Griend in 1992-98. Means +/- SE are plotted.

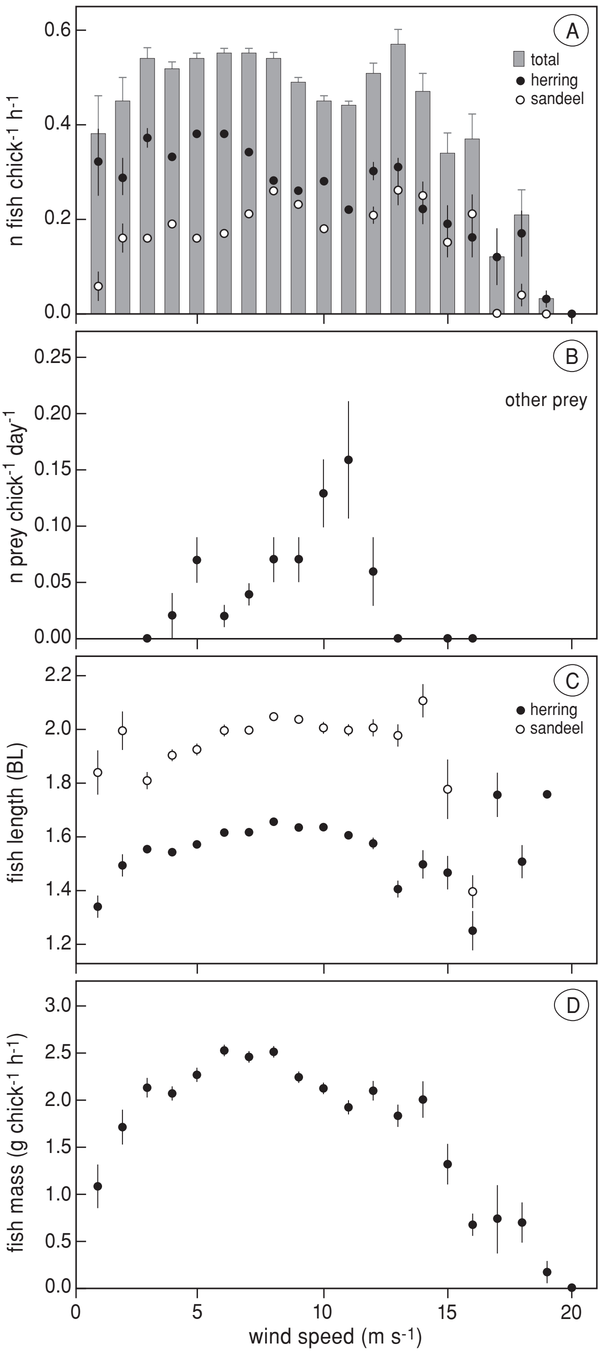

Figure 2.7. The effects of wind speed on the provisioning rate of herring and sandeel (A), other preys (B), prey length (C) and mass provisioning rate (D) of Sandwich Tern chicks on Griend (1992-98). Means ± SE are plotted.

delivery rate of herring gradually decreased, while that of sandeel initially increased with increasing wind speed. Small hatchlings were fed an increasing number of other preys with increasing wind speed, although this trend was broken when wind speed exceeded 11 m s^{-1} (Fig. 2.7). At intermediate wind speeds (5-12 m s^{-1}) significantly longer herring were brought to the chicks than at lower and higher wind speeds (Fig. 2.7). Wind had similar effects on sandeel length, but the slope of the effect did not significantly differ from zero (multiple regression, $t = 0.13$, $n = 5901$, n.s.). The amount of mass brought to the colony initially increased to 2.5 g h^{-1} at wind speeds of 6-8 m s^{-1}, but gradually decreased afterwards (Fig. 2.7).

Food provisioning in relation to the time of the day

No feeding was observed before 4:30 a.m. Almost no feeding occurred after 10:30 p.m. and it completely ceased before 11:00 p.m. The rate of food transport to the chicks was rather low in first hour of the day, but increased to high values directly afterwards (hour 5-6; Fig. 2.8). As the day progressed delivery rate gradually decreased and was more or less stable from 9 a.m. onwards. Note that in the first and last hour of the day delivery rate was actually lower than the extrapolated figures plotted in figure 2.8 because these periods lasted less than 60 minutes. Herring and sandeel peaked at different times of the day. If for a moment not considering the first hour of the day, when the transport of both prey types was low, transport of herring was high early in the morning and late in the evening, with less herring brought to the chicks in the intervening period (Fig. 2.8). The delivery rate of sandeel showed more or less the opposite pattern, with a particular high delivery rate just before noon and a gradual decrease towards dusk. The proportion of herring in the diet varied from more than 82% early in the morning and late in the evening to 50% just before noon. Distinct diurnal patterns were also found in the size of both prey species (Fig. 2.8, Table 2.3). Most obvious, were the small sandeel brought to the colony in the first few hours of the day. Combining delivery rate and prey length resulted in an increasing food mass in the early morning, followed by a decrease between 6 and 8 a.m. (Fig. 2.8). From 8 a.m. onwards the amount of mass brought to the colony was practically stable at a rate of about 2.2 g $chick^{-1}$ h^{-1}.

