



THE SPATIAL AND TEMPORAL LINK BETWEEN  
COMMON TERNS *STERNA HIRUNDO* AND THEIR PREY FISH  
IN THE WADDEN SEA

Von der Fakultät für Mathematik und Naturwissenschaften der  
Carl von Ossietzky Universität Oldenburg  
zur Erlangung des Grades und Titels eines

**Dr. rer. nat.**

angenommene Dissertation

von Andreas Dänhardt  
geboren am 18. März 1973 in Hamburg

Angefertigt am  
Institut für Vogelforschung „Vogelwarte Helgoland“, Wilhelmshaven



Erstgutachter: Prof. Dr. Peter H. Becker  
Zweitgutachter: PD Dr. Ingrid Kröncke  
Tag der Disputation: 19.11.2010



DIESE DISSERTATION WIDME ICH MEINER TOCHTER AMANDA



## ZUSAMMENFASSUNG

Fische stellen im Nahrungsnetz des Wattenmeeres mit die größte Biomasse, wodurch sie sowohl als Konsumenten als auch als Beute eine Schlüsselrolle einnehmen. Fischarten mit dem größten potenziellen Einfluss auf Nahrungsnetzprozesse leben nicht ganzjährig im Wattenmeer, sondern kommen aus den großen Flüssen und aus der Nordsee. Diese Fischarten bilden die Nahrungsgrundlage für Flusseeschwalben (*Sterna hirundo*), die in großen Kolonien entlang der Wattenmeerküste und benachbarter Ästuarie brüten. Seit 2002 hatten Flusseeschwalben im Wattenmeer nur noch unterdurchschnittlichen Bruterfolg, was offenbar mit der Nahrungsversorgung zusammenhängt. Während der Brutsaison der Seeschwalben fehlen Informationen über die räumliche und zeitliche Verteilung von Fischen im Wattenmeer jedoch weitgehend. Das Ziel dieser Promotionsarbeit war daher, die Verteilungsmuster von Abundanz und Größe der Beutefische der Flusseeschwalben auf räumlichen und zeitlichen Skalen zu untersuchen, die für den Jagderfolg als Voraussetzung für den Bruterfolg relevant sind (*Synopse, Kapitel 1*).

Die Daten, auf denen diese Dissertation basiert, wurden in den Jahren 2006 und 2007 erhoben. In den Flusseeschwalben-Brutkolonien am Banter See (53°30' N, 08°05' O) und auf der Insel Minsener Oog im Niedersächsischen Wattenmeer (53°45' N, 08°01' O) wurden nach standardisierter Methodik Brutparameter, die Gewichtsentwicklung der Küken sowie Balz- und Kükenfütterungen aufgenommen. Während der Brutsaison 2007 wurden in ausgewählten Gebieten um Minsener Oog Jagdbeobachtungen durchgeführt. Die saisonale Artenzusammensetzung, Abundanz und Längenverteilung der Fische wurde mit Hilfe schiffsbasierter Hamennetzfänge untersucht, die im zentralen Jadebusen (53°28' N, 08°12' O) und südöstlich vor Minsener Oog (53°44' N, 08°02' O) während der Brutzeit und innerhalb des mittleren Jagdradius der Flusseeschwalben stattfanden. Das Hamennetz bestand auf fünf übereinander angeordneten Netzfächern, wodurch vertikal aufgelöste Informationen über potenzielle Beutefische der Flusseeschwalben gewonnen werden konnten. Veröffentlichte Daten wurden herangezogen, um den Bruterfolg und das Kükenwachstum mit der Abundanzdynamik eines der wichtigsten Beutefische – des Herings (*Clupea harengus*) – in der Nordsee und im Schleswig-Holsteinischen Wattenmeer in Bezug zu setzen.

Die Rekrutierung des Nordseeherings ist ein nützliches Maß, um Kükenwachstum und Bruterfolg der Flusseeschwalben im Niedersächsischen Wattenmeer vorherzusagen (*Kapitel 2*). Die Stärke des gesamten Nachwuchsjahrgangs des Nordseeherings erklärt einen größeren Anteil der Variabilität des Bruterfolges der Flusseeschwalben als räumlich aufgelöste Indices aus der Nordsee und dem Schleswig-Holsteinischen Wattenmeer. Zudem kann mit der Rekrutierung des Nordseeherings der Bruterfolg am Banter See besser erklärt werden als der Bruterfolg von Minsener Oog, wo durch das Fehlen vollwertiger Beutealternativen wie z. B. dem Stint (*Osmerus eperlanus*) eigentlich ein stärkerer Zusammenhang mit mariner Beute wie dem Hering zu erwarten gewesen wäre. Der Anteil erklärter Variabilität auf

Minsener Oog steigt jedoch, wenn Jahre kompletten Brutausfalls stärker gewichtet werden. Daraus folgt, dass die schwachen Nachwuchsjahrgänge des Herings, die seit 2002 beobachtet werden und sich deutlich im Bruterfolg der Flusseeschwalben am Banter See widerspiegeln, den Bruterfolg der Flusseeschwalben auf Minsener Oog ebenfalls beeinflusst haben. Vollziehen Räuber und Beute saisonale Wanderungen, setzt ihre Interaktion zeitliche und räumliche Überschneidung gleichermaßen voraus. Unter Berücksichtigung beider Aspekte wurden die Konzepte der Match-Mismatch-Hypothese und der Central-Place-Foraging-Theorie genutzt, um die Saisonalität der Seevogel-Fisch Interaktion im Wattenmeer zu untersuchen (*Kapitel 3*). Grundannahmen beider Modelle wurden überprüft durch eine vergleichende Untersuchung zwischen der saisonalen Abundanz- und Wachstumsdynamik vierer wichtiger Beutefischarten und dem saisonalen Energiebedarf der Flusseeschwalbenkolonie am Banter See. Entgegen den Annahmen der Match-Mismatch-Hypothese sind sowohl der Energiebedarf der Seeschwalben als auch die Abundanz der Beutefische polymodal, und während des Brutverlaufes nutzen die Seeschwalben mehr als nur einer Beutefischart. Unterschiede in der Nahrungsversorgung und den Brutparametern zwischen 2006 und 2007 zeigen, dass die Beuteabundanz mögliche Effekte zeitlicher und räumlicher Überlappung bei weitem kompensieren kann. Die zeitliche Komponente tritt jedoch in den Vordergrund, wenn die Nahrungsfischdichte unter eine bestimmte Schwelle fällt. Entgegen den Vorhersagen der Central Place Foraging-Theorie werden Heringsartige dem Stint und dem Wittling (*Merlangius merlangus*) vorgezogen, obwohl diese beiden Arten mehr Energie pro erbeutetes Individuum geliefert hätten. Kleine aber energiereiche Beute wie Heringe liefert vergleichsweise viel Energie pro Einheit Jagdaufwand durch ihr konzentriertes Auftreten in individuenreichen Schwärmen. Diese lokal erhöhte Beutedichte kann allerdings verringert sein, wenn Heringe als Reaktion auf zu hohe Wassertemperaturen in tieferes und kälteres Wasser ausweichen. Dies ist ein Mechanismus, wie die Klimaveränderung räumliche Räuber-Beute-Assoziationen beeinträchtigen kann.

Flusseeschwalben würden von Beutefischen unterhalb ihrer maximalen Eintauchtiefe (40–50 cm) nur dann profitieren, wenn aus einer erhöhten Beutedichte in der Tiefe eine erhöhte Beutedichte nahe der Wasseroberfläche folgt. In *Kapitel 4* wird untersucht, ob Abundanz und Längenverteilung der wichtigsten Beutefische der Flusseeschwalben in der gesamten Wassersäule sich in den Fängen aus den Tiefenhorizonten widerspiegeln, die für die Flusseeschwalben erreichbar sind. Die Beutefische sind zumeist außer Reichweite der Seeschwalben und die Fischabundanz innerhalb und außerhalb der Reichweite der Seeschwalben ist nicht in allen Fällen proportional zueinander. Die großen Brutkolonien des Untersuchungsgebietes könnten nur auf Grundlage der oberflächennah auftretenden Fische nicht fortbestehen. Diese Fischarten werden jedoch regelmäßig von den Flusseeschwalben genutzt. Folglich kann die Beuteverfügbarkeit in den Prielen, wie sie durch die Hamennetzfänge repräsentiert wird, nur eine von mehreren Einflussgrößen sein, die die Nahrungsversorgung steuern. Physikalische Faktoren und biologische Interaktionen können jedoch nur dann die



Nahrungsverfügbarkeit erhöhen, wenn die Beuteabundanz grundsätzlich groß genug ist, um ein Zusammentreffen zwischen Räuber und Beute in allen nutzbaren Jagdhabitaten hinreichend wahrscheinlich zu machen.

Nach erfolgreicher Jagd treffen die Seeschwalben individuelle Entscheidungen im Hinblick auf die Verwendung ihrer Beute. Dies wird in *Kapitel 5* thematisiert, in dem die lokale Beutefischdichte, das Jagdverhalten und die Beutenutzung von Flusseeeschwalben auf See und schließlich Fütterungsbeobachtungen auf Minsener Oog zusammenhängend analysiert wird. Qualitativ hochwertige Beute wird überdurchschnittlich oft aus dem Jagdgebiet abtransportiert, während energiearme Beute fast immer vom jagenden Altvogel selbst konsumiert wird. Die Artenanteile der Balz- und Kükenfütterung ähneln denen der Beute, die aus dem Jagdgebiet abtransportiert wird. Übereinstimmend mit anderen Studien erscheint die Nutzung hochwertiger Beute für die Balz- und Kükenfütterung als ein generelles Verhaltensmuster, wonach hohe Anteile minderwertiger Nahrung, die in die Kolonie gebracht werden, als Indiz für eine schlechte Nahrungssituation zu interpretieren wären. Da die Seeschwalben hochwertige Beute zum Füttern nutzen, könnte die Abundanz entsprechender Arten im Meer überschätzt werden, wenn die Schätzungen auf Kolonie-basierten Daten beruhen.

Obwohl der Bruterfolg der Flusseeeschwalben im Wesentlichen mit der Rekrutierung des Nordseeherings erklärt werden kann, haben weitere Faktoren einen Anteil an der verbleibenden Variabilität. Dazu gehören andere Beutefischarten, saisonale Phänomene wie die räumlich-zeitliche Überschneidung der Flusseeeschwalben mit ihrer Beute und deren Abundanz und Wachstum, kleinskalige Jagdbedingungen wie Wetter und Vertikalverteilung der Beute sowie das Verhalten fütternder Altvögel. Oberhalb einer Schwelle, ab der das Überleben adulter Seeschwalben gefährdet wäre, können individuelle Entscheidungen der Altvögel als Mechanismen wirken, nachteilige Umweltbedingungen ggfs. zu kompensieren. Diese Plastizität gegenüber einer variablen Nahrungsversorgung ist jedoch nicht stark genug, um die Assoziation zwischen dem Bruterfolg der Flusseeeschwalben und großskaligen Phänomenen wie die Jahrgangsstärke des Nordseeherings vollständig zu überlagern. Diese ökosystemare Kohärenz beeinflusst den Bruterfolg der Flusseeeschwalben auf lokaler Ebene durch eine erhöhte/verringerte Wahrscheinlichkeit einer hohen/geringen Dichte einer Hauptbeute im Wattenmeer. Bis 2002 war die überregionale Heringsabundanz in der Nordsee offenbar groß genug, kleinskalige Abundanzveränderungen im Wattenmeer auszugleichen.

Die Nahrungsversorgung, Wetterbedingungen und Prädation werden als wichtigste Einflussgrößen auf den Bruterfolg angeführt, jedoch wirkt die Nahrungsversorgung direkt auf die Kondition der Altvögel, wodurch möglicherweise hormonelle Prozesse begünstigt werden, die die Bereitschaft verringern, in den Nachwuchs zu investieren. Dazu gehören eine verringerte Prädatorenabwehr und die Jagdmotivation während Perioden schlechter Nahrungsbedingungen. Die Nahrungsversorgung kann jedoch auch vom Wetter beeinflusst sein, wie in sehr warmen Jahren, in denen die Wassertemperatur eine Toleranzschwelle z. B. der Heringe überschreitet, die dann in tieferes und kälteres Wasser abwandern und

so den Aktionsradius der Flusseeschwalben verlassen. Die Beute der Flusseeschwalben variiert in ihrer Abundanz einerseits aufgrund der Nachwuchsproduktion außerhalb des Wattenmeeres, andererseits bestimmen lokale Lebensraumeigenschaften im Wattenmeer die Habitatqualität für die Fische. Beide Faktoren bestimmen den Energiefluss zu höheren trophischen Ebenen.

## SUMMARY

In the Wadden Sea fish supply among the largest biomass to the food web, making them a key functional group as consumers and prey alike. Fish species with the greatest potential impact on food web processes are not Wadden Sea residents, but originate from rivers and from the North Sea. These fish species are important prey of Common Terns (*Sterna hirundo*), breeding in large colonies along the Wadden Sea coast and adjacent estuaries. 2002 marks the beginning of a series of years with very low or even zero reproductive output of Common Terns, most likely due to poor food supply. During the terns' breeding season, information on fish distribution patterns and abundance dynamics especially of pelagic fish is largely unavailable. The objective of this thesis was thus to investigate distribution and abundance patterns of the Common Terns' most important prey fish species on temporal and spatial scales potentially relevant for successful foraging as a prerequisite for successful reproduction of the Common Terns, as outlined in the *Synopsis (Chapter 1)*.

The data this thesis is based upon were recorded in 2006 and 2007. In the Common Tern breeding colonies Banter See in Wilhelmshaven (53°30' N, 08°05' E) and on the island of Minsener Oog in the Lower Saxon Wadden Sea (53°45' N 08°01' E) breeding parameters, chick weight development, courtship and chick feedings were recorded following standard procedures. During the breeding season 2007, foraging behaviour of Common Terns was observed at selected feeding grounds around Minsener Oog. Seasonal composition, abundance and length distribution of fish were derived from ship-based stow net catches in the central Jade Bay (53°28' N, 08°12' E) and south-east of Minsener Oog (53°44' N, 08°02' E) during the breeding season and within the average foraging range of the Common Terns. The stow net consisted of five stacked net compartments, providing depth-resolved information on potential prey fish of the Common Terns. Published data were used to relate Common Tern breeding success and chick growth dynamics to the abundance of one of the terns' main prey species – the Atlantic herring (*Clupea harengus*) – in North Sea and in the Schleswig-Holstein Wadden Sea.

Evidence was found that “*North Sea herring recruitment predicts chick growth and reproductive performance of Common Terns in the Wadden Sea*” (Chapter 2). North Sea herring recruit abundance explains more variability of Common Tern breeding success than area-resolved abundance indices from the North Sea and from the Schleswig-Holstein Wadden Sea. Herring abundance indices explain more of the variability in breeding success of the more inshore colony at Banter See than terns breeding on Minsener Oog, which, in the absence of prey alternatives such as e.g. smelt (*Osmerus eperlanus*), would be expected to show stronger dependence on marine prey such as herring. However, explained variability in breeding success of Common Terns breeding on Minsener Oog increases, when years with zero breeding success are given more relative weighting. This suggests that the poor herring recruitment since 2002, being clearly seen in the Banter See data, also had a profound effect

on the Common Terns on Minsener Oog. The associations between predators and prey appear to be stronger at larger scales of measurement, suggesting that ecosystem connectivity between the North Sea and the Wadden Sea is strong enough that Common Tern breeding success and chick weight development yield information on herring abundance also beyond the terns' immediate foraging range.

When predator and prey are seasonal migrants, their interaction is a question of the right timing, but also of spatial overlap. To account for both aspects, the framework of the match-mismatch hypothesis and the central place foraging theory are used to investigate "*The seasonality of seabird-fish overlap in the Wadden Sea*" (Chapter 3). Key predictions of both foraging models are tested by comparing the seasonal abundance and growth of four important prey fish species with the seasonal energy requirements of the Common Terns breeding at Banter See. Against the assumptions of the match-mismatch hypothesis, both the energy requirements of the terns and prey fish abundance are polymodal and Common Terns utilize more than one prey species during reproduction. Differential food supply and breeding parameters between 2006 and 2007 suggest that food abundance far outweighs the effects of temporal predator-prey coincidence. The temporal component may only become important when food supply drops below a certain threshold. Against the predictions of the central place foraging theory, clupeids are preferred over smelt and whiting (*Merlangius merlangius*), even though the latter two species would yield more energy per individual fish caught. Small but abundant and energy-rich prey such as herring may yield substantial energy per unit effort by enhancing local prey availability through schooling behaviour. This locally enhanced prey density may in turn be reduced e. g. when herring retreat to deeper and colder water as a reaction to high water temperatures. This illustrates a potential mechanism by which climate change may affect predator-prey interactions.

Common Terns would benefit from prey being located below their maximum diving depth (40–50 cm) only if an increased prey density at depth translates into an increased prey density close to the surface. In Chapter 4 "*Does small-scale vertical distribution of juvenile schooling fish affect prey availability to surface-feeding seabirds in the Wadden Sea?*" it is investigated if local abundance and length composition of the Common Terns' main prey fish in the entire water column are reflected in catches from the depth strata accessible to the terns. Prey fish is usually out of reach of the terns and fish abundance is not proportional between deeper and shallower strata in all cases. Large breeding colonies as found in the area of investigation could not sustain themselves on prey fish density found in the upper water strata, but the regular utilization of these fish species by the Common Terns indicates that prey availability in the tidal channels represented by the stow net can only be one factor determining food supply. Physical factors and biological interactions can only work to enhance food availability to surface feeding seabirds when baseline food abundance is sufficient to generate predator-prey encounter at all foraging sites utilized by the terns.

Upon catch of a prey item the successful forager must decide how to utilize the prey most pro-

fitably. This issue is addressed in Chapter 5: “*To eat or to feed? Prey utilization of Common Terns *Sterna hirundo* in the Wadden Sea*”, which provides an integrated analysis of local fish abundance, foraging behaviour and prey utilization of Common Terns observed at sea and, eventually, of the prey organisms being fed to partners and chicks in the colony on Minsener Oog. High quality prey is carried out of the foraging area disproportionately often, whereas low quality prey is mostly ingested by the foraging adult itself. The proportions of prey being used for provisioning are quite similar to prey being carried out of the foraging area. In agreement with other studies, delivering high quality food items preferably to partners or chicks indeed appears to be a general pattern of seabird behavior, suggesting that large proportions of low quality food being delivered to the colony may indicate a shortage of high quality food. Due to the terns selecting high quality prey for provisioning, the abundance of high quality prey fish in the sea may however be overestimated when derived from colony-based seabird diet studies.

Even though considerable proportions of the variability in Common Tern breeding success can be explained by recruitment fluctuations of herring, residual variability in Common Tern breeding performance could be due to prey fish species other than herring, seasonal phenomena such as spatial and temporal overlap of the terns and their prey fish, fish abundance and growth, small-scale feeding conditions such as weather and vertical prey distribution and also behavioral adaptations of provisioning adults. Beyond a threshold prey abundance, below which adult survival would be compromised, individual decisions by the adult terns can work as a mechanism to compensate for environmental variability. However, this plasticity towards changing food supply is not strong enough to mask the relationship between breeding success of the Common Terns and large scale phenomena such as North Sea herring recruit abundance. This ecosystem connectivity is capable of impacting the breeding success of apex predators such as Common Terns on a local scale by generally increasing or decreasing chances of high prey abundance in the Wadden Sea. Until 2002, large-scale herring recruit abundance in the North Sea was obviously high enough to compensate for small-scale fluctuations in the Wadden Sea. The exceptions were very warm years, when water temperature passed a threshold beyond which herring would leave for deeper and colder water.

Food supply, weather conditions and predation are regarded equally influential on breeding success, but food supply may directly affect adult body condition, potentially creating an endocrine state eventually determining the adults’ energetic investment in their offspring, e. g. via predator defense and foraging motivation during periods of adverse (sub-catastrophic) weather conditions. Nevertheless, food supply may also be influenced by weather, translating into high water temperatures possibly driving temperature-sensitive prey fish such as herring out of the Common Terns’ foraging range. Consequently, the prey of the Common Terns may fluctuate due to its production outside the Wadden Sea (recruitment strength) and also due to proximate living conditions in the Wadden Sea for fish (temperature), both factors determining energy flow to higher trophic levels.



## TABLE OF CONTENTS

---

### Chapter 1: Synopsis

1.1 Rationale of the thesis.....	1
1.2 General introduction.....	1
1.3 Study objectives and chapter outline.....	3
1.4 General overview of methods.....	5
1.5 Questions, hypotheses and key results.....	6
1.6 Conclusions.....	11
1.7 References.....	14

### Chapter 2: North Sea Herring recruitment predicts chick growth and reproductive performance of Common Terns in the Wadden Sea

*(publication status: submitted)*

2.1 Abstract.....	17
2.2 Introduction.....	18
2.3 Material and methods.....	19
2.4 Results.....	24
2.5 Discussion.....	29
2.6 References.....	34

### Chapter 3: The seasonality of seabird-fish overlap in the Wadden Sea

*(publication status: submitted)*

3.1 Abstract.....	37
3.2 Introduction.....	38
3.3 Material and methods.....	39
3.4 Results.....	44
3.5 Discussion.....	52
3.6 References.....	55

### Chapter 4: Does small-scale vertical distribution of juvenile schooling fish affect prey availability to surface-feeding seabirds in the Wadden Sea?

*(publication status: Journal of Sea Research, accepted)*

4.1 Abstract.....	59
4.2 Introduction.....	60
4.3 Material and methods.....	61
4.4 Results.....	65

4.5 Discussion.....	70
4.6 References.....	75

## Chapter 5: To eat or to feed? Prey utilization of Common Terns

*Sterna hirundo* in the Wadden Sea

(publication status: *Journal of Ornithology*, DOI: 10.1007/s10336-010-0590-0)

5.1 Abstract.....	79
5.2 Introduction.....	80
5.3 Material and methods.....	81
5.4 Results.....	85
5.5 Discussion.....	90
5.6 References.....	94

Danksagung .....	97
Lebenslauf .....	99
Erklärung .....	101



## CHAPTER 1

---

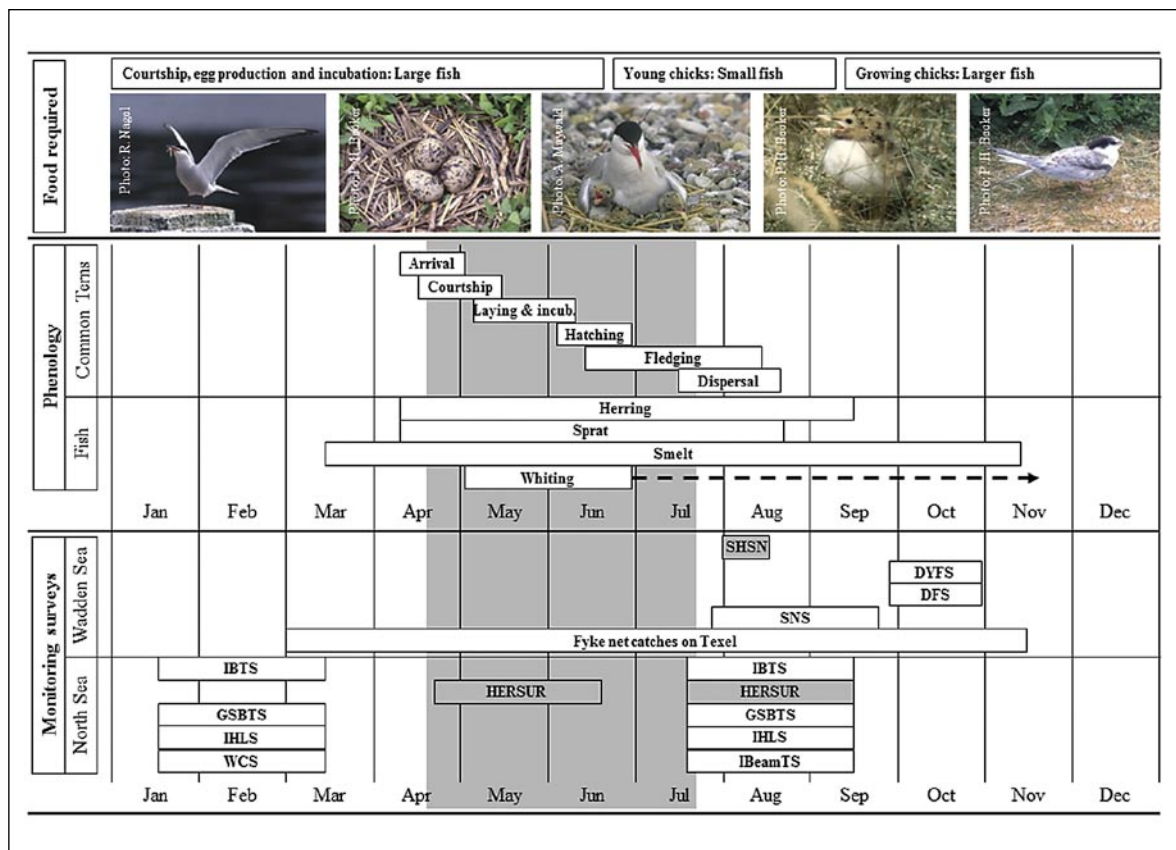
### SYNOPSIS

#### 1.1 RATIONALE OF THE THESIS

The Wadden Sea not only forms part of an international system of breeding and wintering areas for migratory birds, it is also part of an international migration system of fish. Fish supply among the largest biomass to the food web, making them a key functional group as consumers and prey alike. It is well documented that fish most often provide the nutritional basis for top predators such as seabirds during their breeding and migration (e.g. Boecker, 1967; Becker et al., 1987; Brenninkmeijer and Stienen, 1994). Fish species with the greatest potential impact on food web processes are not Wadden Sea residents, but originate from rivers (smelt *Osmerus eperlanus*) and from the North Sea (Atlantic herring *Clupea harengus*, Atlantic sprat *Sprattus sprattus* and the gadoids cod *Gadus morhua* and whiting *Merlangius merlangius*, both being irregularly abundant in the Wadden Sea). These fish species are important prey of Common Terns (*Sterna hirundo*), breeding in large colonies along the Wadden Sea coast and adjacent estuaries. 2002 marks the beginning of a series of years with very low or even zero reproductive output in Common Terns, obviously due to poor food supply. During the terns' breeding season, information on fish distribution patterns and abundance dynamics especially of pelagic fish is largely unavailable (Fig. 1.1), despite the key role fish play in the Wadden Sea food web (Bolle et al., 2009; Jager et al., 2009).

#### 1.2 GENERAL INTRODUCTION

Subject of the present work were Common Terns breeding in two of the largest colonies in the German Wadden Sea: Banter See in Wilhelmshaven and Minsener Oog at the outer Jade in the National Park Lower Saxon Wadden Sea (Becker, 1996, 1998). In mid-April Common Terns arrive from the wintering areas in south-western and southern Africa at the Wadden Sea coast, where the majority of the German breeding populations reproduces. Colonies constitute and courtship starts immediately after arrival, mating commences at the end of April/beginning of May. Incubation lasts 21–24 days, first chicks hatch between the end of May and mid-June, with maximum chick numbers occurring between the middle and the end of June. Chicks fledge at 23–27 days of age. They remain dependent on parent birds until



**Figure 1.1:** Food requirements (top) and phenology of Common Terns and their preferred prey fish (middle), fish monitoring programmes in the Wadden Sea and the North Sea (bottom). The breeding season of the terns and surveys yielding representative data for pelagic fish are highlighted in grey. Dashed arrow indicates presence of whiting in invasion years. Abbreviations of monitoring programmes: SHSN = Schleswig-Holstein Stow net Survey, DYFS = Demersal Young Fish Survey (Germany), DFS = Demersal Fish Survey (Netherlands), SNS = Sole Net Survey, IBTS = International Bottom Trawl Survey, HERSUR = Herring Acoustic Survey, GSBTS = German Small Scale Bottom Trawl Survey (Boxen-Survey), IHLS = International Herring Larvae Survey, WCS = Winter Crangon Survey, IBeamTS = International Beam Trawl Survey.

well after colony dispersal (Becker and Ludwigs, 2004). Common Terns are plunge divers, being restricted to exploiting the top 40–50 cm of the water column. Thus, they depend on fish being close to the surface. Common Terns are single prey loaders, returning to the colony to feed incubating partners and chicks single prey items (Becker and Ludwigs, 2004). Recent feeding observations confirmed earlier findings (Becker et al., 1987; Frank, 1992; Wendeln et al., 1994; Frank 1998), that herring, sprat, smelt and in some years also cod (Becker et al., 2001) and whiting are extensively preyed upon by the terns. Herring older than one year are utilized by adult terns during courtship, egg-formation and incubation. Chicks are fed juvenile herring that have most likely been drifted into the Wadden Sea from the English Channel, where they were spawned the winter preceding the terns' breeding season (Munk and Christensen, 1990; Dickey-Collas et al., 2009). Sprat are a rather unpredictable prey resource, as both locally and externally-spawned cohorts occur in the Wadden Sea (Baumann

et al., 2009). Sprat are usually less abundant than herring, but there are years when sprat outnumber herring by far and thus become proportionally more relevant to the Common Terns and other piscivores (Greenstreet et al., 1999). Smelt is an anadromous species, spawning in February/March in the large rivers discharging into the German Bight. Adult smelt use the Wadden Sea as a transitional area, but appear to accumulate in the Jade Bay and in the estuaries of the rivers Eider, Elbe, Weser and Ems. Juveniles follow in late summer (Lillelund, 1961). Three length classes are present in the Wadden Sea: <8 cm, 8–12 cm and >12 cm. One-year old smelt (8–12 cm) are most abundant, serving as food for both Common Tern adults and chicks. Whiting is one of the key predators in the North Sea food web, being capable of massively reducing the abundance of its prey, both as juveniles (Berghahn, 1996) and adults (Temming et al., 2004, 2007). For juvenile whiting the Wadden Sea is an important but not an essential nursery (Zijlstra, 1978). Whiting and also cod can be very abundant in some years, but it is largely unknown what causes these gadoid invasions in the Wadden Sea. Regardless of the reasons and despite the extreme predation pressure the gadoids exert e. g. on brown shrimp, their mass occurrence provides valuable surplus food for the Common Terns.