Food provisioning in relation to tide

The number of fish transported to the colony was relatively low at incoming tide, when delivery rates of both herring and sandeel were low (Fig. 2.9). Most sandeel was brought to the colony during high tide, while the delivery rate of herring was highest a few hours after high tide. In almost all years, an analogous tidal pattern in delivery rate was found. In 1997 and in 1998, however, a different pattern was found in the delivery rate of herring and in 1996 an additional peak in the delivery rate of sandeel was found around low tide. The proportion of herring in the diet varied between 53% at low tide to 78% at incoming tide. The length of the sandeel fluctuated during the tidal cycle, with relatively

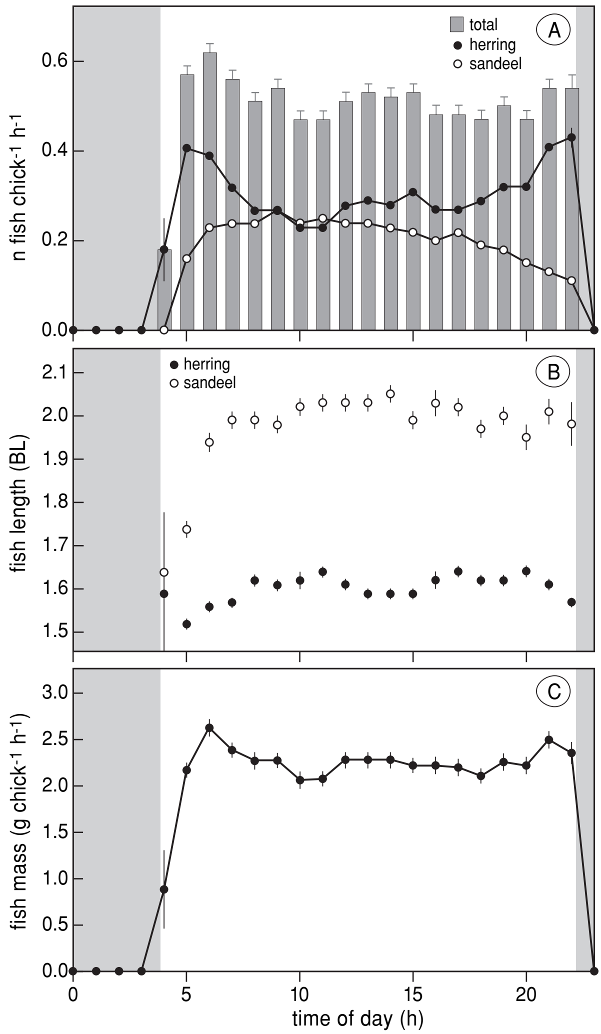

Figure 2.8. Diurnal patterns in provisioning rate of herring and sandeel (A), prey length (B) and mass provisioning rate (C) of Sandwich Tern chicks on Griend (1992-98). Means ± SE are plotted. It was assumed that no feeding occurred during the night (shaded areas).

large sandeel brought to the colony around high tide (Fig. 2.9, Table 2.3). Herring brought to the colony during incoming tide were slightly, but significantly larger than those supplied during other parts of the tidal cycle (Fig. 2.9, Table 2.3). Fish mass brought to the colony peaked around high tide and was relatively low a few hours after low tide (Fig. 2.9, Table 2.3).