### 1.3 STUDY OBJECTIVES AND CHAPTER OUTLINE

The leitmotif of this thesis was to investigate distribution and abundance patterns of the Common Terns' most important prey fish species on temporal and spatial scales potentially relevant for successful foraging as a prerequisite for high reproductive output of the Common Terns. In Chapter 2, entitled "*North Sea Herring recruitment predicts chick growth and reproductive performance of Common Terns in the Wadden Sea*", variability in chick growth and breeding success of the Common Terns breeding at Banter See and on Minsener Oog is sought to be elucidated with inter-annual abundance variation in one of the most important prey fish of the terns, the Atlantic herring. Using published information on herring abundance both in the North Sea (ICES, 2009) and in the Wadden Sea (Vorberg, 2009) along with published (Becker, 1998) and unpublished (P. H. Becker, pers. comm.) data on Common Tern breeding performance and chick growth, the following hypotheses were tested:

- Herring abundance dynamics in the Wadden Sea are proportional to those in the North Sea.
- Herring abundance in the Wadden Sea is a better predictor of Common Tern reproductive performance than more offshore abundance indices.
- Alternatively, larger-scale herring abundance is a better predictor of Common Tern reproductive performance than herring abundance indices from the Wadden Sea, which may be biased due to small-scale variability.

- Breeding success as an integrative measure should be less well predicted by herring abundance than chick weight and growth, which respond more directly to change in food supply.
- Reproductive performance of Common Terns breeding on Minsener Oog should be more closely associated with herring abundance indices than inshore colonies due to a shortage of prey alternatives around the more offshore colonies.

As both the food requirements of the Common Terns and prey fish abundance are clearly seasonal, Chapter 3 focuses on “*The seasonality of seabird-fish overlap in the Wadden Sea*”. Common Terns are especially sensitive to prey abundance variation during their breeding season, because they always have to return to the colony to provision their mates and their young, resulting in a confined foraging area that they can profitably exploit. Theoretically, a foraging tern should seek to maximize energy yield per unit foraging effort by preferring large fish (Orians and Pearson, 1979), so that the energy-demanding transport of single prey items back to the colony eventually pays off. Spatial and temporal mismatch between predator and prey has been suggested to be essential for the reproductive success of the predator (Cushing, 1969, 1990; Durant et al., 2007), assuming that

- the energy demand of the predator and the availability of prey follow a unimodal bell-shaped distribution,
- the closer the temporal match between the maximum energy demand of the predator and peak abundance of prey the better the reproductive performance of the predator,
- that poor temporal match can to some degree be compensated by high prey abundance.

In this chapter, a test of these three assumptions is presented, using seasonal information on prey fish abundance and the energy requirements of the Common Tern breeding colony at Banter See.

Regardless of inter-annual and intra-seasonal patterns, prey *abundance* is not necessarily equivalent to *prey availability*. This is especially true for plunge-diving seabirds such as Common Terns, which can only prey upon fish located no deeper than 40–50 cm below the water surface. Thus, it is discussed in Chapter 4, if “*(Does) small-scale vertical distribution of juvenile schooling fish affect(s) prey availability to surface-feeding seabirds in the Wadden Sea?*”. Using vertically resolved catch data, length and abundance of selected prey fish species were compared between depth horizons accessible to the Common Terns and water strata below the terns’ maximum diving depth. Specifically, it was tested if

- the length composition and abundance of prey fish in reach of the Common Terns represent length composition and abundance of the same fish species in the whole water column, and
- if the breeding performance of Common Terns at Banter See and on Minsener Oog and during two successive years reflects food availability as quantified by the depth-stratified sampling results.

During the breeding season, adult Common Terns have to find a balance between provisioning their mates and young and self-feeding. Once a given prey item is caught this trade-off between somatic and reproductive investment requires individual decisions, coming into focus in Chapter 5: “*To eat or to feed? Prey utilization of Common Terns *Sterna hirundo* in the Wadden Sea*”. Theory predicts that colony-breeding single loaders such as terns should maximize energetic investment in reproduction by bringing only large and energy-rich prey items to their partners or chicks (Orians and Pearson, 1979). This hypothesis is tested by jointly analysing prey fish abundance and at-sea foraging behaviour, prey utilization and courtship and chick feedings of Common Terns breeding on Minsener Oog.

#### 1.4 GENERAL OVERVIEW OF METHODS

The data this thesis is based upon were recorded in the years 2006 and 2007. In the breeding colonies at Banter See in Wilhelmshaven (53° 30' N, 08° 05' E) and on the Wadden Sea island of Minsener Oog (53° 45' N 08° 01' E) breeding parameters and chick weight development were regularly recorded, following standard procedures outlined in Wagener (1998). Feedings of partners and chicks in both colonies were observed both macroscopically and using binoculars (10x40 magnification) from shelters close to the nests. In 2007, foraging behaviour of Common Terns was observed around Minsener Oog from an elevated observation site at the beach and from a small boat using binoculars. The foraging observations in the foraging areas around the island were synchronized with the feeding observations in the colony. Both during foraging observations and feeding observations in the colony, prey items were identified to the lowest possible taxonomic level. To provide information on the prey composition and abundance, fish samples were obtained using a ship-based stow net in the central Jade Bay (53° 28' N, 08° 12' E) and south-east of Minsener Oog (53° 44' N, 08° 02' E). The stow net consisted of five stacked net compartments, providing depth-resolved information on species composition, abundance and size distribution of potential prey fish of the Common Terns. To account for seasonality, sampling took place at least twice per month between April 19<sup>th</sup> and September 5<sup>th</sup> 2006 and April 24<sup>th</sup> and October 10<sup>th</sup> 2007, depending on local wind conditions. Both time and site of the fish sampling were concomitant with the breeding season of the Common Terns and both fish sampling sites were located well within the terns' average foraging range ( $6.3 \pm 2.4$  km, Becker et al., 1993). Absolute catch numbers were normalized to individuals caught per 10 000 m<sup>3</sup> filtered water volume. Published data were used to relate Common Tern breeding success (1981–2009) and chick growth dynamics (1984–2009) (Becker, 1998; P. H. Becker, unpublished data) to herring abundance in the North Sea (1981–2009 and 1984–2009, respectively) (ICES, 2009) and in the Schleswig-Holstein Wadden Sea (Meldorf Bight: 1991–2009, Hörnum Deep: 2001–2009) (Vorberg, 2009). Methodological details are described in the respective chapters.

## 1.5 QUESTIONS, HYPOTHESES AND KEY RESULTS

Prey fed to chicks is mainly comprised of clupeids, which are mostly herring, as documented by the proportions of herring relative to other clupeids in stow net catches. Clupeids are also extensively utilized by adult Common Terns during courtship. Since herring are omnipresent and abundant during the breeding season of the Common Terns and also rich in energy, their abundance is hypothesized to be a suitable predictor of breeding success and chick growth in Common Terns. Using a variety of datasets of herring abundance from the North Sea (ICES, 2009) and from the Wadden Sea (Vorberg, 2009) as potential explanatory variables, evidence was found that indeed “*North Sea Herring recruitment predicts chick growth and reproductive performance of Common Terns in the Wadden Sea*” (Chapter 2). However, regression analyses revealed that the effects of herring abundance on Common Tern reproduction and chick growth dynamics were not straightforward. Even though herring abundance in the Wadden Sea was proportional to that in the North Sea, Common Tern breeding success was related much closer to calculated herring recruit abundance for the whole North Sea than to herring abundance resolved by North Sea area and in the Schleswig-Holstein Wadden Sea. Moreover, herring abundance indices explained more of the variability in breeding success of the more inshore colony at Banter See than of terns breeding on Minsener Oog, which, in the absence of prey alternatives such as e.g. smelt, would be expected to show stronger dependence on marine prey such as herring. However, almost half of the variability in breeding success of Common Terns breeding on Minsener Oog could be explained by North Sea herring recruit abundance, when only data from 1992–2009 were used, i.e. when years with zero breeding success were given more relative weighting. This suggests that the poor herring recruitment since 2002 (Payne et al., 2009), being clearly seen in the Banter See data, also had a profound effect on the Common Terns breeding on Minsener Oog.

The close relationship between North Sea-wide herring recruit abundance and Common Tern breeding success at Banter See was unexpected, as these birds should be able to cope with a lower herring abundance due to the availability of alternative prey. Just that may be the reason that sub-lethal and more subtle responses to fluctuations in prey availability can be observed at Banter See, whereas at Minsener Oog low herring abundance may have more immediate or even catastrophic consequences for chick development and breeding success due to the absence of adequate prey alternatives.

Despite breeding success being an integrative measure, its relationship with North Sea herring recruitment both at Banter See and on Minsener Oog was close and significant. In contrast, relationships encompassing chick growth and weight, thought to be more responsive to changes in food supply (Greenstreet et al., 1999), were weaker or not significant at all. The suitability of herring abundance indices to explain Common Tern reproduction appeared to be influenced by small-scale variability to some degree, indicating that associations between predators and prey appear to be stronger at larger scales of measurement, presumably because

se variation resulting from prey patchiness is reduced. It can thus be stated that ecosystem connectivity between the North Sea and the Wadden Sea is strong enough that Common Tern breeding success and chick weight development yield information on herring abundance even beyond their immediate foraging range.

Exploring long-term relationships between predator and prey e. g. by means of regression analysis requires single values for any given year (Chapter 2), mostly represented by spatial or temporal abundance averages (ICES, 2009). Owing to this methodological necessity, the explanatory power of mean values is likely to be limited by seasonal abundance changes. In Chapter 3, prey abundance and estimated food requirements of predators were thus investigated at a much finer temporal resolution to account for “*The seasonality of seabird-fish overlap in the Wadden Sea*”. If predator and prey are seasonal migrants, their interaction is a question of the right timing. This truism is also valid for Common Terns, depending on an energetically favorable ratio between prey return and foraging investment. Chapter 3 describes how the seasonal abundance and growth (as the two mechanisms governing potential energy yield) of four important prey fish species fit the energy requirements of the Common Terns breeding at Banter See, calculated over the course of the breeding season, and how this was translated into characteristics of phenology and chick growth. Seeking to explain recruitment variation in a predator by means of relating its phenology with that of the prey, the match-mismatch hypothesis states that if the requirement of the predator matches the availability of prey, predator recruitment will be high (Cushing, 1969, 1990). In its original version, the match-mismatch hypothesis assumes

1. a unimodal, bell-shaped distribution of the energy demand of the predator,
2. that the closer the temporal match between the maximum energy demand of the predator and peak abundance of prey the better the reproductive performance, and
3. that poor temporal match can to some degree be compensated by high prey abundance.

In any predator-prey considerations, spatial overlap should also be accounted for besides temporal overlap and prey abundance. This is especially true for seabirds carrying only one prey item at a time and facing a confined foraging range during the breeding season, as they have always to return to the colony to provision their mates and their young. The central place foraging theory provides the conceptual framework for this specific situation and predicts that single-prey loaders such as terns should maximize energy yield per unit foraging effort by preferring large and energy-rich prey, especially to provision their chicks (Orians and Pearson, 1979).

The classical match-mismatch concept is limited in its applicability to the seabird-fish system in the Wadden Sea: Neither the energy requirements of the terns nor prey fish abundance was unimodal, falsifying the first assumption in this particular case. Common Tern reproduction appeared to depend on more than one prey species and a sole temporal match between the

energy requirements of the terns and energy provided by the four prey fish species was not detectable. As expressed in various breeding and chick growth parameters, food supply was much better in 2007 than in 2006, when overall food abundance was lower. This suggests that food abundance far outweighs the effects of temporal coincidence between predator and prey and the temporal component may only become important when food supply drops below a certain threshold. In the light of these results, assumption two had to be rejected, while the validity of assumption three was confirmed.

According to the central place foraging theory (Orians and Pearson, 1979), the Common Terns should have preferred smelt in both years and whiting in 2007 over the clupeids. Instead, clupeids were obviously preferred over smelt. Even though smelt would yield more energy per individual fish, small but abundant and energy-rich prey such as herring may yield substantial energy per unit effort by enhancing local prey availability through schooling behaviour. This locally enhanced prey density may in turn be reduced at times of high water temperatures, e. g. when herring retreat to deeper and colder water (Becker et al., 1997), leaving the Common Terns and other central place foragers with a locally reduced prey density. This illustrates a potential mechanism by which climate change may affect spatial predator-prey overlap in a non-linear fashion. Moreover, the pronounced seasonality of fish abundance may potentially bias fish abundance indices obtained from fish survey data, as an abundance change could mean both fewer individuals at constant phenology or a shift in phenology at constant individual numbers.

In the literature, abundance and availability are not always clearly distinguished, and prey abundance is assumed to be proportional to prey availability. Indeed, better breeding performance of surface-feeding seabirds at times of large prey stocks suggests that prey availability is also a function of prey abundance (Scott et al., 2006). However, this may not be generally so due to predator-specific foraging modes and abiotic forces structuring the aquatic environment (Hunt et al., 1999). In the context of this thesis, it is thus legitimate to ask: “*Does small-scale vertical distribution of juvenile schooling fish affect prey availability to surface-feeding seabirds in the Wadden Sea?*” (Chapter 4). Common Terns can reach no deeper than 40–50 cm below the water surface, approximately corresponding to one body length (Becker and Ludwigs, 2004). They would benefit from prey being located below their maximum diving depth only if an increased prey density at depth translates into an increased prey density in the depth strata close to the surface (Scott et al., 2006). In Chapter 4, vertical patterns of abundance and length distribution of herring, sprat, smelt and whiting are investigated. In addition to Chapters 2 and 3, abundance data on Nilsson’s pipefish (*Syngnathus rostellatus*) were also analysed, representing low quality prey. Depth-resolved stow net catches from two tidal channel systems close the Common Tern breeding colonies at Banter See and on Minsener Oog were used to investigate the vertical distribution of the terns’ main prey fish. More specifically, it was tested if local fish abundance and length composition in the whole water column were also reflected



in catches from the depth strata accessible to the terns and would thus be suitable to predict fish availability to surface-feeding seabirds in the Wadden Sea.

One methodological constraint was the spatial limitation to the deep tidal channels required to deploy the stow net. Strictly speaking, inferences drawn from the vertical fish distribution patterns seen in the stow net catches are only valid for this one type of foraging habitat of the Common Terns. However, schooling fish depend on the tidal channels as they need sufficient water depth to form a school. Consequently, conditions in the tidal channels will clearly have an impact on overall prey availability to the terns. Vertical distribution patterns revealed that prey fish is usually out of reach of the terns. Especially herring and smelt, the Common Terns' main prey, were usually caught below 1 m water depth. Prey fish abundance directly below the water surface was not consistently correlated with abundance in deeper strata, and the patterns appeared to be species- and site-specific rather than driven by overall fish abundance. The hypothesis that high overall abundance inevitably translates into high abundance close to the surface could thus not be maintained. Instead, the observed patterns fit the threat-sensitive predator avoidance hypothesis, stating that the intensity of anti-predator behavior of prey matches the degree of threat posed by the predator (Helfman, 1989; Helfman and Winkelman, 1997). For example, at Minsener Oog, where terns almost exclusively feed on herring, herring were found to avoid the water strata near the surface, despite them being by far the most abundant prey fish at Minsener Oog and ten times more abundant than in the Jade Bay. In the Jade Bay, where predation pressure by seabirds is partly directed also at smelt, herring was caught more frequently also in depth strata accessible to the terns. Likewise, smelt, being among the most frequently utilized prey fish of the Common Terns breeding at Banter See, were also found mostly below the maximum diving depth of the terns. However, the correlations between smelt abundance close to the surface and smelt abundance below the reach of the terns were much weaker than at Minsener Oog.

Large breeding colonies as found in the area of investigation could not sustain themselves on prey fish density found in the upper water strata. However, the regular occurrence of these fish species in the diet of the Common Terns in considerable amounts (Becker et al., 1987; Frank, 1992; Frank and Becker, 1992; Frick and Becker, 1995; Frank, 1998) indicates that prey availability in the tidal channels represented by the stow net catches can only be one factor determining food supply. It can be concluded that physical or hydrographic conditions (Zamon, 2003; Schwemmer et al., 2009) and biological interactions (Camphuysen and Webb, 1999) can only work to enhance food availability to surface-feeding seabirds when baseline food abundance is sufficient to increase chances of predator-prey encounter at all potential foraging sites.

Once encounter with fish has come to a successful end for the Common Terns, they must decide what to do with the prey item caught. At-sea foraging behavior is rather difficult to survey, but as a result of individual decisions of successful foragers in terms of prey utilization, diet studies may suffer substantial bias when solely relying on colony-based data. Seabirds have

been used as indicators of marine change due to their apical position in food webs and their colonial breeding (Cairns 1987; Becker et al. 1987; Montevecchi 1993; Greenstreet et al. 1999; Boyd et al. 2006; Einoder 2009), but inferences about changes in fish populations drawn from seabird diet studies (e.g. Aebischer et al. 1990; Davoren and Montevecchi 2003; Barrett 2007) would clearly benefit when supplemented with information on at-sea foraging behaviour.

Within the framework of the central place foraging theory (Orians and Pearson, 1979) already introduced above, Chapter 5 presents an integrated analysis of local fish abundance represented by stow net catches, foraging behaviour and prey utilization of Common Terns observed in their foraging areas at sea and, eventually, of the prey organisms being fed to partners or chicks recorded in one of the largest breeding colonies in the German Wadden Sea to answer the question “*To eat or to feed? Prey utilization of Common Terns *Sterna hirundo* in the Wadden Sea*”. In accordance with other studies (e.g. Taylor, 1979; Shealer, 1998; McLeay et al., 2009), predictions of the central place foraging theory (Orians and Pearson, 1979) could be confirmed to be valid also for the Common Terns breeding in the Wadden Sea: High quality prey was carried out of the foraging area disproportionately often, whereas almost all low quality prey items were ingested by the foraging adult itself. The proportions of prey being used for provisioning were quite similar to prey being carried out of the foraging area. Delivering high quality food items preferably to partners or chicks indeed appears to be a general pattern of seabird behavior. Similar results have been reported e.g. for auks (Davoren and Burger 1999) and other tern species (Shealer, 1998; McLeay et al., 2009). Even when utilizing anthropogenic food sources such as the cooling water outlet of a power plant, this behavior could be observed (Dänhardt and Becker, 2008). This suggests that large proportions of low quality food being delivered to the colony may indicate a shortage of high quality food. Due to the terns selecting high quality prey for provisioning, the abundance of high quality prey fish in the sea may however be overestimated when derived from colony-based seabird diet studies only. Given the availability of reference catch data, the proportions in which certain prey items are consumed by the foraging tern or used for provisioning could indicate if the respective prey species are “valued” poor or profitable enough to invest the energy of flying back to the colony.

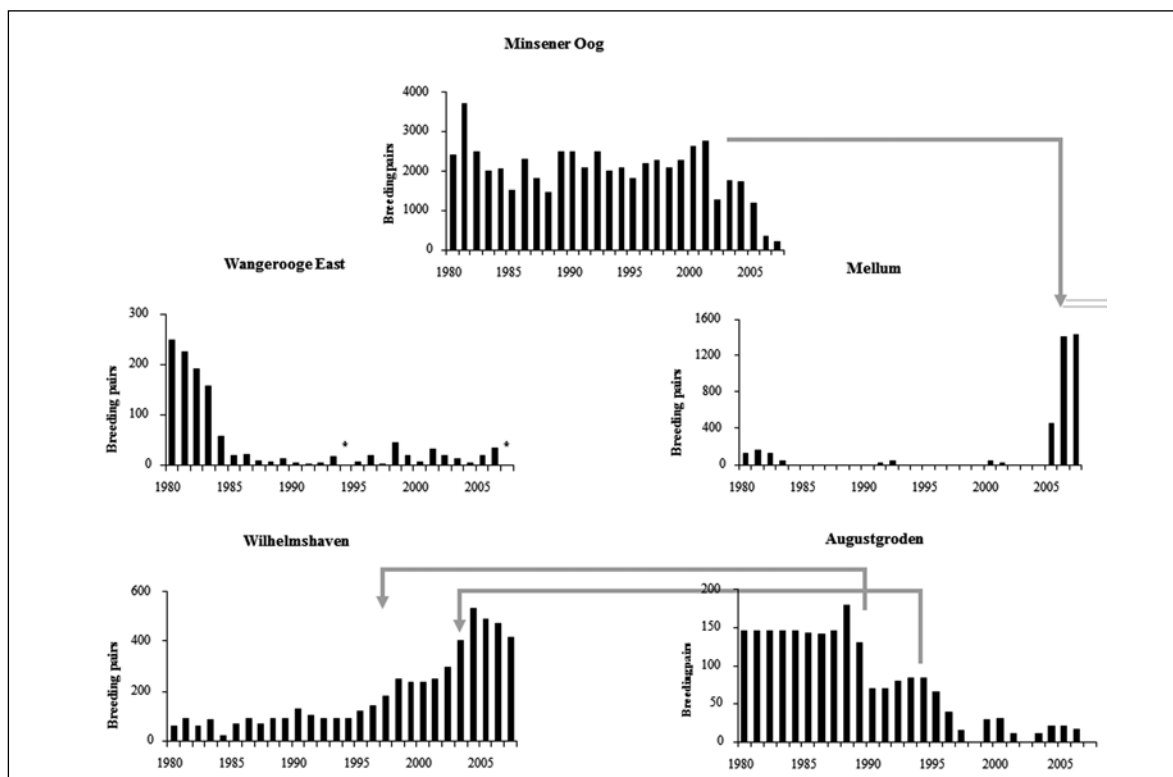
Below a threshold prey abundance, when adult survival would be compromised, individual decisions by the adult terns can work as a mechanism to compensate for environmental variability such as variation of food availability. However, this tolerance towards changing food supply is apparently not strong enough to mask the relationship between breeding success of the Common Terns and large scale herring abundance (Greenstreet et al., 1999).

Despite rich herring supply, low quality food such as pipefish was also ingested by the foraging terns during the study period. This may have been due to either a differential availability of herring and pipefish or due to the absence of selective foraging behaviour. Extensively utilizing low quality prey in the presence of high quality food suggests that Common Terns do not select prey items prior to catching them. This would disagree with the optimal forag-

ing theory that foraging animals should generally seek to maximize energy yield per unit foraging effort (Pyke, 1984; Ydenberg et al., 1994). Nevertheless, it may be energetically justified to catch low quality food to self-feed, when the respective low-value prey species is highly abundant at foraging sites actually promising encounter with high quality food (e. g. Becker et al. 1993; Camphuysen and Webb 1999). In such cases, the catch frequency of low quality prey may provide information to the foraging tern about the overall food situation and, as a consequence, influence its energy partitioning between somatic and reproductive investment.

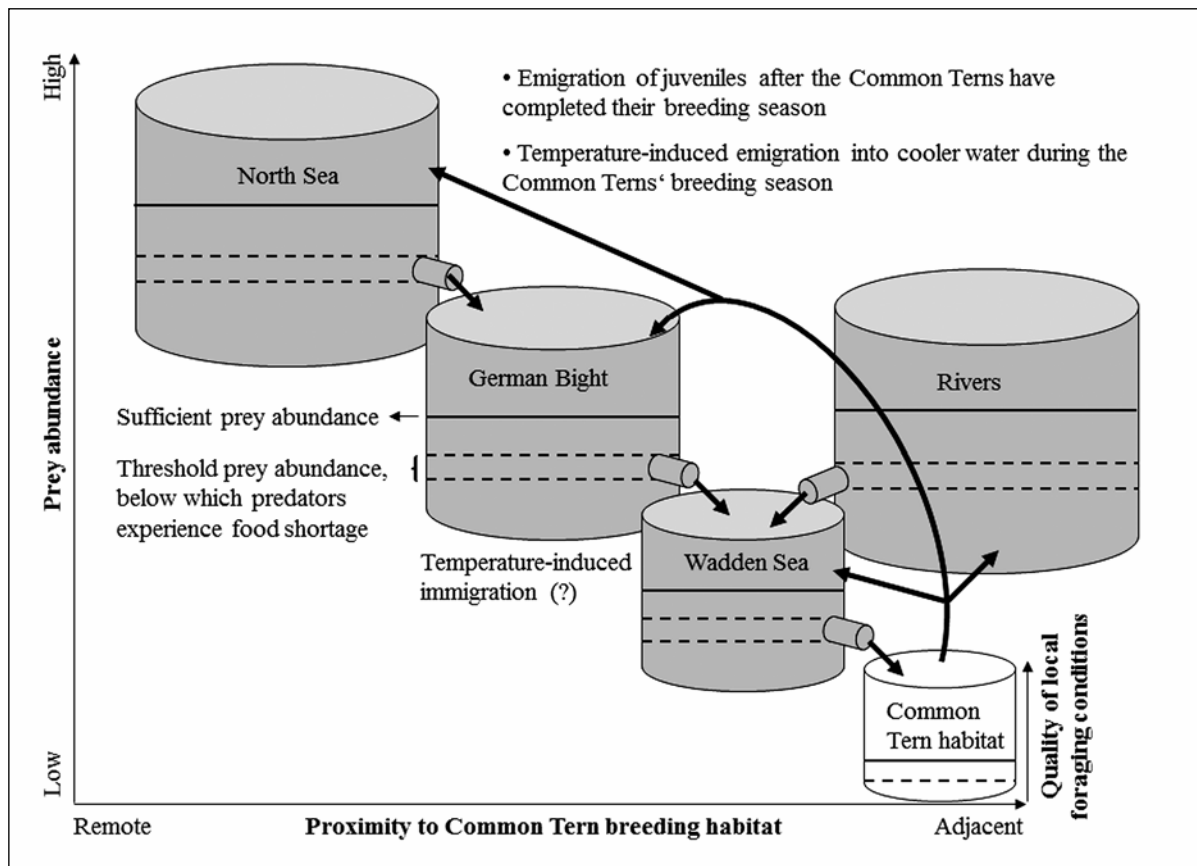
## 1.6 CONCLUSIONS

As a consequence of prolonged periods with poor or even zero breeding success, annual adult mortality of 10% cannot be compensated anymore (Ezard et al., 2006). Before populations actually start to decline, traditional colony sites are abandoned and the breeding population disperses into smaller colonies more vulnerable to predation (Becker and Anlauf, 1988; Becker, 1995, 1998). This development becomes evident in the redistribution of the large Common Tern breeding colonies in the Lower Saxon Wadden Sea (Fig. 1.2).



**Figure 1.2:** Temporal trend of breeding pair numbers of Common Terns in the Lower Saxon Wadden Sea. Arrows indicate migration between colonies. Data from Mellumrat e.V., NLWKN, Institute of Avian Research. \*No data available.

In the Wadden Sea, food web processes involving higher trophic levels such as birds and fish are clearly bottom-up. Foraging conditions determine the quality of the breeding habitat for Common Terns and other avian piscivores, but the stage is set elsewhere for prey abundance eventually becoming available to the Common Terns: The Wadden Sea food web with fish at its core is energetically subsidized with fish biomass coming from the large rivers and from the North Sea. The energy flow between the external sources of prey fish and the eventual spatio-temporal coincidence of the Common Terns and their prey fish are illustrated in Fig. 1.3.