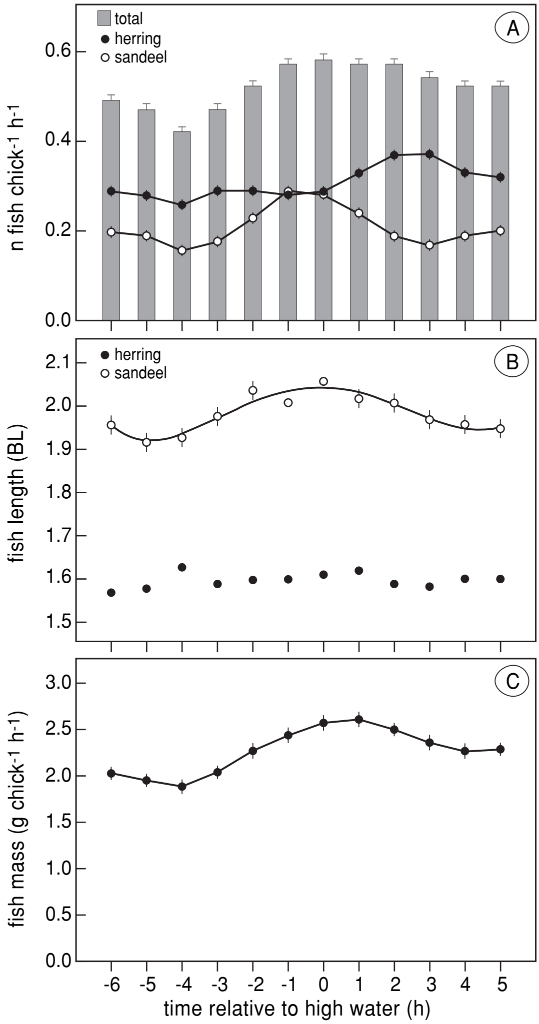

Figure 2.9. Tidal patterns in provisioning rate of herring and sandeel (A), prey length (B) and mass provisioning rate (C) of Sandwich Tern chicks on Griend (1992-98). Means ± SE are plotted.

Fish sampling

At all sampling locations fish abundance showed large standard deviations (Table 2.5), probably reflecting a combined effect of large variation in the occurrence of prey fish in the upper water layer, a patchy distribution of the prey and the small sample size. Especially herring had a patchy distribution and their occurrence at the surface seems very irregular. Most herring were caught in the coastal areas around Vlieland, whereas

Table 2.5. Differences in abundance and occurrence of herring and sandeel between 5 sampling locations in the foraging area of Sandwich Terns breeding on Griend, 1995-98. Fish were caught with an IKMT-net in the upper water layer. Catches were converted to number of fish per 10,000 m^3 water passed through the net.

Sampling Location	Catch per unit effort	% hauls with >10 fish	Number of hauls
Herring			
Vliestroom	0.9 ± 4.3	2.3	88
Westmeep	1.0 ± 4.5	2.2	92
Stortemelk	1181.6 ± 6896.8	11.1	81
Vliesloot	2832.4 ± 11966.5	53.0	83
Oosterom	30.6 ± 96.9	10.0	10
Sandeel			
Vliestroom	25.8. ± 98.2	17.0	88
Westmeep	18.4 ± 76.7	18.5	92
Stortemelk	32.2 ± 138.5	21.0	81
Vliesloot	66.7 ± 449.4	19.3	83
Oosterom	1.3 ± 2.6	0.0	10

the two sampling locations near Griend held relatively few herring. In the Vliesloot more than half of the hauls contained at least 10 herring, indicating a high predictability of the occurrence of this prey species. In the Stortemelk herring were relatively abundant, but occurred only in 11% of the hauls. Sandeel seem to have a more predictable distribution. Most sandeel were caught near Vlieland, but in contrast to herring they were also present in relatively high numbers at the two sampling locations near Griend. At all sampling locations they occurred in 17-21% of the hauls, except for the Oosterom, where almost no sandeel were caught.

Size distribution of the sandeel sampled with the IKMT-net closely matched that brought to the tern colony (Fig. 2.10). In contrast, the herring sampled in the IKMT-net was much smaller than those caught by the terns. It is, however, not clear whether this reflects selective feeding on large herring by the terns or poor sampling methods. Nevertheless some parallels can be seen between variation in herring length as found in the colony and variation in herring length as is reflected in the IKMT-samples (Fig. 2.11). For example the IKMT-catches indicate that the available herring were relatively small during the first week of June in 1998, and in the last week of June in 1996 and 1997. In these periods also herring brought to the colony was relatively small. The catches further indicate that the increase in prey length as observed in the colony was not always accompanied by an increase in length of the fish available. Unfortunately, the numbers of sandeel caught in June were not sufficient for proper comparative analysis.