**Figure 1.3:** Schematic representation of relationship of North Sea- and Wadden Sea-wide prey fish abundance with the food availability of terns. Dashed lines mark the abundance range below which the connectivity between North Sea and Wadden Sea potentially compromises the nutritional basis of the terns. Note that the size of the jars is not proportional to the real spatial relationships between relative fish abundance. It has yet to be clarified if immigration into the Wadden Sea is temperature-induced.

Considerable proportions of the variability in Common Tern breeding success can be explained by recruitment fluctuations of one single prey species, the Atlantic herring (Chapter 2). Unfortunately, the data availability for other fish species preyed upon by the terns (e.g. smelt for the Common Terns at Banter See) is not nearly as good as for herring. But even though their contribution to the observed variability cannot be exactly evaluated, they are likely to

have an influence due to their relevance as food (Chapters 3 and 4). Other factors are likely to be the source of residual variability in Common Tern breeding performance, including seasonal phenomena such as spatial and temporal overlap of the terns and their prey fish, fish abundance and growth (Chapter 3), small-scale feeding conditions such as weather (Becker and Specht, 1991; Becker et al., 1997) and vertical prey distribution (Chapter 4) and also behavioral adaptations of provisioning adults (Chapter 5).

The explained variability in Common Tern breeding success on Minsener Oog increased to almost 50% when years with poor herring recruitment (2002 ff.) were given more relative weighting in the regressions (Chapter 2). This suggests a high degree of ecosystem connectivity and also the relevance of large scale phenomena, being capable of impacting the breeding success of apex predators such as Common Terns. In general, high herring recruit abundance on a large scale will increase chances of high herring abundance in the Wadden Sea (Fig. 1.3). Until 2002, large-scale herring recruit abundance in the North Sea was obviously high enough to compensate for small-scale fluctuations in the Wadden Sea. The exception were very warm years, when water temperature passed a threshold beyond which herring would leave for deeper and colder water.

Food supply, weather conditions and predation have been described to be equally influential on breeding success (Becker, 1998, Becker and Sudmann, 1998). However, food supply may directly affect adult body condition, potentially creating an endocrine and physiological state eventually determining the adults' energetic investment in their offspring (Angelier et al., 2009; Bauch et al. 2010; Kitaysky et al., 2010), including predator defense and foraging motivation during periods of adverse (sub-catastrophic) weather conditions. This idea is supported by the unexpected observation that excluding years with predation and/or adverse weather conditions during breeding and chick raising from the regression analyses between herring recruit abundance and Common Tern breeding performance (Chapter 2) did not improve the relationships. Obviously, the effects of weather and predation on reproductive performance of the Common Terns is at least indirectly affected by food supply, e. g. via the endocrine state of adults. In turn, food supply may also be influenced by weather, translating into high water temperatures possibly driving temperature-sensitive prey fish such as herring out of the Common Terns' foraging range (Becker et al., 1997). Consequently, the prey of the Common Terns may fluctuate due to its production outside the Wadden Sea (recruitment strength) and also due to the proximate living conditions in the Wadden Sea for fish (temperature), both factors determining energy flow to higher trophic levels (Fig. 1.3).

Even though Common Tern breeding success is well explained by herring recruit abundance, there are years when high herring recruitment does not translate into good food supply in the Wadden Sea. For example, in 2007 breeding phenology and chick weight development indicated good food supply, while the recruitment index of North Sea herring was among the lowest on record. In some years, food supply by means of herring may be sufficient in the Wadden Sea despite very low herring recruitment, suggesting that there are either accu-

mulation effects potentially compensating for low baseline abundance or that relatively low abundance in the Wadden Sea is generally sufficient to feed the terns, possibly only through additional prey fish species.

## 1.7 REFERENCES

- Aebischer NJ, Coulson JC and Colebrooke JM (1990) Parallel long-term trends across four marine trophic levels and weather. *Nature* 347: 753–755.
- Angelier F, Clément-Chastel C, Welcker J, Gabrielsen GW and Chastel O (2009) How does corticosterone affect parental behaviour and reproductive success? A study of prolactin in black-legged kittiwakes. *Functional Ecology* 23: 784–793.
- Barrett RT (2007) Food web interactions in the southwestern Barents Sea: Black-legged kittiwakes *Rissa tridactyla* respond negatively to an increase in herring *Clupea harengus*. *Marine Ecology Progress Series* 349: 269–276.
- Bauch C, Kreutzer S and Becker PH (2010) Breeding experience affects body condition: blood metabolite levels over the course of incubation in a seabird. *Journal of Comparative Physiology B* 180: 835–845.
- Baumann H, Mahlzahl AM, Voss R and Temming A (2009) The German Bight (North Sea) is a nursery area for both locally and externally produced sprat juveniles. *Journal of Sea Research* 61: 234–243.
- Becker PH (1995) Effects of coloniality on gull predation on Common Tern (*Sterna hirundo*) chicks. *Colonial Waterbirds* 18: 11–22.
- Becker PH (1996) Flusseeeschwalben (*Sterna hirundo*) in Wilhelmshaven. *Oldenburger Jahrbuch* 96: 263–296.
- Becker PH (1998) Langzeittrends des Bruterfolgs der Flusseeeschwalbe und seiner Einflussgrößen im Wattenmeer. *Vogelwelt* 119: 223–234.
- Becker PH and Anlauf A (1988) Nistplatzwahl und Bruterfolg der Flusseeeschwalbe (*Sterna hirundo*) im Deichvorland. 1. Nestdichte & 2. Hochwasser-Überflutung. *Ökologie der Vögel* 10: 27–58.
- Becker PH and Ludwigs J-D (2004) *Sterna hirundo* Common Tern. *BWP Update* 6: 91–137.
- Becker PH, Frank D and Walter U (1987) Geografische und jährliche Variation der Ernährung der Flusseeeschwalbe (*Sterna hirundo*) an der Nordseeküste. *Journal für Ornithologie* 128: 457–475.
- Becker PH, Frank D and Sudmann S R (1993) Temporal and spatial pattern of Common Tern (*Sterna hirundo*) foraging in the Wadden Sea. *Oecologia* 93: 389–393.
- Becker PH and Sudmann SR (1998) Quo vadis, *Sterna hirundo*? Schlussfolgerungen für den Schutz der Flusseeeschwalbe in Deutschland. *Vogelwarte* 119: 293–304.
- Becker PH, Ludwigs J-D and Wagener M (2001) Neue Chance für den Nordsee-Kabeljau: Seevögel machen bereits im Sommer 2001 auf starken Jahrgang aufmerksam. *Informationen für die Fischwirtschaft aus der Fischereiforschung* 48: 164–165.
- Becker PH, Troschke T, Behnke A and Wagener M (1997) Flüge Küken der Flusseeeschwalbe *Sterna hirundo* verhungern während Hitzeperioden. *Journal für Ornithologie* 138: 171–182.
- Berghahn R (1996) Episodic mass invasions of juvenile gadoids into the Wadden Sea and their consequences for the population dynamics of Brown Shrimp (*Crangon crangon*). *Marine Ecology* 17: 251–260.
- Boecker M (1967) Vergleichende Untersuchungen zur Nahrungs- und Nistökologie der Flusseeeschwalbe (*Sterna hirundo* L.) und der Küstenseeschwalbe (*Sterna paradisaea* Pont.). *Bonner Zoologische Beiträge* 18: 15–126.
- Bolle LJ, Neudecker T, Vorberg R, Damm U, Diederichs B, Jager Z, Scholle J, Dänhardt A, Lüerssen G and Marencic H (2009) Trends in Wadden Sea fish fauna. Part 1 Trilateral Cooperation. *IMARES Report C108/08*, Wageningen.
- Boyd IL, Wanless S and Camphuysen CJ (2006) Top predators in marine ecosystems. Their role in monitoring and management. Cambridge University Press, Cambridge.

- Brenninkmeijer A and Stienen EWM (1994) Pilot study on the influence of feeding conditions at the North Sea on the breeding results of the Sandwich Tern *Sterna sandvicensis*. IBN Research Report 94 (10). Institute for Forestry and Nature Research (IBN-DLO): Wageningen, The Netherlands. 51 p.
- Cairns DK (1987) Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261–271.
- Camphuysen CJ and Webb A (1999) Multi-species feeding associations in North Sea seabirds: Jointly exploiting a patchy environment. *Ardea* 87: 177–197.
- Cushing DH (1969) The regularity of the spawning season of some fishes. *Journal du Conseil International d'Exploration de la Mer* 33: 81–92.
- Cushing DH (1990) Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology* 26: 249–293.
- Davoren GK and Burger AE (1999) Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets. *Animal Behaviour* 58: 853–863.
- Davoren GK and Montevecchi WA (2003) Signals from seabirds indicate changing biology of capelin stocks. *Marine Ecology Progress Series* 258: 253–261.
- Dickey-Collas M, Bolle LJ, Van Beek JKL and Erftemeijer PLA (2009) Variability in transport of fish eggs and larvae. II. Effects of hydrodynamics on the transport of down herring larvae. *Marine Ecology Progress Series* 390: 183–194.
- Durant JM, Hjermann DØ, Ottersen G and Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33: 271–283.
- Einoder LD (2009) A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research* 95: 6–13.
- Ezard TGH, Becker PH and Coulson T (2006) The contributions of age and sex to variation in Common Tern population growth rate. *Journal of Animal Ecology* 75: 1379–1386.
- 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.
- Frank D (1998) Bruterfolgsmonitoring an der Flusseeeschwalbe *Sterna hirundo* als Instrument ökologischer Begleituntersuchungen zu einer Pipeline-Verlegung im Wattenmeer. *Vogelwelt* 119: 235–241.
- Frank D and Becker PH (1992) Body mass and nest reliefs in Common Terns *Sterna hirundo* exposed to different feeding conditions. *Ardea* 80: 57–69.
- Frick S and Becker PH (1995): Unterschiedliche Ernährungsstrategien von Fluss- und Küstenseeschwalbe (*Sterna hirundo* und *S. paradisaea*) im Wattenmeer. *Journal für Ornithologie* 136: 47–63.
- Greenstreet SPR, Becker PH, Barrett RT, Fossum P and Leopold MF (1999) Consumption of pre-recruit fish by seabirds and the possible use of this as an indicator of fish stock recruitment. In Furness RW and Tasker ML (Eds.): *Diets of seabirds and consequences of changes in food supply*. ICES Cooperative Research Report 232: 6–17.
- Helfman GS (1989) Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behavioral Ecology and Sociobiology* 24: 47–58.
- Helfman GS and Winkelman DL (1997) Threat sensitivity in bicolor damselfish: Effects of sociality and body size. *Ethology* 103: 369–383.
- Hunt GL, Mehlum F, Russell RW, Irons D, Decker MB and Becker PH (1999) Physical processes, prey abundance and the foraging ecology of seabirds. In: Adams NJ and Slotow RH (Eds.): *Proc. 22<sup>nd</sup> International Ornithological Congress*, Durban: 2040–2056. Johannesburg: Bird Life South Africa.
- ICES (2009) Report of the herring assessment working group for the area south of 62° N. In ICES CM 2009/ACOM:03, pp. 1–658. International Council for the Exploration of the Sea, Copenhagen.
- Jager Z, Bolle LJ, Dänhardt A, Diederichs B, Neudecker T, Scholle J and Vorberg, R (2009) Fish. In Marencic H and De Vlas J (Eds.) *Quality Status Report 2009*. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven, Germany.
- Kitaysky AS, Piatt JF, Hatch SA, Kitaiskaia EV, Benowitz-Fredericks ZM, Shultz MT and Wingfield JC (2010) Food availability and population processes: Severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Functional Ecology* 24: 625–637.

- Lillelund K (1961) Untersuchungen über die Populationsdynamik des Stintes *Osmerus eperlanus eperlanus* (Linnaeus 1758) in der Elbe. *Archive of Fisheries and Marine Research* 12: 1–128.
- Mcleay LJ, Page B, Goldsworthy SD, Ward TM and Paton DC (2009) Size matters: Variation in the diet of chick and adult Crested Terns. *Marine Biology* 156: 1765–1780.
- Montevocchi WA (1993) Birds as indicators of change in marine prey stocks. In: Furness RW and Greenwood JJD (Eds.): *Birds as monitors of environmental change*. Chapman and Hall, London, p. 217–266.
- Munk P and Christensen V (1990) Larval growth and drift pattern and the separation of herring spawning groups in the North Sea. *Journal of Fish Biology* 37: 135–148.
- Orians GH and Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD and Stairs GR (Eds.) *Analysis of Ecological Systems*. State University Press., Columbus, Ohio, pp. 154–177.
- Payne MR, Hatfield EMC, Dickey-Collas M, Falkenhaus T, Gallego A, Gröger J, Licandro P, Llope M, Munk P, Röckmann C, Schmidt JO and Nash RDM (2009) Recruitment in a changing environment: The 2000s North Sea herring recruitment failure. *ICES Journal of Marine Science* 66: 1–6.
- Piatt JF, Sydeman WJ and Wiese F (2007) Introduction: a modern role for seabirds as indicators. In: Piatt JF and Sydeman WJ (Eds.) *Seabirds as indicators of marine ecosystems*. Theme Section Marine Ecology Progress Series 352: 199–204.
- Pyke GH (1984) Optimal foraging theory: A critical review. *Annual Review of Ecology and Systematics* 15: 523–575.
- Schwemmer P, Adler S, Guse N, Markones N and Garthe S (2009) Influence of water flow velocity, water depth and colony distance on distribution and foraging patterns of terns in the Wadden Sea. *Fisheries Oceanography* 18: 161–172.
- Scott BE, Sharples J, Wanless S, Ross ON, Frederiksen M and Daunt F (2006) The use of biologically meaningful oceanographic indices to separate the effects of climate and fisheries on seabird breeding success. In: Boyd I L, Wanless S and Camphuysen C J (Eds.) *Top predators in marine ecosystems. Their role in monitoring and management*. Cambridge University Press, Cambridge, pp. 46–62.
- Shealer DA (1998) Size-selective predation by a specialist forager, the Roseate Tern. *The Auk* 115: 519–525.
- Taylor IR (1979) Prey selection during courtship feeding in the Common Tern. *Ornis Scandinavica* 10: 142–144.
- Temming A, Floeter J and Ehrich S (2007) Predation hot spots: Large scale impact of local aggregations. *Ecosystems* 10: 865–876.
- Temming A, Götz S, Mergardt N and Ehrich S (2004) Predation of whiting and haddock on sandeel: Aggregative response, competition and diel periodicity. *Journal of Fish Biology* 64: 1351–1372.
- Vorberg R (2009) Monitoring der Fische im Wattenmeer-Untersuchungen zum Vorkommen und zur Verteilung der Fische in der Meldorfer Bucht und in der Nullnutzungszone im Hörnum Tief. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer. 63 pp.
- Wendeln H, Mickstein S and Becker PH (1994) Auswirkungen individueller Ernährungsstrategien von Flussschwärmen (*Sterna hirundo*) auf die Anwesenheit am Koloniestandort. *Vogelwarte* 37: 290–303.
- Ydenberg RC, Welham CVJ, Schmid-Hempel R, Schmid-Hempel P and Beauchamp G (1994) Time and energy constraints and the relationships between currencies in foraging theory. *Behavioral Ecology* 5: 28–34.
- Zamon JE (2003) Mixed species aggregations feeding upon herring and sand lance schools in a nearshore archipelago depend on flooding tidal currents. *Marine Ecology Progress Series* 261: 243–255.
- Zijlstra JJ (1978) The function of the Wadden Sea for the members of its fish fauna. In: Dankers N, Wolff WJ, Zijlstra JJ (Eds.) *Fishes and fisheries of the Wadden Sea*. Report 5 of the final report of the section “Fishes and fisheries” of the Wadden Sea Working Group. Stichting Veth tot Steun aan Waddenonderzoek, Leiden: 20–25.



## CHAPTER 2

NORTH SEA HERRING RECRUITMENT PREDICTS CHICK GROWTH AND  
REPRODUCTIVE PERFORMANCE OF COMMON TERNS IN THE WADDEN SEAAndreas Dänhardt<sup>1\*</sup> and Peter H. Becker

Institute of Avian Research “Vogelwarte Helgoland”,  
An der Vogelwarte 21, 26386 Wilhelmshaven, Germany.

\* Corresponding author

<sup>1</sup> present address: Suerhoper Brunnenweg 13 a, 21244 Buchholz/Nordheide, Germany,  
Phone: + (49) 1 79 / 5 17 15 36, E-mail: andreas@daenhardt.com

## 2.1 ABSTRACT

North Sea autumn-spawning herring is a key prey resource of Common Terns breeding in the Wadden Sea. Their breeding success has been below average since 2002, coinciding with exceptionally low herring recruitment. Time series of herring abundance in the North Sea and in the Schleswig-Holstein Wadden Sea were analyzed to explain long-term reproductive performance and chick development of Common Terns breeding in two colonies in the Lower Saxon Wadden Sea. Area-resolved herring abundance in the North Sea and in the Schleswig-Holstein Wadden Sea were rather poor predictors of breeding success and chick development, whereas the North Sea herring recruitment index was found suitable to estimate breeding success of the Common Terns. The relationships of the tern reproduction measures were stronger with the North Sea herring recruitment index than with more local herring abundance data from the Schleswig-Holstein Wadden Sea. Also, herring abundance data explained more variability of breeding success than of more directly responding measures such as growth rate and maximum weight of chicks. Although Common Terns have a small foraging range during the breeding season, ecosystem connectivity between the North Sea and the Wadden Sea appears to be strong enough that breeding success and chick weight development yield information on herring abundance also beyond the terns' immediate foraging range, suggesting that the Common Terns' recent population decline may be linked to the poor herring recruitment in the North Sea.

## KEYWORDS

*Common Tern, North Sea herring, breeding, chick growth, Wadden Sea, time series, Sterna hirundo, Clupea harengus, ecosystem connectivity*

## 2.2 INTRODUCTION

Resource abundance is linked to seabird demography through a number of functional relationships coming into effect at different spatial and temporal scales. During the breeding season, they include food availability, reproductive performance, chick growth and breeding success (Cairns, 1987, Montevecchi, 1993, Becker and Chapdelaine, 2003, Piatt and Sydeman, 2007). The Wadden Sea in the south-eastern North Sea is Europe's largest intertidal wetland, serving as feeding and breeding habitat for many fish and seabird species (Jager et al., 2009, Koffijberg et al. 2009, Laursen et al. 2009), interacting as predators (seabirds) and prey (fish). The stage for these interactions is set largely outside the Wadden Sea, as the main forage fish are produced in rivers or further offshore in the North Sea.

In the Wadden Sea, the Common Tern (*Sterna hirundo*) is one of the most abundant avian piscivores, feeding mainly on clupeids (Boecker, 1967, Becker et al., 1987, Frank, 1992, 1998, Wendeln et al., 1994, Vincx et al., 2007). The most abundant clupeids in the Wadden Sea are sprat (*Sprattus sprattus*) and autumn-spawning herring (*Clupea harengus*), the latter reproducing along the British east coast (Munk and Christensen, 1990, McQuinn, 1997, Dickey-Collas et al., 2009, Payne et al., 2009). Both clupeid species are common in the Wadden Sea, but herring is much more abundant than sprat (Herrmann et al., 1998, Dänhardt and Becker, 2008, Bolle et al., 2009). Accordingly, clupeid prey of the Common Terns is mainly herring, as indicated by fish remains in regurgitates and fish found in the colonies (Becker et al. 1987). Since 2002, the reproductive success of the Common Terns and other tern species has been far below the long-term average (Dänhardt and Becker, 2008). The low breeding success coincided with exceptionally low recruitment of autumn-spawning North Sea herring, possibly resulting from climate-induced trophic mismatch between zooplankton and first-feeding herring larvae (Payne et al. 2009).

Due to its abundance and energy density (Massias and Becker, 1990, Greenstreet et al., 1999), herring may be the most profitable prey in terms of energy return per unit foraging effort. Herring abundance dynamics may thus be reflected in certain reproductive characteristics of Common Terns breeding in the Wadden Sea. Post-larval herring being produced along the British east coast are drifted into the Wadden Sea (Dickey-Collas et al., 2009), enter the foraging range of the Common Terns at breeding colonies and eventually determine reproductive performance, chick growth dynamics and breeding success. Food availability is likely to be expressed primarily in chick growth rate variation (Mlody and Becker, 1991, Becker and Specht, 1991, Becker, 1998). Within a given period, fast growth would result in

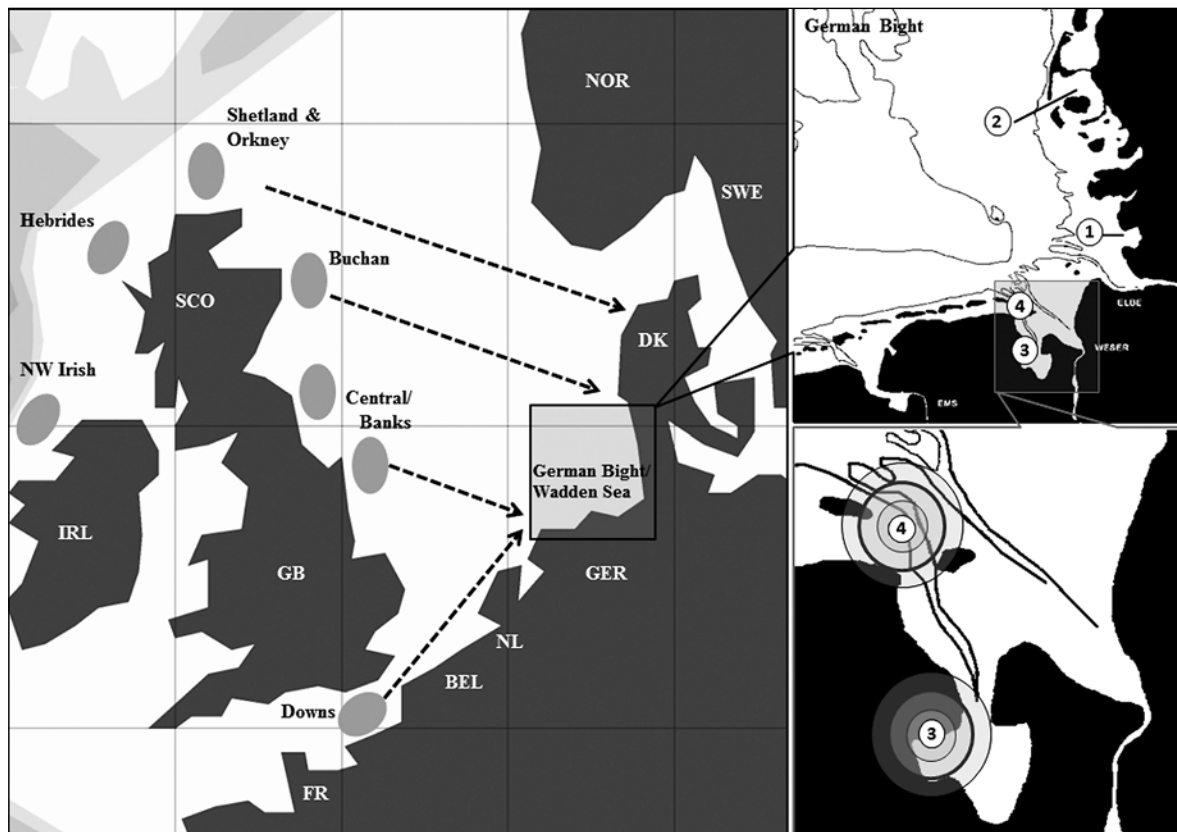
higher maximum weight and – in the absence of predation, flooding and prolonged periods of adverse weather such as heat (Becker et al., 1997), rain or storm (Becker and Specht, 1991) – in higher breeding success. Following this logic, we used a long-term dataset on Common Terns breeding in the Lower Saxon Wadden Sea to investigate, how these three measures change with long-term herring recruitment dynamics from the North Sea (ICES, 2009) and from the Schleswig-Holstein Wadden Sea (Vorberg, 2009), as long time series of herring abundance were not available from the waters around the Lower Saxon breeding colonies (Bolle et al., 2009).

We hypothesize that i) herring abundance in the Wadden Sea is proportional to that in the North Sea and ii) that herring availability to the terns is determined by herring abundance in the Wadden Sea, defining local feeding conditions more directly than herring abundance indices provided by the International Council for the Exploration of the Sea (ICES, 2009). This would result in closer relationships between herring abundance in the Wadden Sea and Common Tern reproductive performance. Alternatively, iii) these relationships could at the same time be biased by small-scale variability within the Wadden Sea brought about e.g. by catch location, daytime, tides, weather or an interaction of these factors. Moreover, iv) due to buffering capabilities of the adult terns and prey alternatives at times of herring shortage the relationship of herring abundance indices with breeding success as an integrative measure should be weaker than with chick weight and growth, which respond more directly to a change in food supply (Greenstreet et al., 1999). Finally, (v) reproductive performance of Common Terns breeding on Minsener Oog should be more closely associated with herring abundance indices than inshore colonies due to a shortage of prey alternatives around the more offshore colonies (Becker et al., 1987, Frank, 1992, Wendeln et al., 1994).

## 2.3 MATERIAL AND METHODS

### FISH SURVEYS AND COMMON TERN BREEDING COLONIES

North Sea autumn spawning herring are potentially relevant as prey to the Common Terns breeding in the Wadden Sea. The herring reproduce along the British east coast, spawning successively later from north to south, with the Downs component spawning in December (Fig. 2.1, left). Owing to its great commercial importance, all stages within the life cycle of the herring are annually surveyed, providing abundance indices as the basis for fisheries management (ICES 2009, Simmonds 2009). Under the auspices of the National Park Administration Schleswig-Holstein Wadden Sea, a stow net survey has been carried out since 1991 (Vorberg, 2009), providing information on species composition and abundance of fish, including herring (Fig. 2.1, top right). Long-term data on Common Tern ecology and demography are collected by the Institute of Avian Research in Wilhelmshaven, with particular focus on two colonies: 1. Banter See in Wilhelmshaven (53° 30' N, 08° 05' E) and 2. on



**Figure 2.1:** Geographic overview of the North Sea (left), the German Bight (top right) and Common Tern breeding areas in the Lower Saxon Wadden Sea (bottom right). Black arrows in the North Sea map denote approximate drift directions of larvae being produced in the main spawning areas of North Sea autumn spawning herring (grey spots). Numbers in the German Bight map indicate the stow net fishing positions in the Schleswig-Holstein Wadden Sea 1) in the Meldorf Bight and 2) in the Hörnum Deep and the Common Tern breeding colonies 3) at Banter See in Wilhelmshaven and 4) on the island of Minsener Oog. The grey circles around the colony sites shown in the Wadden Sea map indicate the foraging range of the Common Terns ( $6.3 \pm 2.4$  km, mean  $\pm$  SD, Becker et al. 1993).

the island of Minsener Oog ( $53^{\circ}45'N$ ,  $08^{\circ}01'E$ ) in the National Park Lower Saxon Wadden Sea (Fig. 2.1, bottom right). Herring abundance indices from the North Sea and from the Schleswig-Holstein Wadden Sea and Common Tern breeding success and chick growth parameters used in this study are summarized in Table 2.1 and are specified below.

#### INDICES OF HERRING ABUNDANCE IN THE NORTH SEA

Not all of the herring abundance indices provided by ICES have the potential to explain variation in e.g. breeding success and chick growth parameters of the Common Terns. Therefore, only life stages that are likely to have direct impact on herring availability to the terns in the Wadden Sea were used in the analyses. For chick provisioning, the Common Terns mainly utilize 0-group herring that were spawned in autumn/winter the year preceding breeding. These young herring are sampled by pelagic oblique trawling at night during the first quarter International Bottom Trawl Survey (IBTS) and provide a direct abundance estimate of poten-

tial food for the tern chicks. From 1977 to 1991, the Isaacs-Kidd-Midwater-Trawl (IKMT) was used, but was replaced with the Methot-Isaacs Kidd Ringnet (MIK) in 1992, which is since used as the standard gear to obtain an index of recruitment strength (Nash and Dickey-Collas, 2005). To account for possible methodological inconsistencies brought about by change in catching gear, the two partial (1977–1991, 1992–2009) and the complete time series (1977–2009) were used in the analyses (Table 2.1). The average density within sub-areas given by the area-resolved MIK-indices was used to explore the relative importance of the different spawning areas for the herring availability in the Wadden Sea. These were in the central western and the southwestern North Sea, the South Bight and the southeastern North Sea (see ICES, 2009). In addition, the herring recruitment index being calculated with the integrated catch-at-age model for the final assessment (ICES, 2009) was used in the analyses (Table 2.1). The 0-ringer recruitment index in a given year closely correlates with year-class strength of 1-ringers in the following year, as derived from the IBTS. These 1-ringers have passed the Wadden Sea during their first year of life as 0-group. When they are caught in the first quarter of their second year of life (with one winter ring) during the IBTS, their abundance should represent their availability to the terns in the Wadden Sea the year before (Greenstreet et al. 1999). As herring older than one year seem to avoid the Wadden Sea and are thus irrelevant as prey for the Common Terns and this index can only retrospectively be related to Common

**Table 2.1:** Time series and years used in the analyses. <sup>1</sup>data collected between May and July. <sup>2</sup>no weight data available for 1993, 2000, 2002–2006, 2008 and 2009. <sup>3</sup>data collected in August, source: Vorberg (2009), <sup>4</sup>Source: ICES (2009).