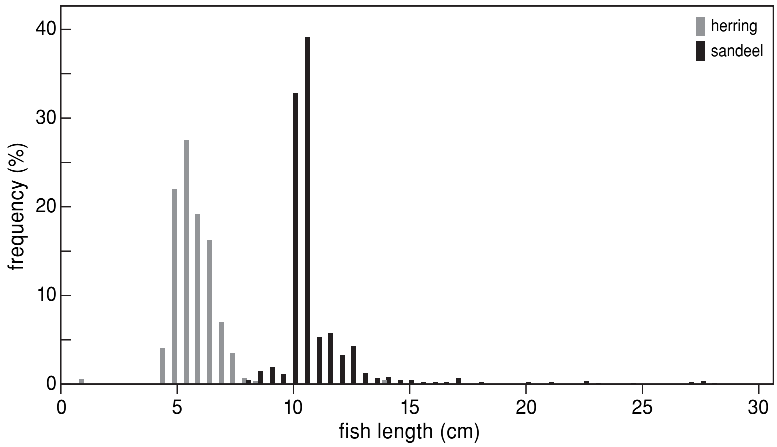

Figure 2.10. Length distribution of herring (n = 264,545) and sandeel (n = 1,625) sampled in the foraging area of Sandwich Terns breeding on Griend, 1995-98. The total length of each fish caught was measured in 0.5 cm classes.

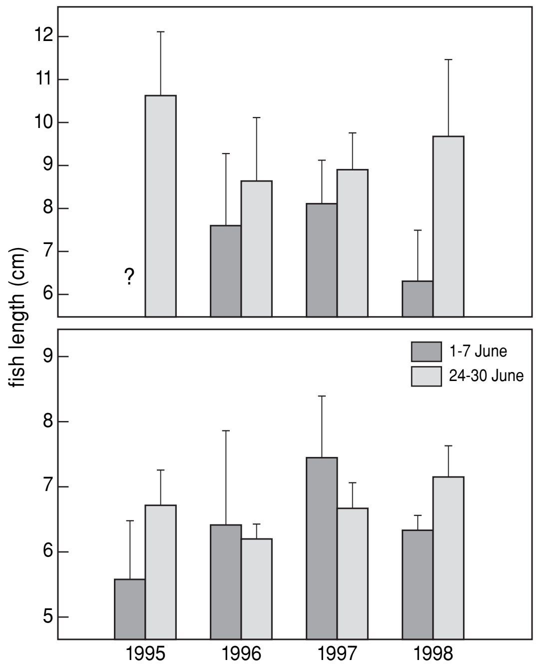

Figure 2.11. Mean length of herring (± SD) that Sandwich Tern parents brought to Griend (upper graph) compared to herring length as sampled in the foraging area of the terns (lower graph) in the first and last week of June, 1995-1998.

DISCUSSION

The diet composition of the Sandwich Terns on Griend reflects the highly specialised prey choice of this species. The observed range in fish size on Griend coincided closely with other studies conducted around the North Sea (Pearson 1968; Veen 1977; Garthe & Kubetzki 1998), although average prey length varies between sites and years. Part of the variation in prey length in our study arises from differences in age composition of the chicks observed, as parents adjusted prey length to meet the increasing energy demands of their growing offspring. Parents with two chicks seem to adjust prey size to the age of their oldest chick and fed too large fish to their second hatchling. However, when age differences and effects of hatching order, time of day, wind and tide were taken into account a year effect was still present (Table 2.3). If such variation in prey size indeed reflects fluctuations in food abundance, we would expect to find similar variations in the fish-sampling programme. However, great care must be taken in interpreting the sampling programme in terms of fluctuations in the food availability of the terns. In the first place the sampling programme only covered a part of the foraging areas of the terns. It was, for example, not possible to sample in the shallow coastal waters north of Vlieland and Terschelling where Sandwich Terns from Griend also frequently foraged. Also in the Wadden Sea only the deeper parts could be sampled, whereas the terns also foraged in shallow waters. In the second place by using a mesh size of 6 mm we selectively sampled for certain prey lengths. Moreover, fish abundance in the upper water layer appears to be highly variable, which requires enormous sample sizes to obtain accurate estimates of food abundance. With some care, one can conclude that large variation in food availability and prey length exists within the foraging area of the terns, and also between and within seasons. As expected, the largest variation was found in herring. The occurrence of suitable herring for Sandwich Terns breeding on Griend depends on a poorly understood system of influx of larvae into the Wadden Sea and migration of older herrings to the coastal areas (Corten & Van de Kamp 1976; Fonds 1978). The timing of these events seems crucial for the breeding performance of the terns as young chicks critically depend on small prey, whereas older chicks need to be fed with larger fish.

Small hatchlings are rather clumsy in handling the fish. After several trials parents sometimes give up feeding the fish to their chick, leaving the fish in the nest or eating it by themselves. When the chicks grow up, supplied fish that are not robbed, are almost instantly eaten by the chick and it practically never happens that a fish is left in the nest or is eaten by the parents. On Griend, the average chick age of fish that fell in the nest or was eaten by the parents, either with or without gull pressure was 4.7, 8.0 and 3.5 days, respectively; much lower than the overall age of chicks during the observations (15.2 days), thus probably largely explaining the smaller fish in these categories. The large size of the fish robbed by Black-headed Gulls and by species other than Sandwich Terns reflects a preference of these pirates for longer fishes. Several studies confirm that pirating Black-headed Gulls mainly take larger prey (e.g. Fuchs 1977; Veen 1977; Gorke 1990; Ratcliffe *et al.* 1997), and also when age differences of the chicks are taken into account robbed prey were significantly longer than other prey (this study). Similarly, pirating gulls may have contributed to the relatively large size of the fish categorised as ‘lost out of sight’. In many occasions, a fish-carrying parent chased by a gull flew out of sight and subsequently returned to the colony without fish. Indeed in years when robbery was severe more prey were lost out of sight (Pearson regression, $r^2 = 0.30$, $P < 0.05$).

Effects of wind

Wind may have several effects on foraging terns. Firstly, terns hovering above a prey may have difficulties remaining stationary at low wind speeds (Dunn 1972), but also when wind is strong more vigorously hovering may be required to maintain stationary. Secondly, wind affects the sea surface itself and the turbidity of the water, with consequences for the terns’ visibility of the fish and vice versa. Moreover, wind can influence the distribution and swimming activity of the prey fish (Corten & van de Kamp 1996; Bégout Anras & Lagardère 1998). Several studies investigating the influence of wind speed on fishing ability of terns found that fishing success (% of successful dives) and capture rate (number of fish caught per unit of time) in Sandwich Terns increase with increasing wind speed (Dunn 1972, 1973). Taylor (1983), however, found that capture rate in Sandwich Terns decreases with increasing wind speed. These contradicting results may be due to differences in diet composition or in characteristics of the foraging area, but the most plausible explanation is that they investigated a different range of wind speed. Dunn’s (1972, 1973) studies covered wind speeds ranging from 0.5-7.0 m s^{-1}, while in Taylor’s (1983) study wind speeds ranged from 3-16 m s^{-1}. In our study, food transport to the colony initially improved and gradually decreased with wind speeds higher than 8 m s^{-1}, but was only seriously affected when wind speed exceeded 14 m s^{-1}, thus far outside Dunn’s (1972, 1973) range. This also explains why Dunn (1975) did not find any adverse effects of wind speed (0-9 m s^{-1}) on chick growth.

Analogous to our study, Frank (1992) found that Common Tern chicks on Minsener Oldeoog (German Wadden Sea) were fed fewer clupeids and more sandeel at high wind speeds. During bad weather, clupeids show a downward migration (Ehrenbaum 1936 in Frank 1992), while shoals break up (Birkhead 1976), as a result of which herring become less available to the foraging terns. Also the horizontal distribution of the prey fish provides a plausible explanation for the effects of wind on the diet composition of terns. Our IKMT-catches showed that herring was predominantly available in the coastal areas around Vlieland. These coastal waters also held relatively large amounts of sandeel, but in contrast to herring sandeel were also caught in relatively large numbers in the Wadden Sea directly north of Griend. Under stormy conditions dominated by northwesterly winds, the sea surface in the coastal areas is extremely rough. Under such conditions, the less exposed Wadden Sea probably provides better foraging conditions for terns than the coastal areas. Thus, if indeed terns switch to forage in the Wadden Sea with strong winds, one should expect an increasing proportion of sandeel. This would also explain the decrease in herring length with strong winds as the Wadden Sea typically holds small herring (Fonds 1978; Corten 1996)). Further observations on the distribution of foraging terns and more insight into the behaviour of their prey fish are, however, needed to effectively explain the observed changes.

When wind speed increased, chicks of less than 6 days old were fed an increasing number of prey other than herring and sandeel, predominantly small and energy low species, like Goby and Brown Shrimp. These alternate preys contribute to fulfil the energy demands of small chicks, but become unimportant when the chicks grow. Even under extremely rough foraging conditions when the provisioning of high energetic preys was severely affected, the parents of older chicks did not switch to less profitable prey species.