Data series	Period		Unit
Common Terns <sup>1</sup>	Banter See	Minsener Oog	
Breeding success	1981–2009	1981–2009	Fledged chicks * pair <sup>-1</sup>
Maximum chick weight	1984–2009	1983–2009 <sup>2</sup>	gram
Chick growth rate during linear phase (age 3–13 days)	1984–2009	1983–2009 <sup>2</sup>	gram * day <sup>-1</sup>
Stow net survey, Schleswig-Holstein Wadden Sea <sup>3</sup>			
Meldorf Bight (3 stations)	1991–2009		n * 10 <sup>6</sup> m <sup>-3</sup> filtered water volume
Hörnum Deep (3 stations)	2001–2009		n * 10 <sup>6</sup> m <sup>-3</sup> filtered water volume
ICES stock indices of autumn-spawning North Sea Herring, IBTS-MIK (IKMT) index <sup>4</sup>			
Central west, southwest, southeast, South Bight	1977–2009		average numbers * m <sup>-2</sup>
Recruitment index from stock summary	1977–2009		numbers * 10 <sup>3</sup>

Tern reproduction parameters, it will not be considered here. Likewise, abundance estimates of very early larvae (larval abundance indices, LAI, from the International Herring Larvae Survey), of herring of two years of age or older and of spawner biomass (acoustic surveys) will not be examined in the present study. Eventually, abundance estimates of all life stages are used in the final stock assessment, but with different weighting (Simmonds, 2009).

#### INDICES OF HERRING ABUNDANCE IN THE WADDEN SEA

Data on pelagic fish abundance in the Lower Saxon Wadden Sea close to the Common Tern breeding colonies are available for the years 2006–2009 (Dänhardt and Becker, 2008 and unpublished data), which is too short to be used in the present context. Longer time series were derived from bottom trawls with poor coverage of the eastern Lower Saxon Wadden Sea (Bolle et al., 2009, their Table 2.1.2). The only long-term data series representing pelagic fish in the Wadden Sea is available from the Schleswig-Holstein Wadden Sea (SH-Wadden Sea) (Fig. 2.1, top right). Starting in 1991, stow net catches have been carried out at three stations in the Meldorf Bight (MB, “Steertloch”, “Kronenloch” and “Norderpiep”), each year in the beginning of August. Since 2001, three catch stations were added in the Hörnum Deep (HD, “T22”, “SB”, “OL”) surrounded by the islands of Amrum, Föhr and Sylt (Fig. 2.1, top right). The opening of the stow net is 9 x 10 m, covering the whole water column. On each of the six stations four hauls are carried out, covering ebb and flood tides during the day and at night. Mesh size is 10 mm in the codend. The filtered water volume was used to quantify catch effort, from which fish numbers  $\times 10^6 \text{ m}^{-3}$  were calculated (Vorberg, 2009). For comparison with other time-series, effort-corrected catch numbers were averaged per station (see results), per area (MB or HD) and for all hauls available in a given year. Against the background of herring migration in the southern North Sea (see above), the effort-corrected herring abundance from the SH-Wadden Sea was assumed to be a measure of prey availability to fish-eating seabirds in the Wadden Sea. Besides exploring the relationship between the stow net herring catches and the variation in breeding success and chick growth parameters of the Common Terns, small-scale effects on the variability in herring catch numbers such as daytime, tide and inter-site differences were also investigated.

#### INDICES OF COMMON TERN BREEDING SUCCESS AND CHICK DEVELOPMENT

Linear chick growth rate is positively correlated with breeding success (Becker, 1998) and with maximum chick weight (Schauroth and Becker, unpublished). Maximum mass affects return probability of a fledgling to the home colony after two years (Ludwigs and Becker, 2006) and it is positively correlated with the chicks’ sub-adult mass measured after return to the colony (Becker et al., 2001). Breeding success and weight development of chicks were thus used as dependent variables, responding more or less directly to changes in food supply. Breeding success integrates extrinsic conditions such as weather, predation and food supply over the whole breeding season, whereas maximum weight and daily growth rate of chicks is

instantaneously impacted by adverse environmental conditions, especially in Common Tern chicks which do not accumulate energy reserves (Mlody and Becker, 1991, Becker, 1998). Information on breeding success was available for the years 1981–2009 both at Banter See and on Minsener Oog (Becker, 1998, 2010). Breeding success is defined as the average number of chicks fledged per breeding pair in a given colony. Maximum weight (in gram) and growth rate during the linear phase of the otherwise sigmoid weight curve (in  $\text{gram} \cdot \text{day}^{-1}$  in 3–13 days old chicks) were used as descriptors of chick weight development (Becker and Wink, 2003). Weight data were available from 1984 to 2009 at Banter See and from 1983 to 2007 on Minsener Oog, where weight could not be measured in 1993, 2000, 2002–2006, 2008 and 2009. Sampling and index calculations followed standard procedures (Wagener, 1998; Becker and Wink, 2003). To control for bias due to effects on breeding success other than food supply, regression analyses were carried out both including and excluding years with predation and adverse weather conditions. This information was only available for Banter See (Becker, 1996, 1998, updated).

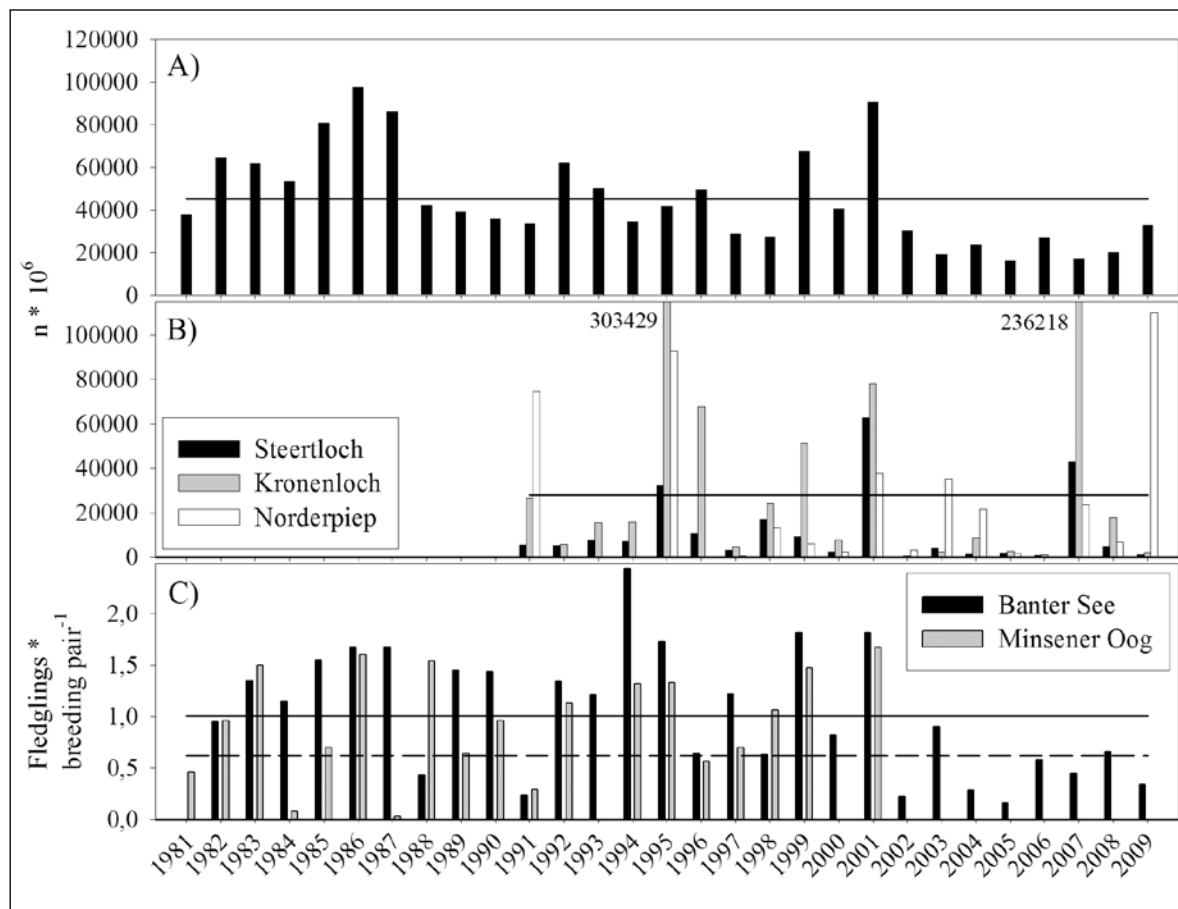
#### STATISTICS

Before investigating the relationships between time series, the mutual influences of variables within the single time series were analyzed. Pearson's product moment correlation coefficient ( $r$ ) was used to quantify relationships among the regional MIK-indices that are potentially relevant to the herring density in the Wadden Sea. These were central west, southwest, southeast and South Bight, as defined in ICES (2009). Also using  $r$ , these four area-resolved measures were related to the North Sea-wide recruitment index eventually used in fish stock assessment. Small-scale variability in herring abundance between and within catch areas in the SH-Wadden Sea was also explored using  $r$ . The impacts of daytime and tide on herring catch numbers in the SH-Wadden Sea were investigated by means of non-parametric Mann-Whitney-U-tests. Regression analysis was applied to examine the influence of chick growth rate on maximum chick weight and the impact of both these parameters on breeding success of the Common Terns.

Regression analyses was also used to analyze, if both herring abundance in the SH-Wadden Sea and Common Tern breeding success and chick growth parameters could be explained by North Sea herring abundance indices. Furthermore, the influence of herring abundance in the SH-Wadden Sea on Common Tern breeding success and chick growth parameters as response variables was also tested by means of regression analyses. Curves were fit to the data using a least-square approach. The assumption of normally distributed residuals was tested by means of probability plots. Where more than three tests were applied to the same dataset, a sequential Bonferroni test was performed to adjust significance levels according to an assumed testwise type I error rate of 5% (Sokal and Rohlf, 1995). All tests were carried out two-sided and were considered significant at  $p \leq 0.05$ .

## 2.4 RESULTS

The best agreement was found between the breeding success at Banter See and the recruitment index of North Sea herring, with the most striking similarity being the below average values since 2002 (Fig. 2.2). The year 2002 also marked the beginning of a series of years with exceptionally low herring abundance in the SH-Wadden Sea, which, in contrast to the other two time series, lasted only until 2006 (Fig. 2.2).



**Figure 2.2:** Time series of A) recruitment of autumn-spawning North Sea herring, B) herring caught during the stow net surveys at three stations in the Meldorf Bight, Schleswig-Holstein Wadden Sea and C) breeding success of Common Terns at the breeding colonies Banter See in Wilhelmshaven and on the island of Minsener Oog in the National Park Lower Saxon Wadden Sea. Horizontal lines denote the long-term average of the respective indices. In the bottom panel (C), the long-term average breeding success is given for Banter See (solid line) and for Minsener Oog (dashed line). The time-series presented in panel B) starts in 1991. Breeding success of Common Terns at Minsener Oog has been zero since 2002.

Abundance patterns in the Wadden Sea did not always fit the larger-scale trends, exemplified by the exceptionally high herring abundance in 2007, when the North Sea herring recruitment index was the second lowest on record. Common Terns breeding on Minsener Oog had zero breeding success since 2002, owing to predation, flooding, adverse weather and poor



food supply. The highest breeding success on record was found in 1994, with below average herring abundance both in the North Sea and in the Wadden Sea. The colony at Banter See appeared to be less affected by predators and weather conditions, but still performed below average (Fig. 2.2).

#### RELATIONSHIPS BETWEEN RECRUITMENT INDICES OF AUTUMN SPAWNING NORTH SEA HERRING

There were close and significant correlations between the area-resolved MIK-indices from the central western, southwestern and southeastern areas and the North Sea herring recruitment index. The MIK-indices from neighboring areas were significantly correlated except for the South Bight, which correlated neither with the recruitment index for the whole North Sea nor with the other three local indices investigated. There were also no significant correlations between the central west and the southeast (Table 2.2).

**Table 2.2:** North Sea herring. Relationships between selected regional MIK-indices and the North Sea-wide recruitment index. Pearson product moment correlation coefficients and significance levels are indicated: \*\*\*,  $p < 0.001$ , \*\*,  $p < 0.01$ . Significant correlations are highlighted in bold.  $n = 33$  years in all cases.

Area	Southwest	Southeast	South Bight	North Sea recruitment
Central west	<b>0.76***</b>	0.27	-0.17	<b>0.49***</b>
Southwest		<b>0.52**</b>	0.14	<b>0.71***</b>
Southeast			0.34	<b>0.79***</b>
South Bight				0.19

SMALL-SCALE VARIABILITY WITHIN STOW NET CATCHES FROM THE SCHLESWIG-HOLSTEIN WADDEN SEA  
Herring catch numbers from MB (all three stations combined) did not correlate with those from the HD (all three stations combined). Catch results also varied between the different stations within one sampling area: For example in MB, herring catch numbers at the sampling sites “Steertloch” and “Kronenloch” were positively and significantly correlated ( $r = 0.68$ ,  $p < 0.001$ ,  $n = 19$ ), whereas no correlation became evident between these two stations and the third, “Norderpiep”.

Besides spatial effects, catch numbers appeared to vary also with daytime. In both areas, herring catches made at night were significantly larger than during the day, but only during ebb tide (Mann-Whitney U-test, HD:  $z = -2.843$ ,  $p < 0.01$ , MB:  $z = -2.789$ ,  $p < 0.005$ ). During flood tide herring catch numbers were similar between day and night. There were no differences in herring catch numbers between ebb and flood.

#### RELATIONSHIPS BETWEEN COMMON TERN BREEDING SUCCESS AND CHICK GROWTH PARAMETERS

Regression analyses at Banter See revealed significant relationships of chick growth rate with both maximum chick weight ( $F = 7.433$ ,  $r^2 = 0.20$ ,  $p < 0.05$ ,  $n = 13$ ) and breeding

success ( $F = 6.941$ ,  $r^2 = 0.19$ ,  $p < 0.05$ ,  $n = 13$ ). This was also the case in maximum chick weight used to explain breeding success ( $F = 6.586$ ,  $r^2 = 0.18$ ,  $p < 0.05$ ,  $n = 13$ ). Against the expectations, excluding years where predation and/or bad weather occurred did not make the relationships closer. Instead, the regressions became insignificant.

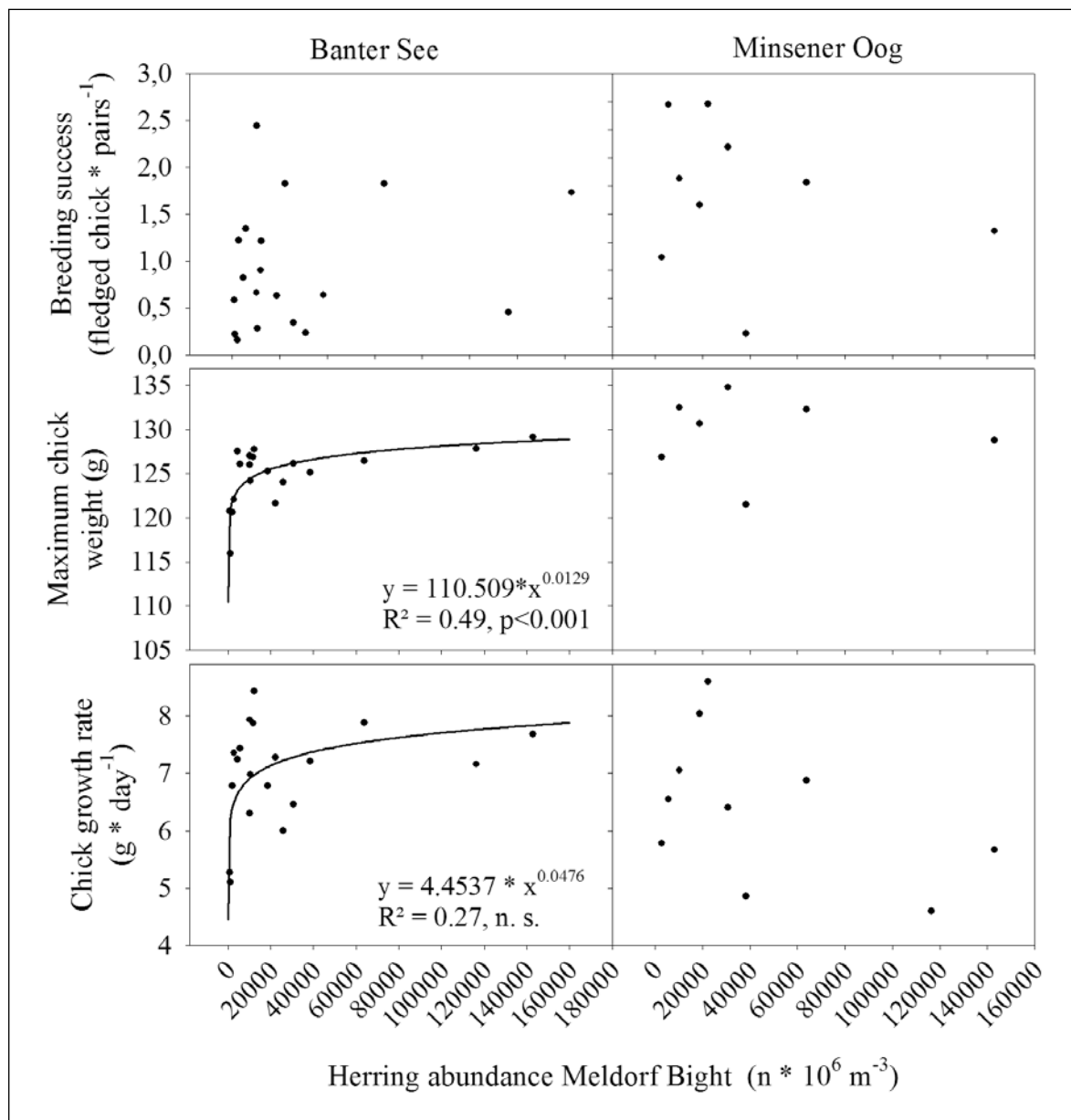
#### HERRING IN THE NORTH SEA AND IN THE SCHLESWIG-HOLSTEIN WADDEN SEA

Including all data from 1991 to 2009, there was no relationship between the recruitment index of North Sea herring and the average catch numbers in the MB and the HD combined. This was mainly attributed to three outliers with disproportionately large catches in the SH-Wadden Sea: Two in the MB (1995 and 2007, both at station “Kronenloch”) and one in the HD (2003, at station “SB”). When these outliers were excluded, the relationships became linear and significant for both areas combined ( $n = 16$ ,  $r^2 = 0.21$ ,  $p < 0.05$ ) and for the MB ( $n = 17$ ,  $r^2 = 0.41$ ,  $p < 0.01$ ), but not for the HD. Regressions of the SH-Wadden Sea time series against the four area-resolved MIK-indices were insignificant in all cases, regardless if outliers were included or not. The three outliers appeared not to have methodological reasons (R. Vorberg, personal communication). Thus, they had to be considered and exemplified the high potential variability operating on small spatial scales.

#### HERRING IN THE SCHLESWIG-HOLSTEIN WADDEN SEA AND COMMON TERNS

Regressions between Common Tern reproduction measures and herring data from the HD could not be carried out due to low sample size. In the analyses only the three stations in the MB were considered. Regression analyses were carried out both with and without the two outliers (see above). None of the Common Tern breeding parameters from Minsener Oog could be explained by the herring abundance in the MB, regardless if resolved by stations or if outliers were excluded. Breeding success and chick growth rate at Banter See could not be explained by the average herring abundance in the MB, whereas the relationship with maximum chick weight at Banter See could be described by a power function, with proportionately small increase beyond ca.  $10\,000 \text{ herring} \cdot 10^6 \text{ m}^{-3}$  (Fig. 2.3). If the data of 1995 and 2007 were excluded (see above), this pattern remained (breeding success and chick growth rate: n.s., maximum chick weight:  $r^2 = 0.40$ ,  $p < 0.01$ ). Without the Bonferroni adjustment (see Material and methods) the herring abundance in the MB and chick growth rate at Banter See were significantly ( $p < 0.05$ ) related by a power function (Fig. 2.3).

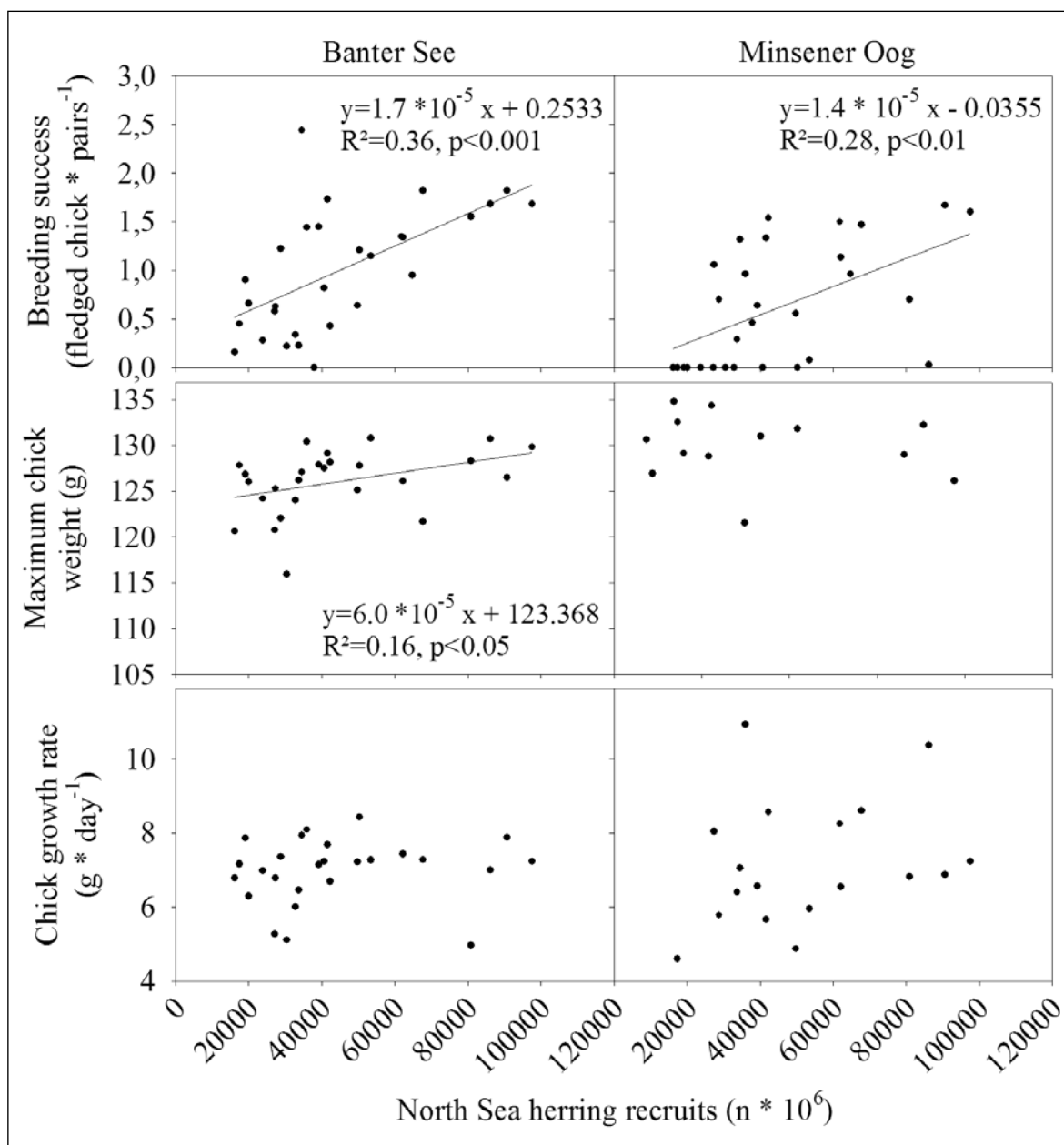
Resolved by the three single stations being sampled in the MB, small-scale spatial effects became evident. Herring catches from the stations “Kronenloch” and “Norderpiep” were not related to any of the Common Tern reproductive parameters, whereas herring abundance at “Steertloch” explained 31 %, 49 % and 46 % of the variability in breeding success ( $p < 0.05$ ), maximum chick weight ( $p < 0.001$ ) and linear chick growth rate ( $p < 0.001$ ) at Banter See, respectively. This pattern remained if the data of 1995 and 2007 were excluded (see above).



**Figure 2.3:** Herring abundance in the Meldorf Bight (all three stations combined) and Common Tern reproductive parameters at Banter See (left column) and on Minsener Oog (right column). Chick growth rate and chick maximum weight could be related to herring abundance via a power function, but only the latter relationship was significant. Parameters, explained variance and significance levels are given.

#### NORTH SEA HERRING AND COMMON TERNS

In contrast to herring abundance in the MB (Fig. 2.3), roughly one third of the variability in breeding success both at Banter See and on Minsener Oog could be explained by the North Sea herring recruitment index. At both colony sites, the relationship was linear and highly significant (Fig. 2.4). At Minsener Oog the linearity and significance of the relationship was attributed to the years 2002–2009 with zero breeding success. The relationship became insignificant if these years were excluded. North Sea herring recruitment had



**Figure 2.4:** North Sea herring recruitment index and Common Tern reproductive parameters at Banter See (left column) and on Minsener Oog (right column). Breeding success at both colonies and chick maximum weight at Banter See were linearly related to herring abundance. Parameters, explained variance and significance levels are given for significant relationships only.

neither an effect on maximum chick weight on Minsener Oog nor on chick growth rate in both colonies, even though the latter suggested an asymptotic and a linear relationship at Banter See and on Minsener Oog, respectively (Fig. 2.4). Using only the years 1981–1991 for the regressions (see Material and methods), all relationships were insignificant, except for breeding success at Banter See ( $F = 6.90$ ,  $r^2 = 0.43$ ,  $p < 0.05$ ). Using only the years 1992–2009, North Sea herring recruitment explained 37% and 48% of the variability

in breeding success at Banter See ( $F = 9.35$ ,  $p < 0.01$ ) and on Minsener Oog ( $F = 14.82$ ,  $p < 0.001$ ), respectively.

Breeding success at Banter See regressed against the MIK-index from the southwestern North Sea revealed a significant relationship ( $F = 6.72$ ,  $r^2 = 0.20$ ,  $p < 0.05$ ). All other area-resolved MIK indices were not suitable to explain variation in breeding success, maximum chick weight or chick growth rate.

## 2.5 DISCUSSION

Long time series allow exploring details of trophic relationships that would remain undetected at shorter time intervals: Neither the poor herring recruitment nor the below-average breeding success of the Common Terns could have been interpreted, when e.g. only data after 2002 were available (Fig. 2.2). High signal-to-noise ratios would be expected due to a variety of factors, including seasonality (IBTS/MIK sampling: first quarter, SH Wadden Sea stow net survey: early August) or gear effects. The latter is difficult to control for, but potentially has profound effects: the low herring recruitment since 2002 clearly seen in the ICES time series (ICES, 2009) and reflected by the Common Tern breeding success data was not detected in bottom trawl surveys from the Dutch Wadden Sea (Tulp et al., 2008, Bolle et al., 2009). Herring catches with bottom trawls in the German Wadden Sea started to decline much earlier than 2002, with regional differences (Bolle et al., 2009). Given the high variability in distribution patterns caused by shallow, tidally influenced habitats and possible methodological bias, the relationship between North Sea herring recruitment and herring abundance in the Wadden Sea is remarkably close.

Our analyses yielded largely unexpected results, most notably Common Tern breeding success being best explained by herring recruit abundance for the whole North Sea, the comparably weak association between Wadden Sea herring data and Common Tern reproductive performance and the stronger relationships of herring abundance indices with the more in-shore colony at Banter See.

### PROPORTIONALITY BETWEEN HERRING ABUNDANCE IN THE WADDEN SEA AND IN THE NORTH SEA

Fish stock data annually collected for management purposes are often the only available measures of food abundance for seabirds. This kind of information has been successfully used to explain reproductive performance of fish-eating seabirds (e.g. Greenstreet et al., 1999, Frederiksen et al., 2005, Furness, 2006, Barrett, 2007, Daunt et al., 2008), indicating that prey fish availability within the foraging range of the respective seabird species represents larger scale prey fish abundance. Although large-scale abundance data are not regarded a precise measure of prey abundance within the foraging range of a given seabird species (e.g. Barrett, 2007), our findings suggest that fish surveys on smaller spatial scales do not

automatically yield the more reliable abundance proxies, especially not in shallow coastal areas with great structural diversity. This is also corroborated by fish abundance in general and herring abundance in particular varying substantially between the Lower Saxon and the SH-Wadden Sea in the years 2005–2009 (Dänhardt and Becker, unpublished data). The proportionality between young herring abundance in the North Sea and in the Wadden Sea may be a methodological issue: An index such as North Sea herring recruitment integrating over an area of almost  $6 \times 10^5 \text{ km}^2$  cannot account for small-scale patchiness, which on the other hand has a profound influence on herring catch numbers in the Wadden Sea. It is generally desirable to obtain prey abundance data from the immediate foraging range of the seabird species of interest. However, small-scale variability needs to be considered when prey abundance is to be translated into prey availability, as exemplified by Common Terns (Becker et al., 1993) and Arctic Terns (Schwemmer et al., 2009) adapting their spatial foraging patterns to the tides. When extreme values are controlled for, herring abundance in the Wadden Sea is proportional to the calculated North Sea herring recruit abundance.

#### COMMON TERN REPRODUCTIVE PERFORMANCE AND HERRING ABUNDANCE IN THE WADDEN SEA AND IN THE NORTH SEA

The only Common Tern reproduction measure being significantly related to herring abundance in the SH-Wadden Sea was maximum chick weight at Banter See. In contrast, breeding success at both colonies and maximum chick weight at Banter See were linearly and significantly related to North Sea herring abundance. Using an additional 19 years of data, the close association between herring recruit density from the southeastern North Sea and the growth rate of fledglings at Banter See found by Greenstreet et al. (1999) between 1991 and 1997 could not be confirmed. This correlation appeared to be specific for this smaller time window, being put into perspective by the longer time series with possibly considerable impacts in the additional years such as poor herring recruitment since 2002 (Payne et al., 2009). The association of maximum chick weight at Banter See with herring abundance in the Wadden Sea was best described by a power function, whereas the relationship with North Sea herring abundance was linear. Herring recruit abundance in the Wadden Sea explained a remarkably large proportion of variability in maximum chick weight at Banter See, even though other prey organisms are also utilized (Frank, 1992; Frick and Becker, 1995). Weight directly depends on food intake (Becker and Ludwigs, 2004), but maximum chick weight will not exceed a physiological threshold, even at very high prey densities. Maximum chick asymptotic mass will not increase any further beyond an average herring density of around 20 000 herring per  $10^6 \text{ m}^3$  fished water volume. In most years, this herring density is not much exceeded, but there are also years without food limitation, possibly due to herring accumulating in the Wadden Sea and generating prey patches sufficient to support ad libitum chick feeding and, as a result, the physiological weight maximum. In turn, the linear relationship between North Sea herring recruit abundance and maximum chick weight at Banter

See indicates, that prey availability to the terns to some degree depends on baseline herring abundance spilling over from the North Sea into the Wadden Sea, where prey fish abundance patterns on larger spatial scales are reflected in the reproductive performance of the Common Terns despite their relatively small foraging range during the breeding season (Becker et al., 1993). However, food abundance is not the same as food availability (Coleman, 2008, Dänhardt and Becker, unpublished data), and there are many factors other than prey density and distribution influencing the eventual foraging success, including weather conditions and tide (Becker and Specht, 1991; Frank and Becker, 1992). Hence, prey density has to be much higher than the seabirds eventually consume to breed successfully (Furness, 2006).

The highest breeding success on record occurred in 1994, with below average herring abundance both in the North Sea and in the Wadden Sea. The extraordinarily high breeding success of the year 1994 was associated with extremely high sprat densities both in the North Sea (ICES, 2009) and in the SH-Wadden Sea (Vorberg, 2009), obviously yielding excess food supply for fish eating species throughout the Wadden Sea. In addition, catches of smelt *Osmerus eperlanus*, another preferred prey fish of the terns breeding at Banter See, were also very high in the SH-Wadden Sea in 1994 (Vorberg, 2009), possibly further improving food supply.

#### CHICK GROWTH AND BREEDING SUCCESS AND THEIR ASSOCIATION WITH HERRING ABUNDANCE

The functional relationships between linear growth rate, maximum chick weight and breeding success were significant, but explained only about 20% of the observed variability, which is obviously attributed to other variables not considered here. In contrast to Cairns' (1987) prediction that breeding success would respond to change in food supply in a sigmoid fashion, the relationship between North Sea herring recruit abundance and breeding success at both Common Tern colonies was clearly linear over a wide range of prey densities. Breeding success is usually regarded largely insensitive to variation in food supply due to various buffering mechanisms by means of adults adjusting their foraging behavior and possible bias due to predation, weather or flooding (Becker and Chapdelaine, 2003). However, breeding success was linearly and significantly related to North Sea herring recruitment both at Banter See and on Minsener Oog, whereas the relationships encompassing chick growth and weight were weaker or not significant at all.

Breeding success was also affected by predation and weather effects in some years. But excluding these two factors did not improve the relationship with herring abundance. On Minsener Oog, the complete breeding failures of the years 2002–2009 were mostly attributed to predation by gulls or corvids and/or to adverse weather conditions during the chick rearing period. Interestingly, the variability of breeding success explained by North Sea herring recruitment almost doubled, when only recent data (1992–2009) were used. Although not intuitive, breeding failure due to predation and adverse weather conditions appears to be at least indirectly related to food supply: Food shortage will impose time and conditional

constraints as well as stress on the adult bird, approximated by levels of the stress hormone corticosterone (Kitaysky et al., 2010). Corticosterone suppresses the pituitary hormone prolactin, known to be involved in initiation and maintenance of parental behavior (Angelier et al., 2009; Bauch et al., 2010). As a consequence, parental motivation to defend their clutches and offspring against predators and to maintain sufficient feeding rates of their young even during prolonged periods of bad weather may be reduced at times of poor food supply (Riechert and Becker, unpublished data).

#### WHY REPRODUCTIVE PERFORMANCE OF COMMON TERNS BREEDING ON MINSENER OOG IS NOT SENSITIVE TO FLUCTUATIONS IN HERRING ABUNDANCE

In contrast to the breeding colony at Minsener Oog, which represents the characteristic breeding habitat for Common Terns in the Wadden Sea (Becker and Ludwigs, 2004), the breeding colony at Banter See is rather untypical: Located on an artificial island on a brackish lake within the city limits of Wilhelmshaven, the clupeid share in chick diet is usually smaller than on Minsener Oog (Frank, 1992; Dänhardt and Becker, 2008). The terns have easy access to a variety of food sources, including freshwater fish, the cooling water discharge of a large power plant nearby and the Jade Bay, offering a consistently high density of smelt, which is rare around Minsener Oog (Dänhardt and Becker, 2008). Nevertheless, both North Sea and Wadden Sea herring abundance were related more closely with reproductive measures from Banter See than from Minsener Oog, confirming the relative importance of herring for the Common Terns also at more inshore colony sites. These rather favorable conditions may support the expression of sub-lethal and more subtle responses to fluctuations in prey availability at Banter See. On Minsener Oog, low herring abundance may have more immediate consequences for chick development and breeding success due to the absence of adequate prey alternatives. Against the initial hypothesis, reproductive performance of Common Terns breeding on Minsener Oog does not reflect fluctuations in herring abundance. The reasons for this are not clear. But even if reproduction dynamics is eventually driven by food supply also on Minsener Oog (see above), the signals in the selected response variables may be masked by catastrophic events more frequently occurring on Minsener Oog.

#### CONCLUSIONS

Due to its commercial importance, the data situation on prey fish stocks is much better in herring than in most other fish species utilized by the terns. Even though there were clear indications that herring is a key prey to the terns in the Wadden Sea, the relative importance of other prey species remains largely unknown due to a lack of long term data series. However, mass occurrences of other species than herring, e. g. sprat, may support good breeding performance, even in years with comparatively low herring density.



The area-resolved MIK-indices were a rather poor indicator of food supply to the Common Terns, even those from the South Bight and from the southwestern North Sea representing the Downs stock, which is most likely the source of herring eventually migrating to the Wadden Sea (Munk and Christensen, 1990; Dickey-Collas et al., 2009). Instead, the herring recruitment index for the whole North Sea calculated from the integrated catch-at-age model (Patterson, 1998; ICES, 2009) was suitable to predict both herring abundance in the MB and Common Tern breeding success at both colonies, even though larvae from the Downs stock were not considered in index estimation (ICES, 2009). Obviously, the calculations and tuning procedures turning the single measurements into the eventual abundance index were able to reproduce the real abundance patterns of North Sea herring encountered by the Common Terns and eventually impacting their breeding success. Associations between predators and prey appear to be stronger at larger scales of measurement, because variation resulting from prey patchiness is reduced. Against the background of large- and medium-scale prey abundance dynamics, scientific focus should be directed at the relative importance of factors affecting breeding performance of seabirds on smaller spatial scales, including foraging behavior and prey availability as a function of seasonality and vertical distribution. Generalist seabirds with a large foraging range are potentially more suitable to reflect the large-scale abundance dynamics of their prey (Montevecchi and Myers, 1995; Barrett, 2007). Conversely, seabird species with a small foraging range such as Common Terns (Becker et al., 1993) would be less suitable. Although a large proportion of the variability in the regressions remains unexplained, ecosystem connectivity between the North Sea and the Wadden Sea appears to be strong enough that Common Tern breeding success and chick weight development yield information on herring abundance also beyond their immediate foraging range. Likewise, breeding success has been shown to severely suffer from the extended period of poor herring recruitment. This demonstrates the key role herring play for the Common Terns, in which population decline is already evident and has resulted in the threat status of Common Terns being revised from “near threatened” to “endangered” in the current version of Germany’s red list of endangered species (Südbeck et al., 2009).

#### ACKNOWLEDGEMENTS

For help with collection of Common Tern reproduction and diet data at Banter See and on Minsener Oog thanks are due to M. Wagener, G. Wagenknecht, U. Walter, M. Wingenroth and to many other colleagues and helpers supporting the field work. The fish abundance data from the Schleswig-Holstein Wadden Sea were collected on behalf of the National Park Administration Schleswig-Holstein Wadden Sea under the auspices of the Trilateral Monitoring and Assessment Program (TMAP). The work received financial support from the Niedersächsische Wattenmeerstiftung (53-NWS-41/04) and from Deutsche Forschungsgemeinschaft (BE 916/1–9).

## 2.6 REFERENCES

- Angelier F, Clément-Chastel C, Welcker J, Gabrielsen GW and Chastel, O (2009) How does corticosterone affect parental behaviour and reproductive success? A study of prolactin in black-legged kittiwakes. *Functional Ecology* 23: 784–793.
- Barrett RT (2007) Food web interactions in the southwestern barents sea: Black-legged kittiwakes *Rissa tridactyla* respond negatively to an increase in Herring *Clupea harengus*. *Marine Ecology Progress Series* 349: 269–276.
- Bauch C, Kreutzer S and Becker PH (2010) Breeding experience affects body condition: blood metabolite levels over the course of incubation in a seabird. *Journal of Comparative Physiology B* 180: 835–845.
- Becker PH (1996) Flusseeeschwalben (*Sterna hirundo*) in Wilhelmshaven. *Oldenburger Jahrbuch* 96: 263–296.
- Becker PH (1998) Langzeittrends des Bruterfolgs der Flusseeeschwalbe und seiner Einflussgrößen im Wattenmeer. *Vogelwelt* 119: 223–234.
- Becker PH (2010) Populationsökologie der Flusseeeschwalbe: Das Individuum im Blickpunkt. Bairlein F and Becker PH (Eds.) 100 Jahre Institut für Vogelforschung „Vogelwarte Helgoland“. Aula Verlag, Wiebelsheim, pp.137–155.
- Becker PH and Chapdelaine G (2003) Further development of seabird monitoring. Tasker ML and Furness RW (Eds.) ICES Cooperative Research Report. International Council for the Exploration of the Sea, Copenhagen, pp. 52–60.
- Becker PH, Frank D and Sudmann SR (1993) Temporal and spatial pattern of Common Tern (*Sterna hirundo*) foraging in the Wadden Sea. *Oecologia* 93: 389–393.
- Becker PH, Frank D and Walter U (1987) Geografische und jährliche Variation der Ernährung der Flusseeeschwalbe (*Sterna hirundo*) an der Nordseeküste. *Journal für Ornithologie* 128: 457–475.
- Becker PH and Ludwigs J-D (2004) *Sterna hirundo* Common Tern. BWP Update 6: 91–137.
- Becker PH and Specht R (1991) Body mass fluctuations and mortality in Common Tern *Sterna hirundo* chicks dependent on weather and tide in the Wadden Sea. *Ardea* 79: 45–56.
- Becker PH, Troschke T, Behnke A and Wagener M (1997) Flüge Küken der Flusseeeschwalbe *Sterna hirundo* verhungern während Hitzeperioden. *Journal für Ornithologie* 138: 171–182.
- Becker PH, Wendeln H and González-Solis J (2001) Population dynamics, recruitment, individual quality and reproductive strategies in Common Terns *Sterna hirundo* marked with transponders. *Ardea* 89: 241–252.
- Becker PH and Wink M (2003) Influences of sex, sex composition of brood and hatching order on mass growth in Common Terns (*Sterna hirundo*). *Behavioral Ecology and Sociobiology* 54: 136–146.
- Boecker M (1967) Vergleichende untersuchungen zur Nahrungs- und Nistökologie der Flusseeeschwalbe (*Sterna hirundo* L.) und der Küstenseeschwalbe (*Sterna paradisaea* pont.). *Bonner Zoologische Beiträge* 18: 15–126.
- Bolle LJ, Neudecker T, Vorberg R, Damm U, Diederichs B, Jager Z, Scholle J, Dänhardt A, Lüerssen G and Marencic, H (2009) Trends in Wadden Sea fish fauna. Part 1 Trilateral cooperation. C108/08.
- Cairns DK (1987) Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261–271.
- Coleman RA (2008) Overestimations of food abundance: Predator responses to prey aggregation. *Ecology* 89: 1777–1783.
- Dänhardt A and Becker PH (2008) Die Bedeutung umweltbedingter Verteilungsmuster von Schwarmfischen für Seevögel im Ökosystem Niedersächsisches Wattenmeer. Institute of Avian Research, Wilhelmshaven. Final report of the project 53-NWS-41/04 of the Niedersächsische Wattenmeerstiftung. 248 pp.
- Daunt F, Wanless S, Greenstreet SPR, Jensen H, Hamer KC and Harris MP (2008) The impact of the sandeel fishery closure on seabird food consumption, distribution and productivity in the northwestern North Sea. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 362–381.
- Dickey-Collas M, Bolle LJ, van Beek JKL and Erftemeijer PLA (2009) Variability in transport of fish eggs and larvae. ii. Effects of hydrodynamics on the transport of downs Herring larvae *Marine Ecology Progress Series* 390: 183–194.

- 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.
- Frank D (1998) Bruterfolgsmonitoring an der Flussseseschwalbe *Sterna hirundo* als Instrument ökologischer Begleituntersuchungen zu einer Pipelineverlegung im Wattenmeer. *Vogelwelt* 119: 235–241.
- Frank D and Becker PH (1992) Body mass and nest reliefs in Common Terns *Sterna hirundo* exposed to different feeding conditions. *Ardea* 80: 57–69.
- Frederiksen M, Wright PJ, Harris MP, Mavor RA, Heubeck M and Wanless S (2005) Regional patterns of kittiwake *Rissa tridactyla* breeding success are related to variability in sandeel recruitment. *Marine Ecology Progress Series* 300: 201–211.
- Frick S and Becker PH (1995) Unterschiedliche Ernährungsstrategien von Fluss- und Küstenseeschwalbe (*Sterna hirundo* und *S. paradisaea*) im Wattenmeer. *Journal für Ornithologie* 136: 47–63.
- Furness RW (2006) Responses of seabirds to depletion of food fish stocks. *Journal of Ornithology* 148: 247–252.
- Greenstreet SPR, Becker PH, Barrett RT, Fossum P and Leopold MF (1999) Consumption of pre-recruit fish by seabirds and the possible use of this as an indicator of fish stock recruitment. Furness RW and Tasker ML (Eds.) *Diets of seabirds and consequences of changes in food supply*. ICES Cooperative Research Report 232: 6–17.
- Herrmann J-P, Jansen S and Temming A (1998) Fische und dekapode Krebse in der Sylt-Rømø-Bucht. Gätje C and Reise K (Eds.) *Ökosystem Wattenmeer – Austausch, Transport und Stoffumwandlungsprozesse*, Springer, Berlin, Heidelberg, New York, pp. 81–88.
- ICES (2009) Report of the Herring assessment working group for the area south of 62°N. ICES CM 2009/ACOM:03, International Council for the Exploration of the Sea, Copenhagen, pp. 1–658.
- Jager Z, Bolle LJ, Dänhardt A, Diederichs B, Neudecker T, Scholle J and Vorberg R (2009) Fish. In Marencic H and DeVlas J (Eds.) *Quality Status Report 2009*. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven, Germany.
- Kitaysky AS, Piatt JF, Hatch SA, Kitaikaia EV, Benowitz-Fredericks ZM, Shultz MT and Wingfield JC (2010) Food availability and population processes: Severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Functional Ecology* 24: 625–637.
- Koffijberg K, Dijkse L, Hälterlein B, Laursen K, Potel P and Schrader S (2009) Breeding birds. In Marencic H and DeVlas J (Eds.) *Quality Status Report 2009*. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven, Germany.
- Laursen K, Blew J, Ens B, Eskildsen K, Günther K, Hälterlein B, Koffijberg K, Potel P and van Roomen M (2009) Migratory birds. In Marencic H and DeVlas J (Eds.) *Quality Status Report 2009*. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven, Germany.
- Ludwigs J-D and Becker PH (2006) Individual quality and recruitment in the Common Tern, *Sterna hirundo*. *Acta Zoologica Sinica* 52 (Supplement): 96–100.
- Massias A and Becker PH (1990) Nutritive value of food and growth in Common Tern (*Sterna hirundo*) chicks. *Ornis Scandinavica* 21: 187–194.
- McQuinn IH (1997) Metapopulations and the Atlantic Herring. *Reviews in Fish Biology and Fisheries* 7: 297–329.
- Mlody B and Becker PH (1991) Körpermasseentwicklung und Mortalität von Küken der Flussseseschwalbe (*Sterna hirundo* L.) unter ungünstigen Umweltbedingungen. *Vogelwarte* 36: 110–131.
- Montevecchi WA (1993) Birds as indicators of change in marine prey stocks. Furness RW and Greenwood JJD (Eds.) *Birds as monitors of environmental change*. Chapman and Hall, London, pp. 217–266.
- Montevecchi WA and Myers RA (1995) Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. *Marine Ecology Progress Series* 117: 1–9.
- Munk P and Christensen V (1990) Larval growth and drift pattern and the separation of Herring spawning groups in the North Sea. *Journal of Fish Biology* 37: 135–148.
- Patterson KR (1998) Integrated catch at age analysis version 1.4. Scottish Fisheries Research Report 38.

- Payne MR, Hatfield EMC, Dickey-Collas M, Falkenhaus T, Gallego A, Gröger J, Licandro P, Llope M, Munk P, Röckmann C, Schmidt JO and Nash RDM (2009) Recruitment in a changing environment: The 2000s North Sea Herring recruitment failure. *ICES Journal of Marine Science* 66: 1–6.
- Piatt JF and Sydeman WJ (2007) Seabirds as indicators of marine ecosystems *Marine Ecology Progress Series* 352: 199–309.
- Schwemmer P, Adler S, Guse N, Markones N and Garthe S (2009) Influence of water flow velocity, water depth and colony distance on distribution and foraging patterns of terns in the Wadden Sea. *Fisheries Oceanography* 18: 161–172.
- Südbeck P, Bauer H-G, Boschert M, Boye P and Knief W (2009) Rote Liste und Gesamtartenliste der Brutvögel (Aves) Deutschlands. Bundesamt für Naturschutz (Eds.) *Naturschutz und biologische Vielfalt* 70 (1): 159–227. Bonn, Bad Godesberg.
- Tulp I, Bolle LJ and Rijnsdorp AD (2008) Signals from the shallows: In search of common patterns in long-term trends in dutch estuarine and coastal fish. *Journal of Sea Research* 60: 54–73.
- Vincx M, Kuijken E and Volckaert F (2007) Higher trophic levels in the southern North Sea. Final report EV/25, D/2007/1191/33, pp. 1–88.
- Vorberg R (2009) Monitoring der Fische im Wattenmeer-Untersuchungen zum Vorkommen und zur Verteilung der Fische in der Meldorfer Bucht und in der Nullnutzungszone im Hörnum Tief. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer. 63 pp.
- Wagener M (1998) Praktische Hinweise für brutbiologische Untersuchungen an der Flussseseschwalbe (*Sterna hirundo*). *Vogelwelt* 119: 279–286.
- Wendeln H (1997) Body mass of female Common Terns (*Sterna hirundo*) during courtship: Relationships to male quality, egg mass, diet, laying date and age. *Colonial Waterbirds* 20: 235–243.
- Wendeln H, Mickstein S and Becker PH (1994) Auswirkungen individueller Ernährungsstrategien von Flussseseschwalben (*Sterna hirundo*) auf die Anwesenheit am Koloniestandort. *Vogelwarte* 37: 290–303.

## CHAPTER 3

## THE SEASONALITY OF SEABIRD-FISH OVERLAP IN THE WADDEN SEA

Andreas Dänhardt<sup>1\*</sup>, Alexander Braasch and Peter H. Becker

Institute of Avian Research “Vogelwarte Helgoland”,  
An der Vogelwarte 21, 26386 Wilhelmshaven, Germany.

\* Corresponding author

<sup>1</sup> present address: Suerhoper Brunnenweg 13 a, 21244 Buchholz/Nordheide, Germany,  
Phone: + (49) 1 79 / 5 17 15 36, E-mail: andreas@daenhardt.com

## 3.1 ABSTRACT

Predator-prey overlap is the prerequisite for trophic interactions, changing seasonally in temperate regions. Both the timing of the predator’s food requirements relative to prey availability and the trade-off between foraging effort and energy yield are central to the predator’s reproductive performance. We used seasonal data on energy requirements of a colony of Common Terns (*Sterna hirundo*) breeding in the German Wadden Sea and on changes in energy made available by forage fish to explain reproductive performance and chick weight development. The temporal dimension of the greatest energy demand of the predator and maximum prey availability in the Wadden Sea appears irrelevant as long as prey abundance is sufficient. During breeding, the spatial overlap between the terns and herring (*Clupea harengus*) may be disrupted by small-scale temperature increase, which can have the same effect as temporal mismatch by decreasing the relative density of prey at times of high energy demand of the predator. Among the prey fish species examined, herring and sprat (*Sprattus sprattus*) should be attractive to the seabirds mainly due to their abundance and less through seasonal length increase, whereas in smelt (*Osmerus eperlanus*) and whiting (*Merlangius merlangius*) an increase in both abundance and size enhances the potential energy return per unit foraging investment by the Common Terns.

## KEYWORDS

*Common Tern, energy requirements, trophic synchrony, phenology, Wadden Sea*

## 3.2 INTRODUCTION

Among avian migrants, terns travel the longest distances between wintering and breeding grounds (Del Hoyo et al., 1996). The annual migration distances travelled by e. g. Common Terns (*Sterna hirundo*) are harshly contrasted by the average foraging range during breeding, when the parent birds are tied to the breeding colony (Becker et al., 1993; Becker and Ludwigs, 2004). In the Wadden Sea, Europe's largest intertidal wetland, the breeding terns depend on prey varying seasonally in size and abundance. Likewise, the terns' energy demand changes over the course of the breeding season. Energy requirements for adults are greatest during egg development and rearing of young, whereas the most critical time for chicks is immediately after fledging, when their energy requirements approach those of adults but foraging skills are still underdeveloped (Safina and Burger, 1988). Thus, prospects for successful reproduction are good, if prey fish enter the terns' foraging range at the right time in high densities, providing energy return per unit foraging effort sufficient to feed the incubating partner, to raise the chicks and, eventually, to self-feed. Both abundance and size of the prey fish determine the energy return on foraging investment: Chances for successful foraging increase at high prey densities, but net energy yield may be smaller when only small prey items are caught. To some degree, low prey density may be compensated by large and energy-rich prey.

The relevance of spatio-temporal overlap between predators and prey has been first conceptualized in Hjort's (1914) critical period hypothesis, providing the foundation of the match-mismatch hypothesis later formulated and developed by Cushing (1969, 1990, 1995). Originating from plankton-fish systems, the match-mismatch hypothesis was extended to higher trophic levels, e. g. by Durant et al. (2005). It states that if there is a temporal mismatch between the food requirement of the predator and prey availability, then reproductive success of the predator will be low. This general formulation can be specified, that during the time of the greatest energy demand of the predator the energy yield per unit foraging effort should correspondingly be high. The spatio-temporal mismatch between predators and prey has been related to divergent changes in predator and prey phenologies as a result of climate change, potentially disrupting food webs (e. g. Parmesan and Yohe, 2003; Edwards and Richardson, 2004; Durant et al., 2007).

In colonial seabirds, the spatial component of predator-prey overlap becomes more important during breeding, when provisioning breeders have to return to the colony to feed partners and offspring. Thus, energetic investment per unit energy return is enhanced compared to the non-breeding season and the foraging range is at the same time spatially confined. During

that time, adult birds have to balance the demands of their chicks with maintaining their own body condition (Wendeln and Becker, 1999; Quillfeldt et al., 2010). Single-prey loaders such as terns could maximize their return on investment by preferring large, energy-rich prey to deliver to the colony, because flying from the foraging area back to the colony requires energy beyond the actual foraging process. In turn, provisioning chicks or breeding partners with small prey of low absolute energy content would be less profitable (Massias and Becker, 1990). Consequently, food yielding less energy should be ingested by the successful forager itself (Wilson et al., 2004; Sonntag and Hüppop, 2005; Dänhardt et al., 2010). This concept is known as the central place foraging theory (Orians and Pearson, 1979).

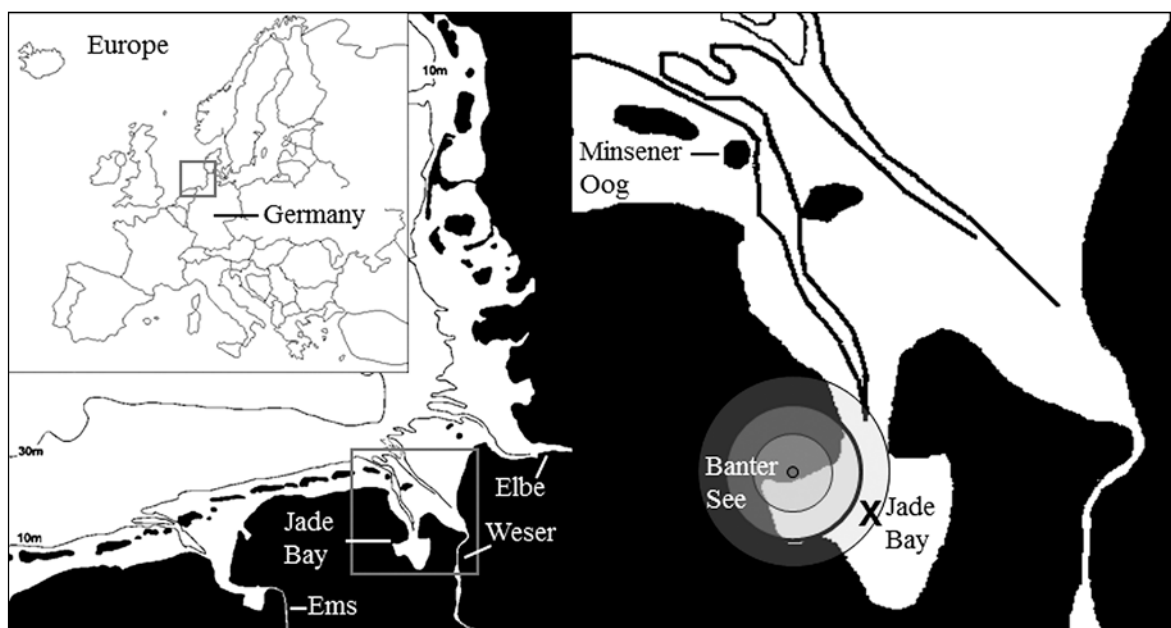
Within the framework of the match-mismatch hypothesis and the central place foraging theory, we use information on seasonal energy requirements of a Common Tern colony breeding in the German Wadden Sea and data on seasonal change of energy made available through their key prey fish species to explain reproductive performance and chick weight development. In addition, we test three key assumptions of the match-mismatch hypothesis: i) The energy demand of the predator and the availability of prey follow a unimodal bell-shaped distribution, ii) the closer the temporal match between the maximum energy demand of the predator and peak abundance of prey the better the reproductive performance, and iii) poor temporal match can to some degree be compensated by high prey abundance.