Diurnal rhythms

Several authors found diurnal rhythms in feeding activity in fish-eating birds (e.g. Cairns 1987; Hamer & Thompson 1997). In terns, peaks in feeding activity were found early in the morning and late in the evening (Dunn 1972; Hulsman 1977; Frank 1992). Dunn (1972) argued that such diurnal patterns could result from changing energy requirements of the chicks during the day, the peak in feeding activity at dawn would then result from the hunger state of adults and chicks after a night without food, while the peak at dusk follows the need for a final feeding bout before the night falls. A few studies have related the diel pattern in feeding activity in birds to vertical movements of their prey (Sjöberg 1985; Piersma *et al*. 1988; Richner 1995). Many fish show diurnal rhythmicity and move vertically in the water column as light or feeding conditions change (Thorpe 1978). *Clupea harengus* migrates upwards to the surface at dusk where they tend to disperse near the surface; they reform and move to deeper waters at dawn (Blaxter & Parrish 1965; Laevastu & Hayes 1981). Diving Sandwich Terns can reach a maximum depth of 2 m (Borodulina 1960; Dunn 1972), and thus are depending on fish present near the water surface. Furthermore, foraging Sandwich Terns utilise visual cues and therefore do not feed during darkness (Smith 1975), when herring is most available in the upper water column. Thus parallel to the pattern in herring transport to Griend, *Clupea harengus* is typically available for foraging terns during the early morning hours and before the night falls. *Ammodytes tobianus*, like other *Ammodytes* spp. (Thorpe 1978; Yamashita *et al*. 1985), are buried in the sediment at night and swim near the surface during daylight (Macer 1966; Reay 1970). So, the patterns of vertical migration in *Clupea harengus* and *Ammodytes* perfectly match the patterns found in the colony. Unfortunately, we do not know of any publications on vertical movements in *Sprattus sprattus* and *Hyperoplus lanceolatus*, but it is likely that they resemble the migration patterns of *Clupea harengus* and *Ammodytes tobianus*. This strongly suggests that the observed diel patterns in food transport to the ternery are related to the vertical movements of the tern's prey fish. Although this pleads against Dunn's (1972) hypothesis that these patterns arise from changing energy requirements of the chicks, his view can not be excluded. In this respect, it would be interesting to investigate how Sandwich Terns organise their activities during the day in colonies where only sandeel is available.

Interestingly, in the first two hours of the light period relatively small sandeel were brought to the colony. This suggests that these small prey were found closer to the colony and as a consequence parents returned to the colony sooner. In this way some parents could partly satisfy the hunger of their chicks, but the low rate of food transport in the first hour of the day suggests that most parents did not chose for this option.

Tidal rhythms

Several studies on terns report variation in food transport to the colony throughout the tidal cycle (Dunn 1972; Hulsmann 1977; Frank 1992). Combining observations in the colony with radio-tracking results, Becker *et al.* (1993) showed that Common Terns visited specific foraging areas in the Wadden Sea and North Sea depending on the tide. Sandeel were mainly caught by these terns at the North Sea during incoming tide, while herring were mainly caught in the Wadden Sea at high tide. Aerial counts of foraging Sandwich Terns performed in 1994 indicate that terns breeding on Griend also use different foraging areas during a tidal cycle (Essen *et al.* 1998). During low tide, foraging terns concentrated around the gullies in the Wadden Sea and North Sea. Observations in the colony showed that fishing success was low during this part of the tidal cycle. Just before high tide terns were mainly seen foraging in the deep waters between Vlieland and Terschelling. Colony observations showed that herring and sandeel could be caught here in equal numbers and that relatively long sandeel were available here. During receding tide, relatively high numbers of herring were brought to Griend and according to the aerial counts in 1994 during his stage of the tidal cycle the terns mainly foraged around the west point of Terschelling. Surprisingly, the waters around the east point of Vlieland, where IKMT-catches indicate a high abundance of herring, were largely avoided during receding tide. We have no explanation for this than herring being only available around Vlieland during other parts of the tidal cycle, since the fish-sampling project did not account for differences during the tidal cycle. Many species of fish, however, have synchronised their activities with the tidal cycle or show horizontal movements oscillating with the tide (Gibson 1978; Aprahamian *et al.* 1998). It was beyond the scope of this study, but it would be challenging to further extend the sampling programme and to pay more attention to the distribution of the foraging terns during the entire tidal cycle.

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REFERENCES

Aprahamian, M.W., G.O. Jones & P.J. Gough 1998. Movement of adult Atlantic salmon in the Usk estuary, Wales. J. Fish Biol. 53: 221-225.

Bailey, R.S. 1991. The interaction between sandeels and seabirds - a case history at Shetland. International Council for the Exploration of the Sea (ICES) 165: 1-12.

Becker, P.H., D. Frank & S.R. Sudmann 1993. Temporal and spatial pattern of Common Tern (*Sterna hirundo*) foraging in the Wadden Sea. Oecologia 93: 389-393.

Bégout Anras, M.-L. & J.-P. Lagardère 1998. Variabilité météorologique et hydrologique. Conséquences sur l'activité natatoire d'un poisson marin. Comptes Rendus de l'Académie des Sciences de la Vie 321: 641-648.

Birkhead, T.R. 1976. Effects of sea conditions on the rates at which Guillemots feed chicks. British Birds 69: 490-492.

Blaxter, J.H.S. & B.B. Parrish 1965. The importance of light in shoaling, avoidance of nets and vertical migration by herring. J. Cons. Perm. int. Explor. Mer 30: 40-57.

Borodulina, T.L. 1960. Biology and economic importance of gulls and terns of southern-USSR water bodies. Akad. Nauk SSR. Trudy Inst. Morf. Zhiv. 32: 1-132.

Cairns, D.K. 1987. The ecology and energetics of chick provisioning by Black Guillemots. Condor 89: 627-635.

Campredon, P. 1978. Reproduction de la Sterne caugec, *Thalasseus sandvicensis* Lath., sur le Banc d'Arguin (Gironde). Aperçu de sa distribution hivernale. L'Oiseau et R.F.O. 48: 123-150, 263-279.

Corten, A. & G. van de Kamp 1979. Abundance of herring larvae in the Dutch Wadden Sea as a possible indication of recruitment strength. Int. Counc. Explor. Sea. C.M. 1979/H: 26.

Corten, A. & G. van de Kamp 1996. Variation in the abundance of southern fish species in the southern North Sea in relation to hydrography and wind. ICES J. Mar. Sc. 53: 1113-1119.

Corten, A. 1996. Ecoprofiel haring. RIVO/DLO-rapport CO59/95. Rijksinstituut voor Visserij Onderzoek, IJmuiden.

Daan, S. 1981. Adaptive daily strategies in behavior. In: J. Aschoff (ed.), Handbook of behavioral neurophysiology, 4: Biological rhythms; p. 275-297. Plenum Press, New York.

Dunn, E.K. 1972. Studies on terns with particular reference to feeding ecology. PhD. Thesis. University of Durham, Durham.

Dunn, E.K. 1973. Changes in fishing ability of terns associated with windspeed and sea surface conditions. Nature 244: 520-521.

Dunn, E.K. 1975. The rôle of environmental factors in the growth of tern chicks. J. Anim. Ecol. 44: 743-754.

Ehrenbaum, E. 1936. Naturgeschichte und wirtschaftliche Bedeutung der Seefische Nordeuropas. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Essen, K., J.H.M. Schobben, H.J.M. Baptist, C.J.N. Winter & J. Jol 1998. Foerageergedrag van de Grote Stern *Sterna sandvicensis*. Werkdocument RIKZ OS-98.117. Rijksinstituut voor Kust en Zee, Den Haag.

Evans, R.M. 1982. Foraging-flock recruitment at a Black-billed Gull colony: implications for the information centre hypothesis. Auk 99: 24-30.

Fonds, M. 1978. The seasonal distribution of some fish species in the western Dutch Wadden Sea. In: N. Dankers, W.J. Wolff & J.J. Zijlstra (eds), Fishes and fisheries of the Wadden Sea. Stichting Veth tot steun aan Waddenonderzoek, Leiden.

Frank, D. 1992. The influence of feeding conditions on food provisioning of chicks in Common Terns *Sterna hirundo* nesting in the German Wadden Sea. Ardea 80: 45-55.

Fuchs, E. 1977. Kleptoparasitism of Sandwich Terns *Sterna sandvicensis* by Black-headed Gulls *Larus ridibundus*. Ibis 119: 183-190.

Garthe, S. & U. Kubetzki 1998. Diet of Sandwich Terns *Sterna sandvicensis* on Juist (Germany). Sula 12: 13-19.

Genstat 5 Committee 1993. Genstat 5 Reference Manual. Clarendon Press, Oxford.

Gibson, R.N. 1978. Lunar and tidal rhythms in fish. In: J.E. Thorpe (ed.), Rhythmic activity of fishes. Academic Press, London.

Gorke, M. 1990. Die Lachmöwe (*Larus ridibundus*) in Wattenmeer und Binnenland. Seevögel 11: 1-48.