### 3.3 MATERIAL AND METHODS

#### FISH SAMPLING

Fish samples were obtained using a ship-based stow net in the central Jade Bay (53° 28' N, 08° 12' E) in the Lower Saxon Wadden Sea, Northern Germany. Between April 19<sup>th</sup> and September 5<sup>th</sup> 2006 and April 24<sup>th</sup> and October 10<sup>th</sup> 2007 sampling took place at least twice per month, depending on local wind conditions. Both time and site of the fish sampling were concomitant with the breeding season in one of the largest German colonies of Common Terns at Banter See in Wilhelmshaven (53° 30. 40' N, 08° 06. 20' E). The fish sampling site was located well within the average foraging range of Common Terns in the Wadden Sea ( $6.3 \pm 2.4$  km, Becker et al., 1993; Fig. 3.1).

Stow nets are passive catching gear utilizing the water current as encountered in rivers and in tidal marine areas such as the Wadden Sea. They are largely unselective towards mobile species and are thus representative especially of pelagic fish (Breckling and Neudecker, 1994), the Common Terns' main prey. The stow net covered the water column from the water surface down to 4–5 m at absolute water depths of 5–8 m, depending on the tides. The net opening was 5 m wide and 4–5 m high, depending on the strength of the water current pushing against the net surface and lifting the lower beam. Haul duration was  $45 \pm 5$  minutes. The stretched mesh size decreased from 40 mm close to the mouth to 10 mm in the cod end.



**Figure 3.1:** Area of investigation. The dot indicates colony location at Banter See; the circles around the colony denote the average ( $\pm$  SD) foraging range of the Common Terns ( $6.3 \pm 2.4$  km, after Becker et al. 1993). The cross indicates the stow net catching position in the central Jade Bay.

Water flow was recorded by means of four propeller flow meters (Hydrobios, Kiel). Absolute catch numbers were normalized to individuals per 10 000 m<sup>3</sup> filtered water volume ( $No_{10000}$ ) by

$$No_{10000} = No_{absolute} / (PC_{end} - PC_{start} \times 0.3 \times Net_{height} \times Net_{width}) \times 10000$$

with  $No_{absolute}$  = absolute fish numbers,  $PC_{end}$  i.e.  $PC_{start}$  = propeller count at the end i.e. the start of a haul, 0.3 = meters per rotation of the propeller flowmeter (value provided by manufacturer),  $Net_{height}$  = average net height in m (varying with the current pressure),  $Net_{width}$  = net width in m (constant). The catches were sorted by species, individuals were counted and standard length ( $\pm 1$  mm) was measured (Muus and Nielsen, 1999). For further analyses (see below) the average effort-corrected catch numbers per catching date were used.

#### INDIVIDUAL NUMBERS OF COMMON TERNS

The breeding colony at Banter See is subject to long-term investigations on Common Tern population ecology (Becker, 1998; Becker et al., 2001b; Ezard et al. 2007). In 2006 and 2007 470 and 420 pairs, respectively, were breeding at the colony site. Starting upon the arrival of the first Common Terns in the colony in mid-April, the total numbers of breeders and non-breeders marked with transponders were recorded daily during the entire breeding period (for details see Ezard et al., 2007 and Becker et al., 2008). As the focus of this study is on the reproductive part of the colony and as the number of non-breeders was negligible in both



years, only breeding birds and their reproductive output were included in the analyses. The proportions of the marked birds (~ 60 %) were extrapolated to all birds present in the colony, divided into egg-producing females, self-feeding adults (males and non-egg-producing females), chicks younger and older than 13 days, yielding the eventual figures for subsequent energetic calculations.

Terns concentrate in the colonies shortly after their arrival from the wintering grounds, but stay in the area for several weeks after fledging (Schauroth and Becker, 2008). Thus, the decrease in colony energy demand towards the end of the breeding season reflects colony dispersal rather than a true decline in energy demand to be met by prey fish. Despite some post-fledging mortality the energy demand can be assumed to remain high between leaving the colony site and the start of migration in late August/early September (Becker and Ludwigs, 2004). Colony counts were terminated on September 14<sup>th</sup> and on August 2<sup>nd</sup> in 2006 and 2007, respectively.

#### FEEDING OBSERVATIONS

Feedings of partners and chicks in the colony were observed with the naked eye and using binoculars (10 x 40 magnification) from wooden shelters in the colony a few meters away from the nests. Prey items were identified to the lowest possible taxonomic level. Prey length was recorded as multiples of average bill length of adult birds (3.7 cm; Becker and Ludwigs, 2004). Bill lengths were multiplied with 3.7 to acquire actual prey length in cm. Herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and twaite shad (*Alosa fallax*) could not be distinguished and were thus summarized as clupeids. Plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and sole (*Solea solea*) were noted as flatfish. Whiting (*Merlangius merlangius*) and cod (*Gadus morhua*) were recorded as gadids; identification of gobies (*Pomatoschistus spec.*), pipefish (*Syngnathus spec.*) and sandeel (*Ammodytes spec.* or *Hyperoplus spec.*) was also not possible down to species level. Judging from the stow net catches, where species identification was always carried out except for gobies, clupeids were mainly herring, flatfish were mainly plaice, gadids were mainly whiting, pipefish were mainly Nilsson's pipefish (*Syngnathus rostellatus*) and sandeel were mainly lesser sandeel (*Ammodytes tobianus*) (for details see Dänhardt and Becker, 2008). Where identification was not possible, prey items were recorded as "unidentified". Prey items being fed in proportions less than 1 % during courtship and chick rearing periods were pooled as "others".

#### ENERGY REQUIREMENTS OF COMMON TERNS

Individual energy requirements of the Common Terns vary over the course of the breeding season and are thus not strictly proportional to individual numbers. Before mating, male and female birds have only to self-feed and require an average of 355 kJ \* day<sup>-1</sup> (Klaassen et al., 1992a). This value multiplied by individual numbers per day was thus used to approximate the mean daily energy demand of the colony before mating. After mating, females require

additional energy for egg formation, the provision of which is increasingly shifted from the female to the male partner. The energetic costs for egg formation depend on egg mass (EM in g; 19.8 g, Wendeln et al., 2000), clutch size (CS, 2.3 in 2006 and 2.6 in 2007), energy content per unit egg mass (EC, 6.81 kJ \* g<sup>-1</sup> fresh weight in semi-precocial species; Bezzel and Prinzing, 1990) and production efficiency (set at 75 %; Hilton et al., 2000). The additional energy required to produce a clutch of a given size ( $E_{\text{clutch}}$ ) was calculated as

$$E_{\text{clutch}} = 19.8 \text{ g} * \text{CS} * 6.81 \text{ kJ} * \text{g}^{-1} * (100/75)$$

$E_{\text{clutch}}$  was then divided by 16, as egg production was assumed to last from 10 days before to 5 days after laying the first egg, and added to the daily energy requirements of egg-producing females. Eventually, the daily energy demand of all egg-producing breeding pairs in the colony ( $E_{\text{clutch} * \text{day}^{-1}}$ ) was calculated as

$$E_{\text{clutch} * \text{day}^{-1}} = (2 * 355 \text{ kJ} * \text{day}^{-1} + (E_{\text{clutch}}/16)) * (n_{\text{adults}} - n_{\text{self-feeding adults}}).$$

The average daily energy demand of younger and older chicks was calculated separately, using the gross energy intake interpolated between fast and slow growing Common Tern chicks (Klaassen et al., 1992b, their Figure 3): The gross energy intake of 7 days old chicks (155 kJ \* day<sup>-1</sup>) was used to represent the energy demand of young chicks (0–13 days); the gross energy intake of 20 days old chicks (210 kJ \* day<sup>-1</sup>) was used to represent the energy demand of older chicks (14 days until fledging) (Klaassen et al., 1992b). Average energy requirements were multiplied by the number of chicks younger and older than 13 days and summed up to get a figure of the energy demand of all chicks. Chick age of 13 days marks the turning point between the linear and the asymptotic growth phase (Klaassen et al., 1994). As adults need more energy when provisioning chicks, the daily energy requirements of chick-feeding birds was set at 434 kJ \* day<sup>-1</sup>, following Galbraith et al. (1999). Finally, summing up the energy demands of self-feeding adults, egg-producing adults, chick-feeding adults and all chicks yielded an approximation of the total daily energy demand of the entire breeding colony over the course of the breeding season (Fig. 3.2). For subsequent comparisons with the abundance and energy of prey fish, only the total daily energy requirement of the breeding colony was used.

#### ENERGY CONTENT OF PREY FISH

The energy densities at length of herring, sprat and smelt (*Osmerus eperlanus*) were taken from Fischer (2009); values for whiting were obtained from Pedersen and Hislop (2001). These fish species are the most important prey of Common Terns in the Wadden Sea and of the focal colony (Becker et al., 1987; Frank, 1992; Wendeln et al., 1994; Wendeln, 1997). Standard length (SL) and individual energy content of these four species were related by

Herring:  $\text{kJ} * \text{Individual}^{-1} = 0.3800 * \text{SL}^{2.7458} (r^2 = 0.97)$

Sprat:  $\text{kJ} * \text{Individual}^{-1} = 0.4548 * \text{SL}^{2.7312} (r^2 = 0.91)$

Smelt:  $\text{kJ} * \text{Individual}^{-1} = 0.2431 * \text{SL}^{2.9472} (r^2 = 0.99)$

Whiting:  $\text{kJ} * \text{Individual}^{-1} = 0.0244 * \text{SL}^{3.2713} (r^2 = 0.99)$

The length-specific energy content was multiplied with the average fish length for each fish sampling date to account for seasonal changes in fish size distribution. Finally, the average energy density by prey species per unit water volume was calculated by multiplying the average energy content with individual numbers per 10000 m<sup>3</sup> fished water volume. To determine how much energy a Common Tern would gain per individual fish caught throughout the season, the average prey fish length was translated into energy available per successful foraging event.

#### BREEDING PERFORMANCE AND CHICK GROWTH OF COMMON TERNS

At Banter See, the total colony was under investigation to study reproductive success of clutches from the first laying cycle (checks every other day between May 1<sup>st</sup> and June 9<sup>th</sup>; for methodological details see Wagener (1998) and Wendeln and Becker (1999)). The laying pentad was the five-day-period of the year when the first egg of a clutch was laid; clutch size referred to eggs per clutch, the breeding success was defined as the number of chicks fledged per breeding pair.

All chicks were ringed on the day they were first found. Subsequently, a sub-sample of all newly hatched chicks was weighed at every check by means of a digital balance in a special wind protected box (accuracy  $\pm 1$  g; Wagener, 1998). Three parameters of mass growth were investigated: Growth rate ( $\text{g} * \text{day}^{-1}$ ) during the linear phase of the body mass development, (3–13 days of age), peak mass (maximum mass record (g) of a chick = asymptotic mass) and pre-fledging mass (last mass record (g) of a chick before it leaves the colony site as a fledgling). For further details see Becker and Wink (2003). Peak mass and pre-fledging mass were calculated only for chicks which fledged, growth rate was determined also for chicks which died before fledging.

#### STATISTICS

The degree of association between the energy demand in the colony and energy density in the foraging area was determined using Spearman's rank correlation coefficient ( $r_s$ ). Inter-annual comparisons of Common Tern breeding parameters were tested for significance using a Mann-Whitney-U-test (egg laying pentad, clutch size and fledglings per breeding pair) and student's t-test (growth rates, pre-fledging and fledging weight of chicks). Coefficients of variation (CV) were used to compare the degree of relative variability in abundance and energy content between the main prey fish species (Sokal and Rohlf, 1995). Both correlations and differences were considered statistically significant at  $p \leq 0.05$ .

### 3.4 RESULTS

#### FEEDING OBSERVATIONS

In 2006, 688 and 2809 courtship and chick feedings were observed, respectively. In 2007, 134 and 1366 prey deliveries to partners and chicks, respectively, were recorded. In both years courtship prey consisted of fish that were 7.2 cm long on average (range 2–15 cm), chicks were fed prey fish with a mean length of 8.8 cm (range: 2–20 cm). The length classes of prey fish consumed by the terns was consistent with the length classes observed in the stow net catches, so all length classes caught were used to calculate energy availability.

Clupeids and smelt were the dominant prey items, together supplying ca. one half of all prey (Table 3.1). In June 2007, large numbers of whiting occurred in the Lower Saxon Wadden Sea and made up 12% of chick food. Brown shrimp, fish larvae, pipefish and gobies were also present in the feedings in higher proportions, but these prey types were not included in the analyses, because they were regarded poor prey due to their size (fish larvae, gobies) or their high content of indigestible tissue (brown shrimp, pipefish). Furthermore, stow nets do

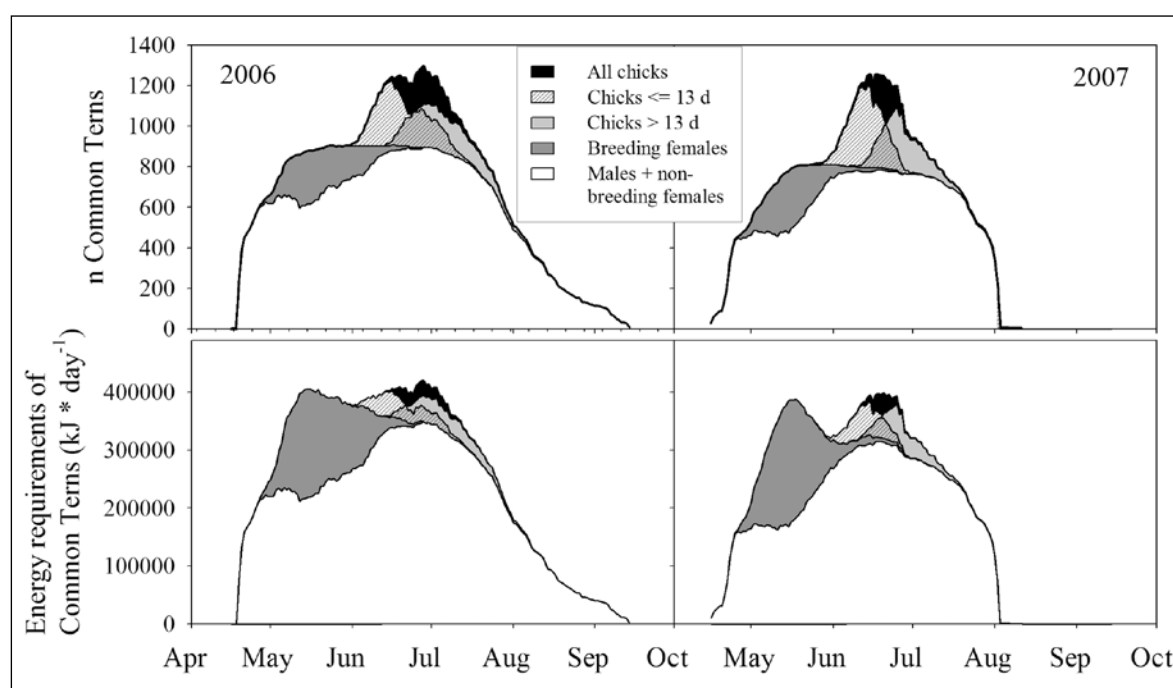
**Table 3.1:** Composition of Common Tern prey in 2006 and 2007 at Banter See fed to partners during courtship and chicks, sorted by relative importance. The prey groups used in the analyses are highlighted in bold.

Prey organism	2006		2007		$\Sigma$
	Courtship %	Chicks %	Courtship %	Chicks %	
<b>Clupeids (herring, sprat, twaite shad)</b>	<b>26.2</b>	<b>25.7</b>	<b>6.0</b>	<b>32.7</b>	<b>27.1</b>
<b>Smelt (<i>Osmerus eperlanus</i>)</b>	<b>24.4</b>	<b>16.0</b>	<b>63.4</b>	<b>17.8</b>	<b>18.9</b>
Brown shrimp ( <i>Crangon crangon</i> )	12.6	12.0	11.9	5.9	10.4
Unidentified	13.5	8.2	3.0	8.7	8.9
Fish larvae	8.3	7.7	15.7	7.2	7.5
Pipefish ( <i>Syngnathus spec.</i> )		8.0	5.0		5.8
Goby ( <i>Pomatoschistus spec.</i> )	10.9	4.1		1.3	4.1
Flatfish (Plaice, flounder, sole)		5.8		2.7	4.0
Insects		5.6		1.1	3.5
<b>Gadids (whiting, cod)</b>				<b>12.2</b>	<b>3.3</b>
Shore crab ( <i>Carcinus maenas</i> )		4.4		2.4	3.2
Others	3.1	1.9		1.6	1.9
Lesser sandeel ( <i>Ammodytes spec.</i> )	1.0	1.2			0.8
Perch ( <i>Perca fluviatilis</i> )				1.5	0.4
N	688	2809	134	1366	4997

not yield representative abundance estimates of demersal species. Thus, brown shrimp was not considered in the analyses, even though they were fed in considerable proportions. Due to their abundance and nutritional value, herring, sprat, smelt and whiting were assumed to be decisive for the terns and were thus used in subsequent analyses (Table 3.1).

#### COMMON TERN NUMBERS AND ENERGY DEMAND

In both years, colony formation started in mid-April, and adult numbers kept increasing until May 22<sup>nd</sup>. Courtship behaviour, represented by the difference between all individuals in the colony and self-feeding adults (Fig. 3.2) was observed from April 27<sup>th</sup> until June 27<sup>th</sup> and from April 24<sup>th</sup> until June 27<sup>th</sup> in 2006 and 2007, respectively.



**Figure 3.2:** Seasonal variation of Common Tern numbers and energy consumption at the Banter See colony in 2006 (left) and 2007 (right). Individual numbers (top) and estimated energy requirements (bottom) of Common Terns of the entire colony are presented, divided into males and non-egg-producing females (white area), egg-producing females (dark grey area) and chicks (black area), resolved into younger ( $\leq 13$  days, hatched area) and older ( $> 13$  days, grey area) chicks. Individuals and energy demands of the different classes add up to the colony total, represented by the outer contour of the area plots. Surplus energy needed by parents to provision their young is considered in the energy demand of non-breeding adults (white area).

In 2006, courtship peaked in the first two weeks of May, whereas in 2007 courtship behaviour was evident throughout the whole month of May (Fig. 3.2). Courtship ceased when chicks started hatching (2006: May 31<sup>st</sup>, 2007: May 25<sup>th</sup>). In 2006, chick numbers peaked around June 19<sup>th</sup> and June 28<sup>th</sup>. In 2007, maximum chick numbers were counted on June 15<sup>th</sup>. In 2006, the number of chicks declined more gradually than in 2007, when many chicks died due to a stormy weather period starting on June 27<sup>th</sup>. After that, the colony started to break up until

recording of individual numbers ended on August 2<sup>nd</sup>. In 2006 the Common Terns stayed at the colony site until September. The seasonality of energy demand of self-feeding adults and chicks resembled individual numbers, whereas energy requirements of the colony peaked in early May due to egg-producing pairs. In 2007, the period of egg formation was more synchronized than in 2006, with numbers of egg-producing pairs steeply decreasing in the second half of May. In contrast, the decrease of egg producing pairs was more gradual in 2006 (Fig. 3.2).

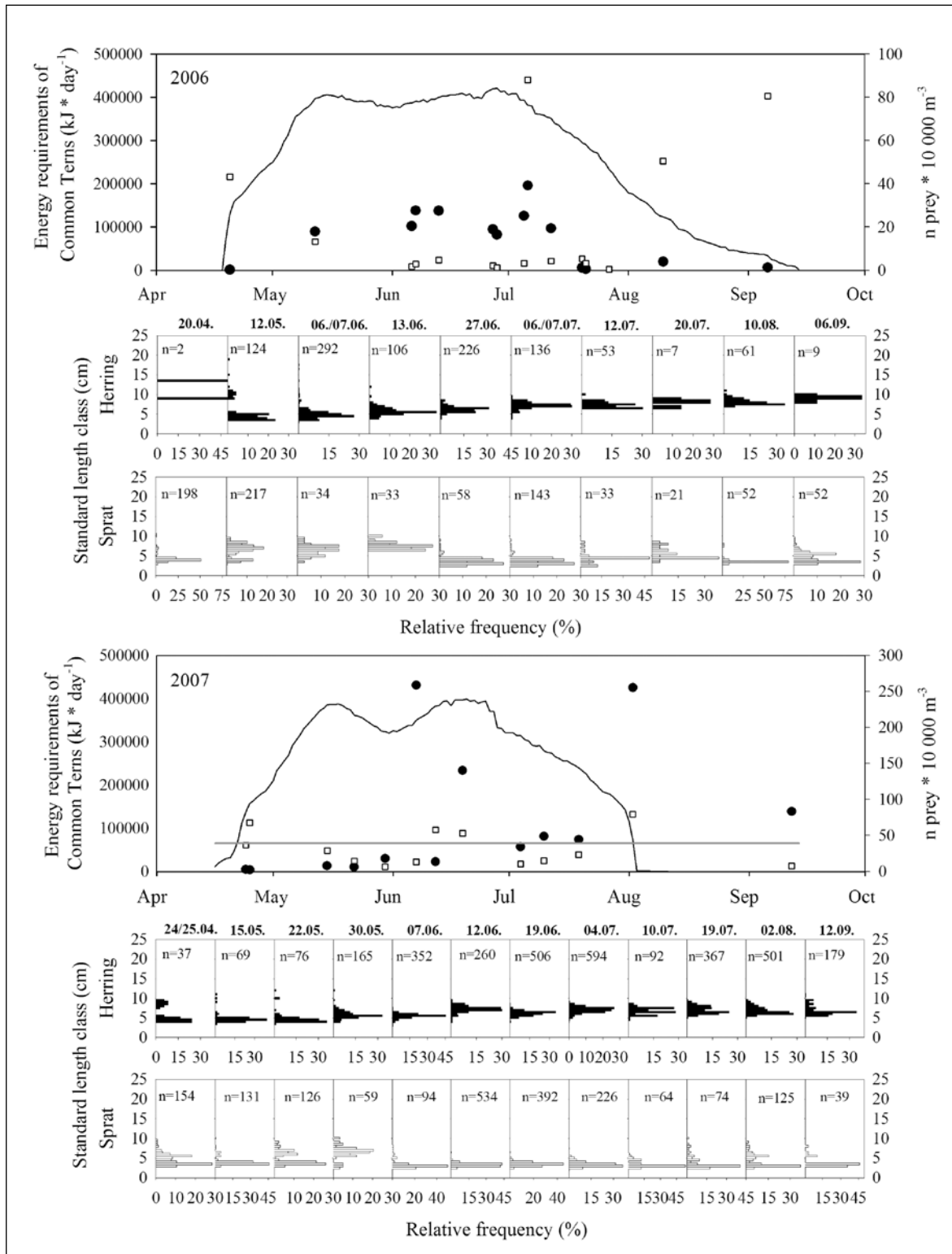
#### SEASONAL DYNAMICS OF ABUNDANCE AND LENGTH OF PREY FISH

##### *Herring*

Herring were much more abundant in 2007 than in 2006, but abundance was also much more variable. The temporal match between the colony's energy demand and herring density was also closer in 2007 than in 2006, with peak herring abundance around the time of maximum chick numbers and shortly after fledging. During courtship and egg formation, herring was abundant in neither of the two years examined, being reflected in the proportions fed to partners in 2007, but not in 2006 (Table 3.1). In both years, the energy provided by herring did not correlate with the energy demand of the Common Terns, except in self-feeding adults in 2006 ( $r_s = 0.613$ ,  $p < 0.05$ ,  $n = 14$ ). Towards the end of the chick rearing period 2006, herring numbers and, thus, energy dropped sharply. In contrast, herring numbers in 2007 kept increasing well until after the chicks had fledged (Fig. 3.3). When individual Common Tern numbers (adults + chicks) in the colony peaked in 2007, the energy provided by herring was well above the maximum of the previous year. As the chicks grew, the energy provided by herring also increased, mainly through a numerical increase and – to a lesser degree – through growth. In 2006, only very few herring were present by the end of April. In mid-May, two length groups of herring were caught: few individuals of 10–13 cm SL and the bulk of 3–6 cm long post-larvae. The older herring were not observed after May 12<sup>th</sup>, whereas the post-larvae could be tracked throughout the whole season, growing to 8–10 cm long juveniles within four months. During the highest energy demand of the Common Tern colony between mid-June and mid-July, herring were 6–8 cm long. In the beginning of the season 2007, two length groups of herring were detected, with the larger individuals being only occasionally caught until the end of May. Unlike the previous year, the SL of herring changed less throughout the season with a period of zero length increase between mid-June and mid-September. During the Common Tern chick rearing period, the average SL of herring did not change (Fig. 3.3).

##### *Sprat*

Sprat was slightly more abundant in 2007 than in 2006, but there was hardly any temporal coincidence with the colony's energy demand (Fig. 3.3). In both years, sprat appeared to provide less energy as the colony's demand increased, being expressed in negative correlations. This trend was however not significant except in 2007 in self-feeding adults ( $r_s = -0.664$ ,



**Figure 3.3:** Seasonality of total energy requirements of the Common Tern breeding colony at Banter See, Wilhelmshaven, and abundance and length frequency distribution of herring (filled circles and bars, respectively) and sprat (open rectangles and bars, respectively) in the Jade Bay in 2006 (top) and 2007 (bottom). The total energy requirements are identical with the outer contour of the area plots in Fig. 3.2. The horizontal line in the 2007 graph denotes maximum herring abundance of the year 2006.

$p < 0.05$ ,  $n = 12$ ). Even though sprat provided only 50 % of the energy of herring in 2006 and 10 % in 2007, this species might have temporarily supplemented the terns' diet. In 2006 larger sprat were present during the early chick rearing period, and sprat numbers appeared to increase half way through colony break-up. There was no directional length development throughout the season, with larger individuals present only until the end of May/beginning of June. Among all four prey fish species examined, sprat were the smallest (Fig. 3.3), providing the least energy per individual fish.

### *Smelt*

In both years, smelt density was similar to that of herring in 2006, but yielded energy in the order of magnitude of herring in 2007 (Fig. 3.3), due to the presence of on average larger individuals. Over the course of the whole breeding season smelt numbers did not fluctuate as strongly as in herring and sprat, potentially providing a consistent nutritional basis for the Common Terns. Smelt catches in 2006 peaked at the end of June (Fig. 3.4), when chick numbers were highest in the colony. However, all correlations between energy demand of the Common Terns and energy provided by smelt were insignificant due to a differential pattern of seasonality. Smelt numbers peaked earlier in 2007 than in 2006, supplying food for courtship and egg formation. This was expressed in large proportions of smelt in the courtship feedings in 2007 (Table 3.1). Compared to herring and sprat, a wider range of length classes of smelt was observed in both years. Individuals were larger, large smelts were more common and smelt grew faster, starting at 6–8 cm SL in late April and increasing to 10–15 cm SL by mid-September (Fig. 3.4).