Götmark, F. 1990. A test of the information-centre hypothesis in a colony of Sandwich Terns *Sterna sandvicensis*. Anim. Behav. 39: 487-495.

Hamer, K.C. & D.R. Thompson 1997. Provisioning and growth rates of nestling Fulmars *Fulmarus glacialis*: stochastic variation or regulation? Ibis 139: 31-39.

Heubeck, M. 1988. Shetland's seabirds in dire straits. BTO News 158: 1-2.

Hulsman, C. 1977. Feeding and breeding biology of six sympatric species of tern (Laridae) at One Tree Island, Great Barrier Reef. PhD. Thesis. University of Queensland, Queensland.

Isenmann, P. 1975. Über einen Versuch zur Messung der Fütterungshäufigkeit von fast flüggen Jungvögeln bei der Brandseeschwalbe (*Sterna sandvicensis*) in der Camarque (Süd-Frankreich). Vogelwarte 28: 159-160.

Klaassen, M., B. Zwaan, P. Heslenfeld, P. Lucas & B. Luijckx 1992. Growth rate associated changes in the energy requirements of tern chicks. Ardea 80: 19-28.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Laevastu, T. & M.L. Hayes 1981. Fisheries oceanography and ecology. Fishing News Books, London.

Macer, C.T. 1966. Sandeels (Ammodytidae) in the south-western North Sea; their biology and fishery. Fishery Investigations London 24: 1-55.

Monaghan, P., J.D. Uttley, M.D. Burns, C. Thaine & J. Blackwood 1989. The relationship between food supply, reproductive effort and breeding success in Arctic Terns *Sterna paradisaea*. J. Anim. Ecol. 58: 261-274.

Norusis, M.J. 1990. SPSS?PC+ 4.0. Base Manual. SPSS, Chicago.

Pearson, T.H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37: 521-552.

Piersma, T., R. Lindeboom & M.R. van Eerden 1988. Foraging rhythm of Great Crested Grebes *Podiceps cristatus* adjusted to diel variations in the vertical distribution of their prey *Osmerus eperlanus* in a shallow eutrophic lake in The Netherlands. Oecologia 76: 481-486.

Ratcliffe, N., D. Richardson, R. Lidstone Scott, P.J. Bond, C. Westlake & S. Stennett 1997. Host selection, attack rates and success rates for Black-headed Gull kleptoparasitism of terns. Colonial Waterbirds 20: 227-234.

Reay, P.J. 1970. Synopsis of biological data on North Atlantic sandeels of the genus *Ammodytes*. FAO Fisheries Synopsis 82. Food and Agriculture Organization of the United Nations, Rome.

Richner, H. 1995. Wintering Cormorants *Phalacrocorax carbo carbo* in the Ythan Estuary, Scotland: numerical and behavioural responses to fluctuating prey availability. Ardea 83: 193-197.

Shealer, D.A. 1998. Differences in diet and chick provisioning between adult Roseate and Sandwich Terns in Puerto Rico. Condor 100: 131-140.

Sjöberg, K. 1985. Foraging activity patterns in the Goosander (*Mergus merganser*) and the Red-breasted Merganser (*M. serrator*) in relation to patterns of activity in their major prey species. Oecologia 67: 35-39.

Smith, A.J. 1975. Studies of breeding Sandwich Terns. British Birds 68: 142-156.

Suddaby, D. & N. Ratcliffe 1997. The effect of fluctuating food availability on breeding Arctic Terns (*Sterna paradisaea*). Auk 114: 524-530.

Taylor, I.R. 1983. Effect of wind on foraging behaviour of Common and Sandwich Terns. Ornis Scand. 14: 90-96.

Thorpe, J.E. 1978. Rhythmic activity of fishes. Academic Press, London.
Vader, W., T. Anker-Nilssen, V. Bakken, R.T. Barrett & K.-B. Strann 1990. Regional and temporal differences in breeding success and population development of fisheating seabirds in Norway after collapses of herring and capelin stocks. Transactions 19th IUGB Congress (Trondheim 1989), p. 143-150.
Veen, J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (*Sterna s. sandvicensis* Lath.). Behaviour 20 (Supplement): 1-193.
Waltz, E.C. 1987. A test of the information-centre hypothesis in two colonies of Common Tern *Sterna hirundo*. Anim. Behav. 35: 48-59.
Yamashita, Y., D. Kitagawa & T. Aoyama 1985. Diel vertical migration and feeding rhythm of the larvae of the Japanese Sand-eel *Ammodytes personatus*. Bull. Jap. Soc. Scientific Fisheries 51: 1-5.