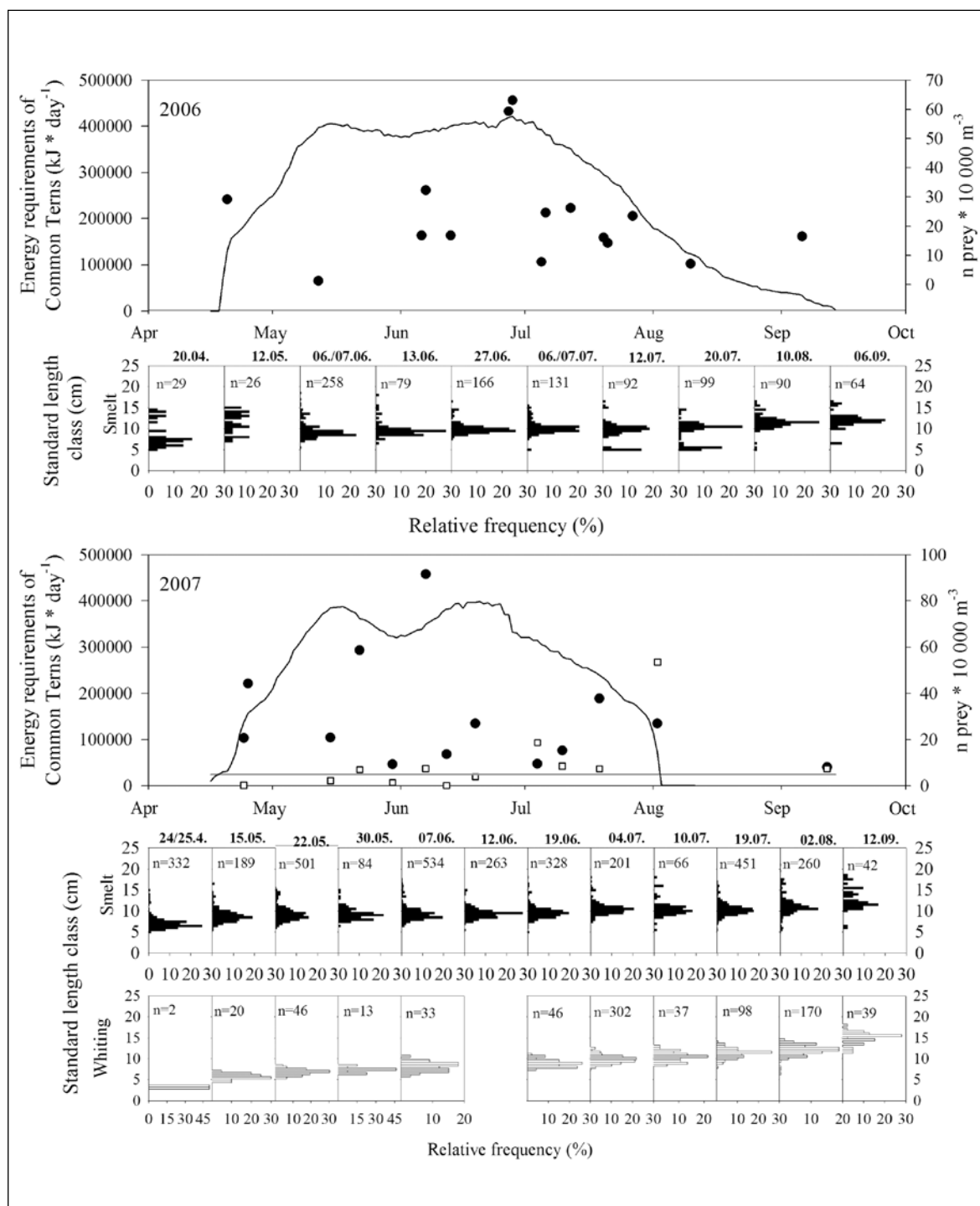
### *Whiting*

In 2006, whiting was caught only between mid-June and mid-July and was ten times less abundant than in 2007 (grey line in bottom panel of Fig. 3.4), when large numbers of juveniles immigrated into the Wadden Sea in June and stayed also after the investigations had been terminated. As in herring in 2007, but without strong fluctuations, whiting numbers steadily increased over the course of the breeding season (Fig. 3.4, bottom panel). The correlations between the colony's energy demand and energy provided by whiting were negative, but not significant. Among the four prey fish species examined, whiting grew fastest, starting at 5–7 cm in mid-May and increasing to 12–18 cm by mid-September (Fig. 3.4, bottom panel).

### SEASONALITY OF ENERGY SUPPLY BY THE FOUR MAIN PREY FISH SPECIES

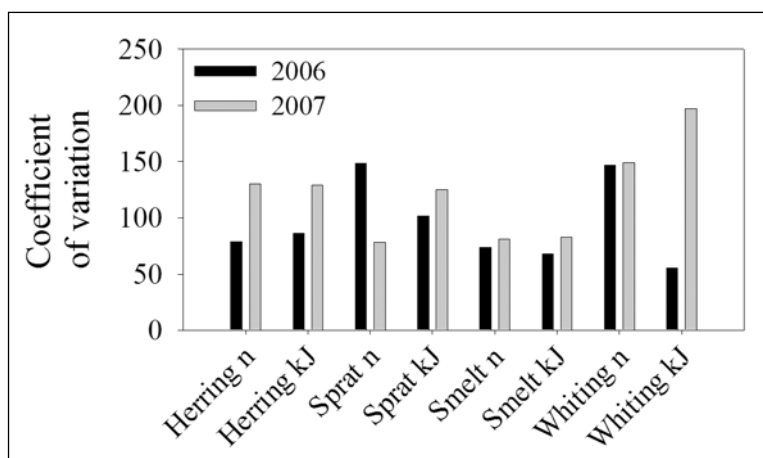
Taken together, the seasonal energy supply by herring, sprat, smelt and whiting significantly matched the energy demand of the Common Terns only in the case of chicks older than 13 days in 2006 ( $r_s = 0.648$ ,  $p < 0.05$ ,  $n = 10$ ). Correlations between the energy requirements of the Common Terns and the added energy supplied by the four main prey species were otherwise not significant.





**Figure 3.4:** Seasonality of total energy requirements of the Common Tern breeding colony at Banter See, Wilhelmshaven, and abundance and length frequency distribution of smelt (filled circles and bars, respectively) in 2006 (top) and 2007 (bottom) and whiting (open rectangles and bars, respectively) only in 2007 (bottom) in the Jade Bay. On June 12<sup>th</sup> only one whiting was caught. The total energy requirements are identical with the outer contour of the area plots in Fig. 3.2. The grey line in the bottom panel denotes maximum catch numbers of whiting in 2006 (not shown).

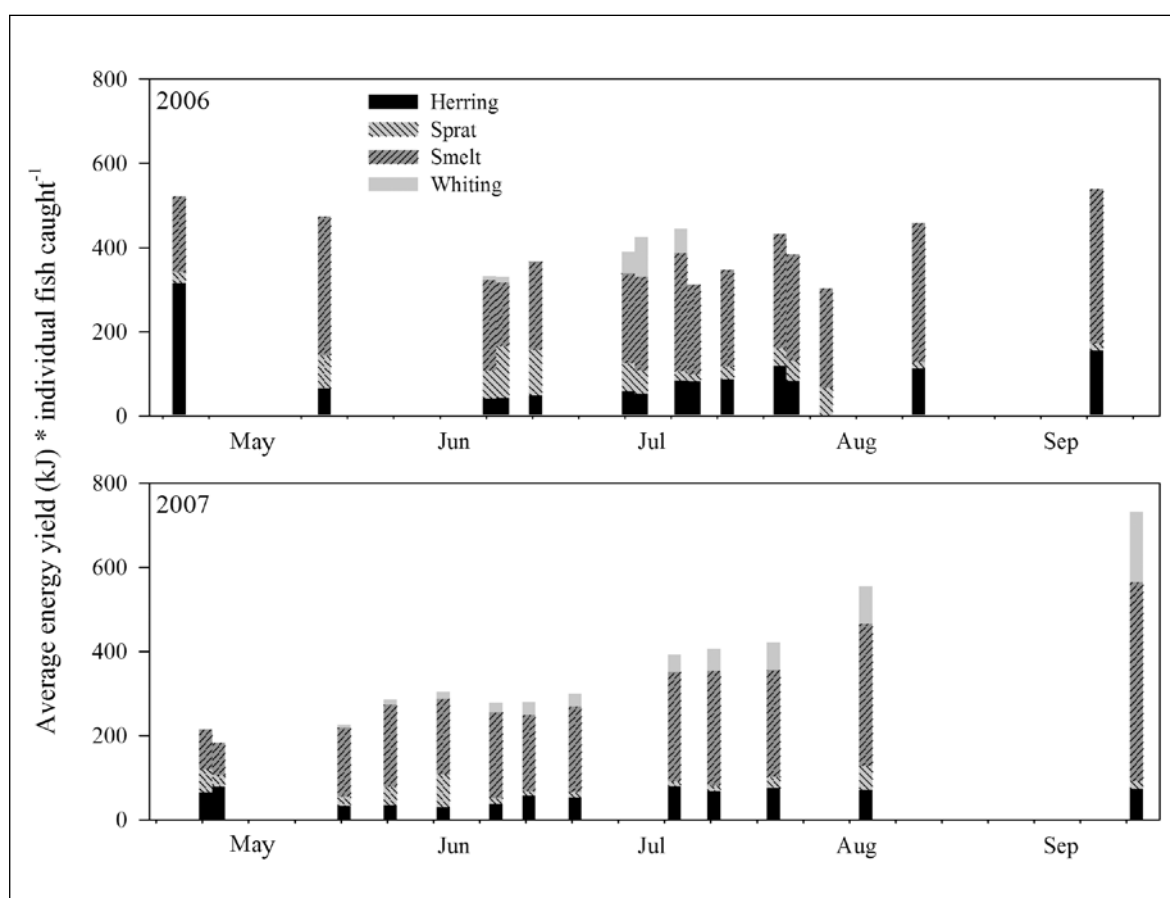
The seasonal variation in numbers and energy provided by the four main prey fish species to the Common Terns was uniform neither among species nor between years. The CV of herring numbers was lower in 2006 than in 2007, owing to some very large catches in 2007. In both years, the relative variability in abundance was reflected by the relative variability in energy (Fig. 3.5), being attributed to a more or less even size distribution (Fig. 3.3). This was contrasted by sprat, in which abundance was almost twice as variable in 2006 than in 2007. However, this pattern was not repeated in the mean energy content per 10 000 m<sup>-3</sup> fished water volume due to large variations in the length-frequency distributions (Fig. 3.3). In smelt, neither abundance nor energy content per 10 000 m<sup>3</sup> fished water volume varied substantially in both years (Fig. 3.5). In whiting, CV of abundance did not vary between years, whereas the variability in energy content per 10 000 m<sup>-3</sup> fished water volume was four times as high in 2007 as in 2006 (Fig. 3.5). Similarly-sized whiting were caught during only one month in 2006, whereas in 2007 whiting were present throughout the whole season, growing almost 10 cm within four months (Fig. 3.4).



**Figure 3.5:** Coefficients of variation of mean abundance and mean energy provided to the Common Terns by herring, sprat, smelt and whiting over the course of the breeding seasons 2006 (black bars) and 2007 (grey bars).

The energy yield per individual fish caught varied with the season, between prey species and also between years. In 2007, the energy yield per successful foraging trip gradually increased over the course of the season, whereas in 2006 a directional development was less clear (Fig. 3.6). Though less abundant, herring caught in 2006 yielded more energy than in 2007. During the chick rearing period, herring and sprat, though very abundant, yielded on average the smallest amount of energy of the four prey fish examined to a successful forager due to the small size of individuals and, thus, energy yield per successful foraging event. During the chick rearing period, the contribution of sprat was minimal in 2007, whereas in 2006 energy per individual sprat exceeded that of herring in May and June (Fig. 3.6).

The combined effects of steadiness, abundance (Fig. 3.4) and energy yield per successful foraging event (Fig. 3.6) made smelt the most profitable prey to the Common Terns. Successively more energy was made available through smelt and also through whiting in



**Figure 3.6:** Average energy yield per individual fish caught, divided by main prey fish species of the Common Terns in 2006 (top) and 2007 (bottom).

2007, reflecting the seasonal growth trajectories of these two species (Fig. 3.4). In 2006, maximum energy from the four main prey fish species could be obtained during courtship and after the colony counts had been terminated. In 2007, energy yield per successful foraging trip was highest after all chicks had fledged, which was mainly attributed to mass growth of smelt and whiting (Figs. 3.4 and 3.6).

#### REPRODUCTIVE PERFORMANCE AND CHICK GROWTH OF THE COMMON TERNS

Reproductive success as well as chick growth were significantly higher in 2007 than in 2006: On average, eggs were laid about 5 days earlier, clutches were larger, chicks grew faster with almost 2 g more daily weight gain and achieved higher peak and pre-fledging mass, respectively. However, the breeding success in 2007 was lower than in 2006, owing to starvation of many older chicks, caused by food shortage as a result of adverse weather conditions during the late season. The recession from peak- to pre-fledging mass, which was higher in 2007 than in 2006 (2006:  $-8.1 \pm 0.5$  g,  $n = 272$ ; 2007:  $-11.1 \pm 0.6$  g,  $n = 222$ ;  $t = -3.755$ ,  $p < 0.001$ ,  $t$ -test), was an indicator of these adverse feeding conditions (Table 3.2).

**Table 3.2:** Reproduction and chick growth parameters of Common Terns breeding at Banter See, Wilhelmshaven, in 2006 and 2007 (mean  $\pm$  SE). In 2007 a bad weather period reduced the breeding success despite otherwise favourable foraging conditions. Test of inter-year differences at Banter See: <sup>A)</sup>Mann-Whitney-U-test, <sup>B)</sup>t-test. All test results were significant at  $p < 0.001$ .

Parameter	2006	2007	Statistics
Reproduction <sup>A</sup>			z
N clutches studied	442	411	
Egg laying date [pentad]	29.1 $\pm$ 0.1	28.2 $\pm$ 0.1	-6.427
Clutch size [eggs * clutch <sup>-1</sup> ]	2.3 $\pm$ 0.0	2.6 $\pm$ 0.0	-7.144
Fledglings * pair <sup>-1</sup>	0.57 $\pm$ 0.03	0.45 $\pm$ 0.03	-3.355
Chick mass growth (N) <sup>B</sup>			t
Growth rate [g * day <sup>-1</sup> ]			
Chicks not fledged	3.2 $\pm$ 0.3 (71)	5.6 $\pm$ 0.3 (77)	-5.607
Chicks fledged	5.3 $\pm$ 0.3 (76)	7.2 $\pm$ 0.2 (93)	-6.323
Peak mass [g]	120.7 $\pm$ 0.6 (272)	127.8 $\pm$ 0.7 (222)	-7.917
Pre-fledging mass [g]	112.6 $\pm$ 0.7 (272)	116.7 $\pm$ 0.7 (222)	-4.148

### 3.5 DISCUSSION

Predictions derived from conceptual framework such as the match-mismatch hypothesis or the central place foraging theory always require simplifying assumptions. These predictions are at the same time limited in their general validity and also hard to test in nature. For example, the theoretical ideal of one predator responding to only one type of prey is rarely encountered, yet it is a central element of the match-mismatch hypothesis (Cushing, 1969; 1990). In the present study, this “mismatch” between theory and practice became evident e. g. in 2007, when the relative contributions of the four prey fish species were not separable in their effect on Common Tern breeding performance. In terms of predators maximizing their net energy gain per unit foraging effort, as predicted by the central place foraging theory (Orians and Pearson, 1979), the Common Terns should have preferred smelt in both years and whiting in 2007 over the clupeids. This was not the case, suggesting that decisions of individual predators with respect to their foraging tactics and energetics are not straightforward to disentangle. Even though smelt and whiting would be expected to be the more profitable prey, North Sea herring recruit abundance explained more than one third of the variability in Common Tern breeding success at Banter See (Dänhardt and Becker, unpublished data). Together with the high proportions of clupeid prey being fed both to partners and chicks, this emphasizes the general importance of herring and, in some years, also sprat (Frank, 1992;

Wendeln, 1997; Greenstreet et al., 1999). Even though smelt was found to be extensively utilized by the terns (Wendeln, 1997), the proportions of smelt and clupeids in the feeding observations appeared to be inversely related in 2006 and 2007, indicating that herring was preferred over smelt, even though smelt would yield more energy per individual fish. Herring form large schools even at young age encountered in the Wadden Sea, potentially generating locally enhanced prey availability to the terns with substantial energy yield per unit effort through small but abundant and energy-rich prey (Massias and Becker, 1990). As a consequence, exploiting these herring patches may be energetically more beneficial than skipping such occasions to pursue larger prey such as smelt, yielding more energy per individual fish. This suggests that exploiting herring schools will maximize energy return per unit foraging investment, as predicted by the central place foraging theory, or that the original prediction may be biased by some degree of opportunism during foraging (e. g. Camphuysen and Webb, 1999; Fauchald and Erikstad, 2002).

Neither the seasonality of energy demands of the terns nor prey fish abundance was found to be unimodal, violating an assumption of the match-mismatch concept (Cushing, 1969, 1990; Durant et al., 2005). The strong dependency of e. g. herring recruitment on seasonal events such as plankton production was masked by other factors determining presence and abundance of the terns' prey fish in the Wadden Sea. Moreover, only peak abundance of smelt fell within the core breeding season of the terns, whereas abundance of all other prey species examined peaked either before or after the period of highest energy requirements of the Common Terns. The temporal match between the maximum energy demand of the terns and peak abundance of their prey was thus a poor predictor of reproductive performance in the two years under study. Judging from reproduction and chick growth performance, 2007 provided much better conditions than 2006, despite the apparent temporal mismatch between predator and prey. This suggests that food abundance is not only capable of compensating poor temporal match to some degree (Durant et al. 2005, 2007), but far outweighs the effects of temporal coincidence between predator and prey. The temporal component may only become important when food supply drops below a certain threshold. Around this threshold abundance, small temporal mismatch can be compensated by larger prey abundance (Durant et al., 2005).

Climate change comes into ecological effect mostly via altered temperature regimes, potentially disrupting food webs (e. g. Parmesan and Yohe, 2003). Among the processes governing prey fish availability in the Wadden Sea, water temperature may directly affect spatio-temporal overlap of predators and prey. In 2006, herring abundance in the Jade Bay and the daily mean water temperature were positively correlated up to the beginning of June ( $r_s = 0.63$ ,  $p < 0.003$ ), thereafter the correlation was negative ( $r_s = -0.52$ ,  $p < 0.006$ ), culminating in the sudden disappearance of all herring in the third quarter of July, possibly due to water temperatures exceeding 23 °C (Dänhardt and Becker, 2008). Common Tern chicks have earlier been reported to starve during periods of high water temperatures, due to herring

leaving the Wadden Sea (Becker et al., 1997). Local water temperature may thus be a factor determining spatial predator-prey overlap in a non-linear fashion. On a comparatively small scale (i.e. within the confined foraging range of breeding Common Terns) this mechanism of a sudden drop in key prey abundance through behavioural thermoregulation (Ward et al., 2010) exemplifies how Common Tern reproduction may potentially be impacted by climate change, projected to increase average water temperatures (IPCC, 2007). Whereas a sudden intra-seasonal prey decline can have catastrophic consequences for predators, a gradual intra-seasonal prey decline, e.g. by predation, may be compensated through growth of the respective prey species.

The clear inter-specific and inter-annual differences in abundance and growth patterns of the prey fish species as well as weather-related factors indicate that the Common Terns' breeding environment is largely unpredictable. After arrival in the breeding area the onset of breeding is associated with smelt abundance, and also the abundance of larger herring spawning in spring in the Wadden Sea (Wendeln, 1997; Dänhardt and Becker, unpublished data). The availability of courtship food is independent of the availability of smaller herring (0-group of winter spawners), which are key to chick development (Massias and Becker, 1990). Their abundance cannot be foreseen by the adult terns when they mate. However, the large fluctuations of herring and also sprat may be alleviated by a rather constant smelt density with growing energy content per individual. Common Terns breeding on the Wadden Sea islands (e.g. Minsener Oog) do not have access to smelt or freshwater fish (Wendeln, 1997) and are thus much more directly impacted by a shortage in clupeids. This is expressed in complete breeding failure during the study period, which is largely uncommon at Banter See, possibly mainly due to smelt as a prey alternative (Dänhardt et al., unpubl. data). Whiting are usually neither steady nor abundant, but they are opportunistically utilized as prey in invasion years (Berghahn, 1996), as was also described for another gadoid fish, the cod (*Gadus morhua*) (Becker et al., 2001b).

Although facing a largely unpredictable prey field, Common Terns breeding earlier in the season produce more offspring (Wendeln et al., 2000; Arnold et al., 2004). Besides individual characteristics such as age and condition (Wendeln and Becker, 1999; Ezard et al., 2007) the initiation of breeding may be modulated by environmental conditions such as water temperature possibly triggering immigration of prey fish. In 2006 and 2007, advantages of early breeding in terms of prey abundance were not reflected in prey abundance at the onset of breeding. However, there are years when 1+ year old herring and large smelt are present already in late April (Dänhardt and Becker, unpublished data), potentially providing rich food supply.

Finally, the strong seasonality of fish abundance has consequences for the utility and interpretation of fish survey data, potentially biasing abundance indices: An abundance change could mean fewer individuals at constant phenology of the target species or a shift in phenology at constant individual numbers.

#### ACKNOWLEDGEMENTS

We thank K.-H. Rostek and many volunteers for their support during the fish sampling and C. Bauch, J. Spieker, J. Sprenger and G. Wagenknecht for collecting and analysing data on Common Tern breeding performance and feeding. Thanks are also due to T. Ezard, M. Martinez Benito, A. Ostendorp, S. Kreutzer, J. Riechert, L. Schmidt, V. Blum and many others for supporting the field work in the colony. The financial support provided by Niedersächsische Wattenmeerstiftung (53-NWS-41/04) and Deutsche Forschungsgemeinschaft (BE 916/1–9) is gratefully acknowledged.

#### 3.6 REFERENCES

- Arnold JM, Hatch JJ and Nisbet ICT (2004) Seasonal declines in reproductive success of the Common Tern *Sterna hirundo*: Timing or parental quality? *Journal of Avian Biology* 35: 33–45.
- Becker PH (1998) Langzeittrends des Bruterfolgs der Flusseeschwalbe und seiner Einflussgrößen im Wattenmeer. *Vogelwelt* 119: 223–234.
- Becker PH and Wink M (2003) Influences of sex, sex composition of brood and hatching order on mass growth in Common terns (*Sterna hirundo*). *Behavioural Ecology and Sociobiology* 54: 136–146.
- Becker PH and Ludwigs J-D (2004) *Sterna hirundo* Common tern. BWP Update, 6: 91–137.
- Becker PH, Frank D and Walter U (1987) Geografische und jährliche Variation der Ernährung der Flusseeschwalbe (*Sterna hirundo*) an der Nordseeküste. *Journal für Ornithologie* 128: 457–475.
- Becker PH, Frank D and Sudmann SR (1993) Temporal and spatial pattern of Common tern (*Sterna hirundo*) foraging in the Wadden Sea. *Oecologia* 93: 389–393.
- Becker PH, Wendeln H and González-Solis J (2001a) Population dynamics, recruitment, individual quality and reproductive strategies in Common Terns *Sterna hirundo* marked with transponders. *Ardea* 89: 241–252.
- Becker PH, Ludwigs J-D and Wagener M (2001b) Neue Chance für den Nordsee-Kabeljau: Seevögel machen bereits im Sommer 2001 auf starken Jahrgang aufmerksam. *Informationen für die Fischwirtschaft aus der Fischereiforschung* 48: 164–165.
- Becker PH, Troschke T, Behnke A and Wagener M (1997) Flüge Küken der Flusseeschwalbe *Sterna hirundo* verhungern während Hitzeperioden. *Journal für Ornithologie* 138: 171–182.
- Becker PH, Ezard THG, Ludwigs J-D, Sauer-Gürth H and Wink M (2008) Population sex ratio shift from fledging to recruitment: Consequences for demography in a philopatric seabird. *Oikos* 117: 60–68.
- Berghahn R (1996) Episodic mass invasions of juvenile gadoids into the Wadden Sea and their consequences for the population dynamics of Brown Shrimp (*Crangon crangon*). *Marine Ecology* 17: 251–260.
- Bezzel E and Prinzing R (1990) *Ornithologie*. UTB Ulmer, Stuttgart.
- Breckling P and Neudecker T (1994): Monitoring the fish fauna in the Wadden Sea with stow nets (part 1): A comparison of demersal and pelagic fish fauna in a deep channel. *Archive of Fisheries and Marine Research* 42: (1): 3–15.
- Camphuysen CJ and Webb A (1999) Multi-species feeding associations in North Sea seabirds: Jointly exploiting a patchy environment. *Ardea* 87: 177–197.
- Cushing DH (1969) The regularity of the spawning season of some fishes. *Journal du Conseil International de l'Exploration de la Mer* 33: 81–92.
- Cushing DH (1990) Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology* 26: 249–293.
- Cushing DH (1995) *Population production and regulation in the sea: a fisheries perspective*. Cambridge University Press, Cambridge.

- Dänhardt A and Becker PH (2008) Die Bedeutung umweltbedingter Verteilungsmuster von Schwarmfischen für Seevögel im Ökosystem Niedersächsisches Wattenmeer. Institute of Avian Research, Wilhelmshaven. Final report of project 53-NWS-41/04, Niedersächsische Wattenmeerstiftung, 248 pp.
- Dänhardt A, Freseman T and Becker PH (2010) To eat or to feed? Prey utilization of Common Terns *Sterna hirundo* in the Wadden Sea. *Journal of Ornithology*, DOI: 10.1007/s10336-010-0590-0
- Del Hoyo J, Elliott A and Sargatal J (1996) Hoatzins to auks. In *Handbook of birds of the world*, Vol. 3. Lynx Editions, Barcelona.
- Durant JM, Hjermann DØ, Anker-Nilssen T, Beaugrand G, Mysterud A, Pettorelli N and Stenseth NC (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters* 8: 952–958.
- Durant JM, Hjermann DØ, Ottersen G and Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33: 271–283.
- Edwards M and Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430: 881–884.
- Ezard THG, Becker PH and Coulson T (2007) The correlation between age, phenotypic traits and reproductive success in Common terns (*Sterna hirundo*). *Ecology* 88: 2496–2504.
- Fauchald P and Erikstad KE (2002) Scale-dependent predator-prey interactions: The aggregative response of seabirds to prey under variable prey abundance and patchiness. *Marine Ecology Progress Series* 231: 279–291.
- Fischer V (2009) Die Qualität pelagischer Fische als Seevogelnahrung. Diploma thesis University of Hamburg, Hamburg.
- 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.
- Galbraith H, Hatch JJ, Nisbet ICT and Kunz TH (1999) Age-related changes in efficiency among breeding Common Terns *Sterna hirundo*: Measurement of energy expenditure using doubly-labelled water. *Journal of Avian Biology* 30: 85–96.
- Greenstreet SPR, Becker PH, Barrett RT, Fossum P and Leopold MF (1999) Consumption of pre-recruit fish by seabirds and the possible use of this as an indicator of fish stock recruitment. In Furness RW and Tasker ML (Eds.): *Diets of seabirds and consequences of changes in food supply*. ICES Cooperative Research Report 232: 6–17.
- Hilton GM, Furness RW and Houston DC (2000) A comparative study of digestion in north atlantic seabirds. *Journal of Avian Biology* 31: 36–46.
- Hjort J. (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapport pour la Réunion Conseil International pour l'Exploration de la Mer* 20: 1–228.
- IPCC (2007) *Climate change 2007: the physical science basis. Summary for policy makers*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge.
- Klaassen M, Becker PH and Wagener M (1992a) Transmitter loads do not affect the daily energy expenditure of nesting Common Terns. *Journal of Field Ornithology* 63: 181–185.
- Klaassen M, Zwaan B, Heslenfeld P, Lucas P and Luijckx B (1992b) Growth rate associated changes in the energy requirements of tern chicks. *Ardea* 80: 19–28.
- Klaassen M, Habekottè B, Schinkelshoek P, Stienen E and van Tienen P (1994) Influence of growth rate retardation on time budgets and energetics of Arctic Tern *Sterna paradisaea* and Common Tern *S. hirundo* chicks. *Ibis* 136: 197–204.
- Massias A and Becker PH (1990) Nutritive value of food and growth in Common Tern *Sterna hirundo* chicks. *Ornis Scandinavica* 21: 187–194.
- Muus BJ and Nielsen JG (1999) *Die Meeresfische Europas in Nordsee, Ostsee und Atlantik*. Kosmos Naturführer, 336 pp.
- Orians GH and Pearson NE (1979) On the theory of central place foraging. In Horn DJ, Mitchell RD and Stairs GR (Eds.) *Analysis of Ecological Systems*. Ohio State University Press., Columbus, Ohio, pp. 154–177.



- Parmesan C and Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- Pedersen J and Hislop JRG (2001) Seasonal variations in the energy density of fishes in the North Sea. *Journal of Fish Biology* 59: 380–389.
- Quillfeldt P, Michalik A, Veit-Köhler G, Strange IJ and Masello JF (2010) Inter-annual changes in diet and foraging trip lengths in a small pelagic seabird, the thin-billed prion *Pachyptila belcheri*. *Marine Biology* 157: 593–598.
- Safina C and Burger J (1988) Prey dynamics and the breeding phenology of Common Terns (*Sterna hirundo*). *The Auk* 105: 720–726.
- Schauroth C and Becker PH (2008) Post-fledging body mass increase in Common Tern *Sterna hirundo*: Influence of age, sex and year. *Ibis* 150: 50–58.
- Sokal RR and Rohlf FJ (1995) *Biometry*, WH Freeman, New York.
- Sonntag N and Hüppop O (2005) Snacks from the depth: Summer and winter diet of Common Guillemots *Uria aalge* around the island of Helgoland. *Atlantic Seabirds* 7: 1–14.
- Wagener M (1998) Praktische Hinweise für brutbiologische Untersuchungen an der Flußseeschwalbe (*Sterna hirundo*). *Vogelwelt* 119: 279–286.
- Ward AJW, Hensor EMA, Webster MM and Hart PJB (2010) Behavioural thermoregulation in two freshwater fish species. *Journal of Fish Biology* 76: 2287–2298.
- Wendeln H (1997) Body mass of female Common Terns (*Sterna hirundo*) during courtship: Relationships to male quality, egg mass, diet, laying date and age. *Colonial Waterbirds* 20: 235–243.
- Wendeln H and Becker PH (1999) Effects of parental quality and effort on the reproduction of Common Terns. *Journal of Animal Ecology* 68: 205–214.
- Wendeln H, Becker PH and González-Solis J (2000) Parental care of replacement clutches in Common Terns (*Sterna hirundo*). *Behavioural Ecology and Sociobiology* 47: 382–392.
- Wendeln H, Mickstein S and Becker PH (1994) Auswirkungen individueller Ernährungsstrategien von Flusseeschwalben (*Sterna hirundo*) auf die Anwesenheit am Koloniestandort. *Vogelwarte* 37: 290–303.
- Wilson LJ, Daunt F and Wanless S (2004) Self-feeding and chick provisioning diet differ in the Common Guillemot *Uria aalge*. *Ardea* 92: 197–208.



## CHAPTER 4

---

DOES SMALL-SCALE VERTICAL DISTRIBUTION OF JUVENILE SCHOOLING  
FISH AFFECT PREY AVAILABILITY TO SURFACE-FEEDING SEABIRDS  
IN THE WADDEN SEA?

Andreas Dänhardt<sup>1\*</sup> and Peter H. Becker

Institute of Avian Research “Vogelwarte Helgoland”,  
An der Vogelwarte 21, 26386 Wilhelmshaven, Germany.

\* Corresponding author

<sup>1</sup> present address: Suerhoper Brunnenweg 13 a, 21244 Buchholz/Nordheide, Germany,  
Phone: + (49) 1 79 / 5 17 15 36, E-mail: andreas@daenhardt.com

#### 4.1 ABSTRACT

Food availability is a key variable influencing breeding performance and demography of marine top predators. Due to methodological reasons, proportionality between fish abundance and availability is often assumed without being explicitly tested. More specifically, better breeding performance of surface-feeding seabirds at times of large prey stocks suggests that prey availability is also a function of prey abundance. Using vertically resolved stow net sampling we tested whether local abundance and length composition of pelagic fish are reliable predictors of the availability of these fish to surface-feeding Common Terns (*Sterna hirundo*) breeding in the German Wadden Sea. Prey fish were found to concentrate below the maximum diving depth of the terns. Individuals caught close to the surface were in most cases smaller than conspecifics caught at greater depth. Correlations between fish abundance within and out of reach of the terns were both species- and site-specific rather than driven by overall fish abundance. Vertical distribution patterns of the terns' main prey fish could be explained as anti-predator behavior, reducing prey availability to the terns. In 2007, when breeding performance was much better than in 2006, herring and whiting were much more abundant, suggesting that overall prey abundance may also increase prey availability in habitats other than those represented by the stow net sampling.

## KEYWORDS

*Breeding performance, pelagic schooling fish, prey availability, Sterna hirundo, surface-feeding, vertical distribution, Wadden Sea*

## 4.2 INTRODUCTION

Life-history theory predicts that an animal's behaviour will be generally directed at maximizing lifetime reproductive output (Stearns, 1992). In that, sufficient prey availability to maintain a positive energy budget is essential, especially in apex predators in bottom-up-controlled ecosystems such as seabirds in the North Sea (Furness and Tasker, 1999; Wanless et al., 2005; Frederiksen et al., 2007). Against this background, seabirds have repeatedly been proposed as indicators of status and change of their marine environment (e.g. Cairns, 1987, 1992; Montevecchi, 1993; Boyd et al., 2006; Piatt et al., 2007; Einoder, 2009). However, type and strength of functional relationships between prey abundance and the responses in avian predators are rarely direct or linear and thus difficult to predict. Using measures of prey availability to explain reproductive traits and demography of predators is often limited by uncertainty about distribution and abundance of aquatic prey such as fish, especially when fish abundance indices from fishery research surveys are used as surrogate measures of food availability (Greenstreet et al., 1999; Rindorf et al., 2000; Frederiksen et al., 2005; Barrett, 2007). This approach is based on the assumption that medium- to large-scale prey abundance, as quantified by the respective survey indices, is proportional to prey availability to the seabird species of interest. Even though survey data of fisheries research programs have proven useful in studies of seabird trophic ecology (e.g. Barrett and Krasnov, 1996; Lewis et al., 2001; Fauchald and Erikstad, 2002; Barrett, 2007), prey *abundance* may not necessarily be proportional to prey *availability* at a given time in a given place, depending on the predator-specific foraging mode and forces structuring the aquatic environment (Hunt et al., 1999). For example, small surface-feeders such as terns or kittiwakes are restricted to the topmost water strata and would not benefit from prey being located below their maximum diving depth (0.5 m for Common Terns *Sterna hirundo*, Becker and Ludwigs, 2004). In turn, prey resources at greater water depths might be easily accessed by pursuit-divers such as auks and shags, exploiting a larger water volume in the vertical dimension (Barrett and Krasnov 1996; Regehr and Rodway, 1999). In order to enhance food supply for surface-feeding seabirds, an increased prey density at depth must translate into an increased prey density in the depth strata close to the surface (Scott et al., 2006). Some of the observed variance in indices of large-scale fish abundance can explain e.g. breeding success. At smaller spatial scales, e.g. within the foraging range around breeding colonies, information on spatial and temporal distribution of prey fish abundance is usually not available.

During the breeding season, larid gulls and terns are among the most common seabirds in the Southern North Sea and in the Wadden Sea. The breeding performance of Common Terns has been found to be vulnerable to reduced food supply in the vicinity of the colonies (Mlody and Becker, 1991; Becker, 1996; Furness and Tasker, 2000), affecting e. g. breeding success, laying date, chick growth rate and chick weight at fledging (Thyen et al., 1998). Good breeding performance of surface feeders at times of large prey stocks suggests that prey availability is also a function of prey abundance, suggesting that predator-prey-interactions are more likely to occur at large stock size. The critical density threshold below which breeding performance is impaired might be reached earlier in surface-feeders than in pursuit divers, which have the ability to exploit a larger water volume and to actively seek locations of high prey density (Regehr and Rodway, 1999; Scott et al., 2006).

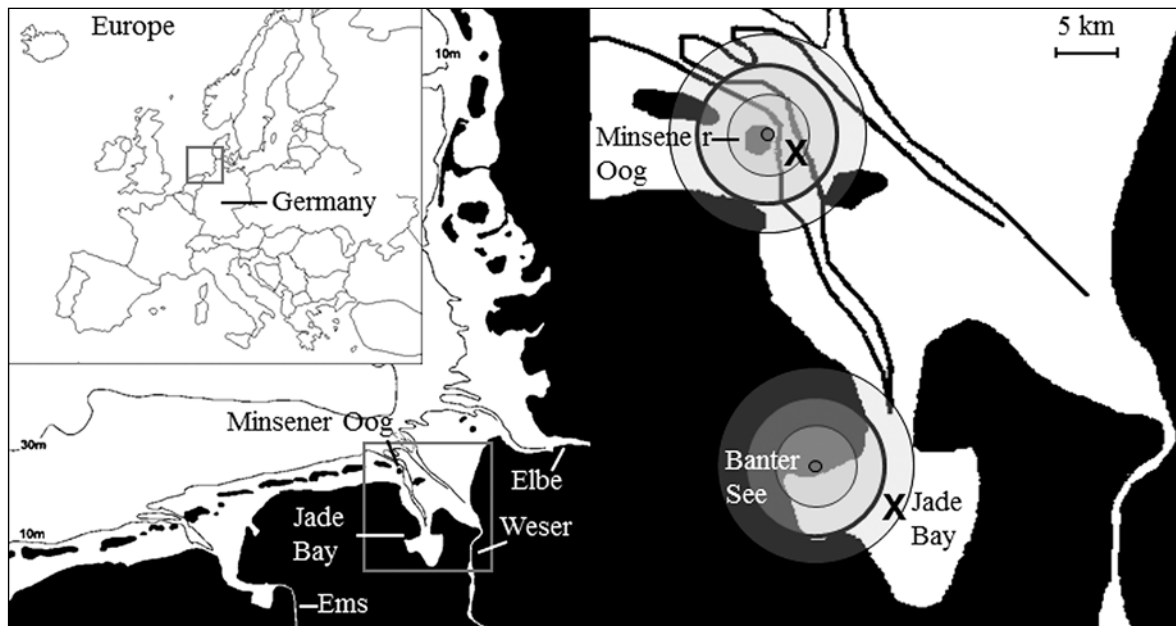
Earlier investigations identified herring (*Clupea harengus*), sprat (*Sprattus sprattus*), smelt (*Osmerus eperlanus*), whiting (*Merlangius merlangius*), Nilsson's pipefish (*Syngnathus rostellatus*) and sandeel (*Ammodytes spec.*) as important prey species of the Common Terns (Becker et al., 1987; Frank, 1992; Frank and Becker, 1992; Frick and Becker, 1995; Frank, 1998). The vertical distribution of size and abundance of these species were obtained from vertically resolved stow net catches carried out in two tidal channel systems within the foraging range of Common Terns breeding in the Lower Saxon Wadden Sea, Northern Germany.

In this study, we explored the vertical distribution of the terns' main prey fish and tested two hypotheses: 1) The length composition and abundance of prey fish in reach of the plunging Common Terns represent length composition and abundance of the same fish species in the whole water column (i. e. local fish abundance and length composition are reliable predictors of fish availability to surface-feeding seabirds in the Wadden Sea), and 2) The breeding performance of Common Terns in two colonies and during two successive years reflects food availability as quantified by the depth-stratified sampling results.

### 4.3 MATERIAL AND METHODS

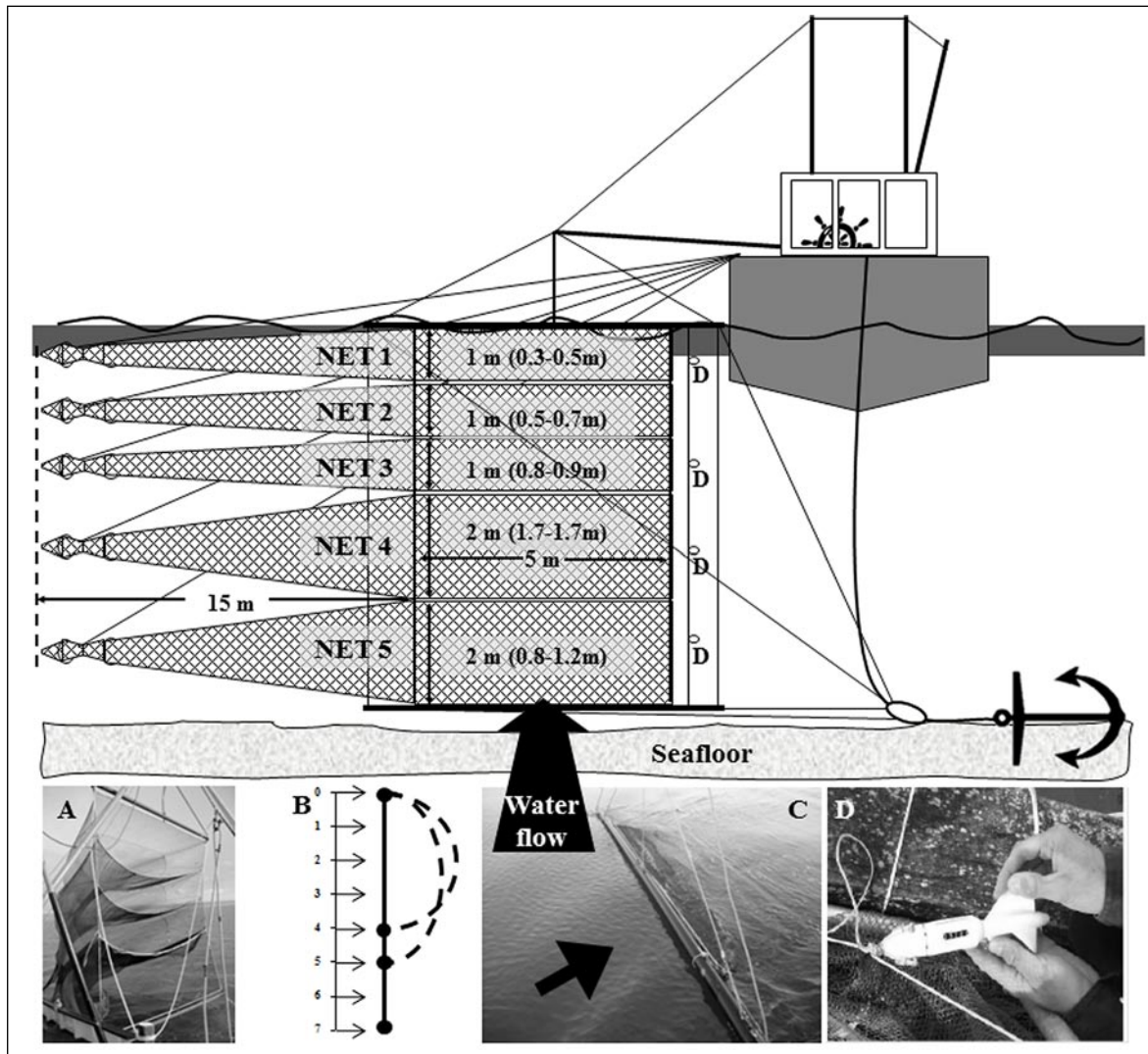
#### VERTICAL DISTRIBUTION OF FISH ABUNDANCE AND LENGTH

Fish samples were obtained using a ship-based stow net in the central Jade Bay (53° 28' N, 08° 12' E) and south-east of the island of Minsener Oog (53° 44' N, 08° 02' E), Lower Saxon Wadden Sea, Northern Germany. Between April 19<sup>th</sup> and September 5<sup>th</sup> 2006 and April 24<sup>th</sup> and October 10<sup>th</sup> 2007 sampling took place at least twice per month, depending on local wind conditions. Both time and place of the fish sampling were concomitant with the breeding season in two of the largest German colonies of Common Terns: Minsener Oog at the outer Jade (53° 45' N, 08° 01' E) and Banter See in Wilhelmshaven (53° 30' N, 08° 05' E). Both fish sampling sites were located well within the average foraging range ( $6.3 \pm 2.4$  km, Becker et al., 1993) of the Common Terns (Fig. 4.1).



**Figure 4.1:** Area of investigation. Dots indicate colony locations on Minsener Oog and at Banter See, crosses indicate catching positions with the stow net near Minsener Oog and in the central Jade Bay. Circles indicate foraging range (mean  $\pm$  SD, after Becker et al. 1993).

Stow nets are passive catching gear and are largely unselective and thus representative especially of pelagic fish (Breckling and Neudecker, 1994). Stow nets utilize water movement as encountered in rivers or in tidally influenced marine areas such as the Wadden Sea. The stow net was fixed between an upper beam and a lower beam, the weight of the latter stretching the net between the water surface and 4–5 m water depth. The beams were attached to the anchor chain through cable ropes, ensuring perpendicular positioning of the net mouth in the water column. The stow net consisted of five stacked net compartments, resolving catches by water depth. Hanging loosely, the openings of the three topmost nets were 1 m high and 5 m wide, the two bottommost ones were 2 by 5 m, resulting in an overall mouth opening of 7 x 5 m (Fig. 4.2). However, the resistance of the filtering net surface against the water current caused the lower beam to be lifted, so that the vertical net opening changed as a function of the current velocity, varying between 4 and 5 m. To account for the tidal dependence of the vertical net opening, the mean depth of the lower beam of the duration of the respective haul was recorded with a thin tape measure to be used in subsequent calculations ( $N_{\text{Height}}$ , see below). Catches were obtained from the water surface down to 4–5 m at absolute water depths of 5–8 m, depending on the gauge height. The resulting vertical openings of each net chamber at 4–5 m depth of the lower beam (Fig. 4.2) were 1: 0.3–0.5 m, 2: 0.5–0.7 m, 3: 0.8–0.9 m, 4: 1.7–1.8 m, 5: 0.8–1.2 m. Adding an allowance for wave height, the two topmost net chambers represented the depth strata accessible for the plunge-diving terns, whereas depth horizons sampled by net chambers 3, 4 and 5 were inaccessible for the terns. Hereafter, net chambers 1 and 2 and net chambers 3, 4 and 5 are referred to as top nets and bottom nets, re-



**Figure 4.2:** Vertically-resolving stow net. Vertical dimensions of the stow net chambers given in the figure refer to zero water movement (overall net height 7m). The height of the single net chambers at 4 and 5 m overall net height are given in brackets (see text for details). A) Overview stow net (four of five net chambers are shown), B) side view of stow net at 4, 5, and 7m total net height, C) operating stow net, upper beam on calm water surface, D) propeller flow meter. Black arrows indicate direction of the water current.

spectively. Haul duration was  $45 \pm 5$  minutes. The stretched mesh size decreased from 40 mm close to the mouth to 10 mm in the cod end. Water flow was recorded by means of four propeller flow meters (Hydrobios, Kiel) placed next to the net chambers (Fig. 4.2). Absolute catch numbers were normalized to individuals caught per 10000 m<sup>3</sup> filtered water volume by

$$No_{10000} = No_{absolute} / (PC_{End} - PC_{Start} \times 0.3 \times Net_{Height} \times Net_{Width}) \times 10000$$

with  $No_{10000}$  = fish numbers per 10000 m<sup>3</sup> fished water volume,  $No_{absolute}$  = absolute fish numbers,  $PC_{End}$  = propeller count at the end of a haul,  $PC_{Start}$  = propeller count at the start of a

haul, 0.3 = meters per rotation of the propeller flowmeter (value provided by manufacturer),  $\text{Net}_{\text{Height}}$  = net height in m (varying with the current pressure),  $\text{Net}_{\text{Width}}$  = net width in m (constant).

The catches from each net chamber were sorted by species, individuals were counted and standard length ( $\pm 1$  mm) was measured (see Muus and Nielsen, 1999). Analyses of the vertical fish distribution were limited to key prey fish species of the terns, namely herring, smelt, sprat, whiting and Nilsson's pipefish (referred to as "pipefish" hereafter). For pipefish, no length measurements were carried out.

#### BREEDING PERFORMANCE AND CHICK GROWTH OF COMMON TERNS

Both Common Tern colonies studied are subject to long-term investigations of reproductive success and ecology (Becker, 1998). In 2006, 340 pairs were breeding on Minsener Oog and 470 at Banter See; in 2007, 197 and 420 pairs, respectively, were counted.

At both sites reproductive output and chick growth was studied based on checks during the entire breeding period. At Minsener Oog, a sample of clutches from the first laying cycle was fenced to study the fate of eggs and chicks (see for details Becker and Finck, 1985). At Banter See, the total colony was under investigation to study reproductive success of clutches from the first laying cycle from pentad (= 5d period of the year) 25–32 (May 1<sup>st</sup> to June 9<sup>th</sup>; for methodological details see Wendeln and Becker, 1999). The laying pentad was the 5-day-period when the first egg of a clutch was laid; clutch size referred to eggs per clutch, the breeding success was defined as number of chicks fledged per breeding pair.

All newly hatched chicks were ringed and weighed at every check by means of a digital balance in a wind protected box (Wagener, 1998; accuracy  $\pm 1$  g). Three parameters of mass growth were investigated: Growth rate ( $\text{g} \cdot \text{day}^{-1}$ ) during the linear phase of the body mass development from 3 to 13 d of age (at Banter See a sub-sample of chicks was investigated); peak mass (maximum mass record (g)) of a chick and pre-fledging mass (last mass record (g) of a chick before it leaves the colony site as a fledgling). These parameters were calculated only for chicks which fledged, growth rate was determined also for chicks which died before fledging. For further details see Becker and Wink (2003).

#### STATISTICS

The distribution and, consequently, means and variance in fish length could not be reliably determined due to very low sample sizes in the two topmost net chambers. Thus, parametric tests were not applicable. Instead, non-parametric statistics (Mann-Whitney-U-test) were applied to test for length differences in fish caught in the top and the bottom nets, where sample size was sufficient. The degree of association between catch numbers from these two depth ranges was determined using Pearson's product-moment correlation coefficient (Sokal and Rohlf, 1995). A sequential Bonferroni test was performed to adjust significance levels of the correlations according to an assumed experimentwise type I error rate of 5 % (Sokal and Rohlf, 1995).

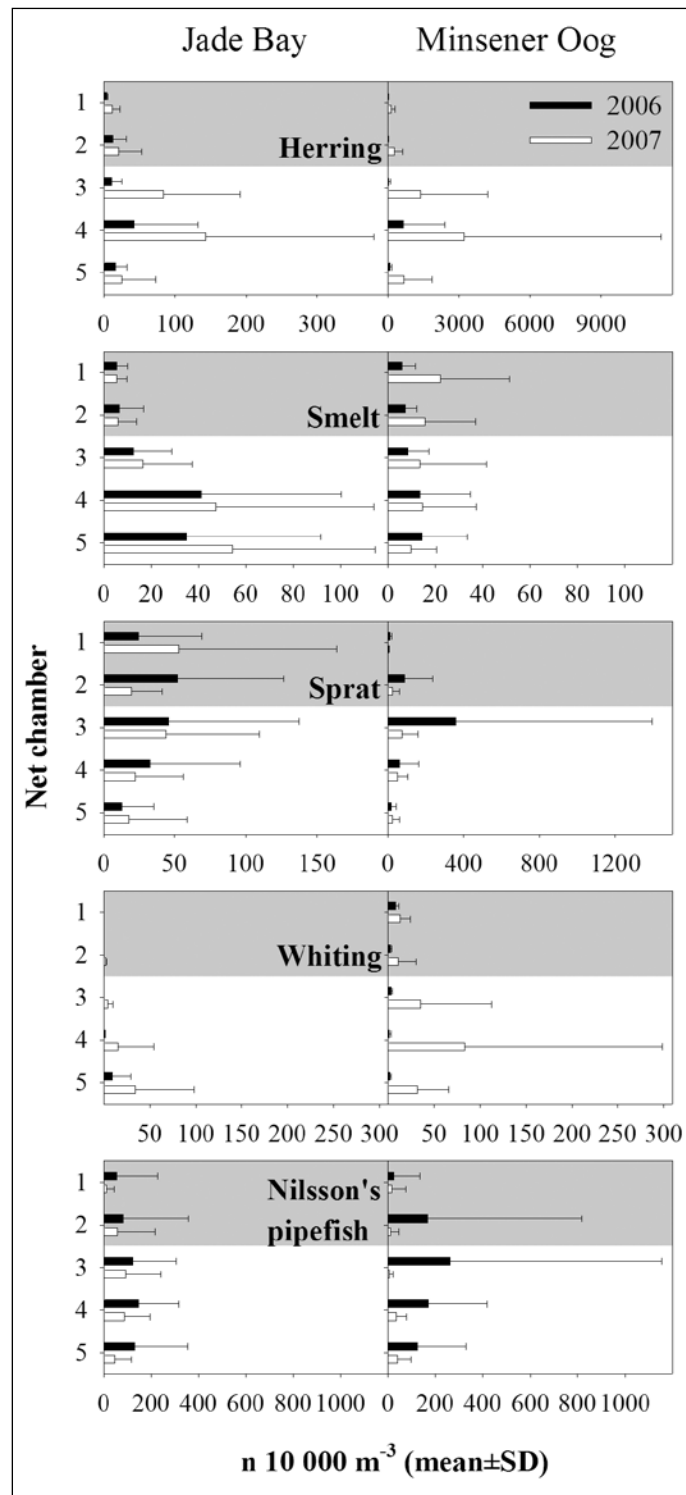


Inter-annual comparisons of Common Tern breeding parameters were tested for significance using a  $\chi^2$ -test (egg laying pentad), analyses of variance (clutch size, fledglings per breeding pair), a generalized linear model (weight gain of chicks) and a Kruskal-Wallis-test (maximum weight of chicks and chick weight at fledgling). Both correlations and differences were considered statistically significant at  $p < 0.05$ .

#### 4.4 RESULTS

##### SPATIAL AND INTERANNUAL ABUNDANCE PATTERNS

The abundance of the fish species examined differed between years and catch locations (Fig. 4.3). Herring and whiting were more abundant in 2007 than in 2006 by approximately one order of magnitude at both locations, whereas there were more sprat and pipefish in 2006 than in 2007. Smelt abundance was rather uniform between years. Largest catches of herring, sprat, whiting and pipefish were obtained at Minsener Oog, whereas smelt abundance was on average only half of that in the Jade Bay (Fig. 4.3). At Minsener Oog, herring was by far the most abundant fish species in the catches, followed by pipefish, sprat, whiting and smelt in order of decreasing catch numbers. Also in the Jade



**Figure 4.3:** Vertical abundance distribution of herring, smelt, sprat, whiting and Nilsson's pipefish caught in 2006 (black bars) and 2007 (grey bars) in the central Jade Bay (left) and at Minsener Oog (right). Note different scaling of x-axes in herring and sprat. Depth horizons exploitable for the terns are highlighted in grey.

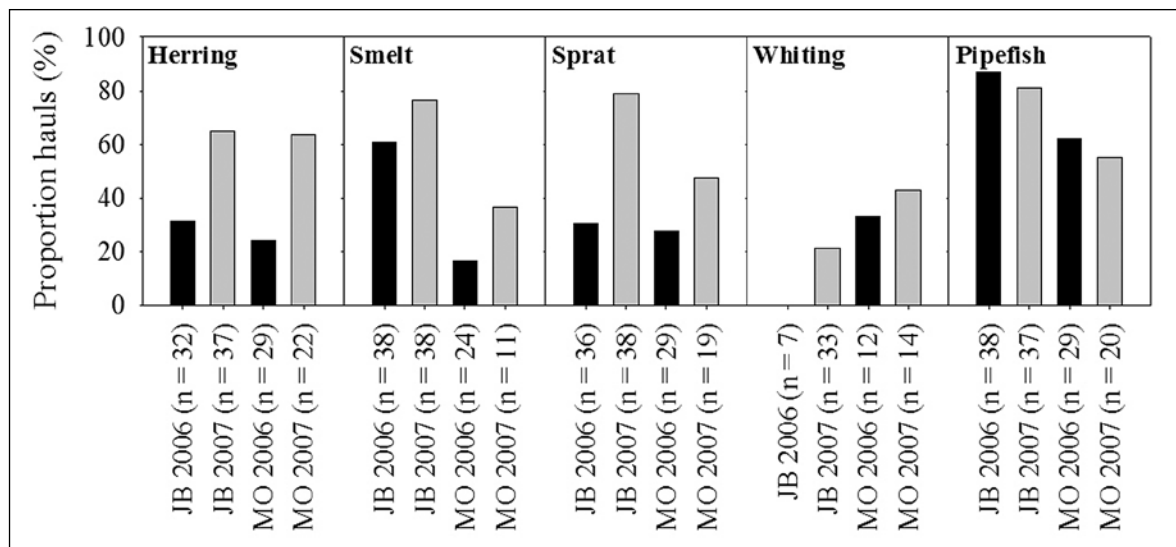
Bay, herring was the most abundant species, but except for whiting in 2006 the other species were present in the same order of magnitude (Fig. 4.3). Since hardly any sandeel were caught they were not considered in the analyses.

#### VERTICAL DISTRIBUTION OF ABUNDANCE

Across all fish species examined, abundance differed clearly between the five depth horizons sampled. Fish abundance was usually lowest in the water layers accessible for the terns. The exceptions were sprat in the Jade Bay, smelt at Minsener Oog and pipefish at both locations (Fig. 4.3). Abundance was highest in depth strata below the terns' maximum foraging depth. This pattern was most pronounced in herring (at both sites) and smelt (only in the Jade Bay) (Fig. 4.3), the two most important prey species of the terns.

The vertical abundance patterns within one species were not uniform between years in all cases. Smelt catches at Minsener Oog were higher at the top in 2007 than in 2006, highest numbers of pipefish were caught by the three bottom nets in 2007, contrasting the rather uniform abundance distribution in 2006 in this species (Fig. 4.3). There were also differences in vertical distribution patterns between catch locations: Smelt was rather evenly distributed over the water column at Minsener Oog, whereas in the Jade Bay smelt was most abundant in the two bottommost net chambers. Sprat in the Jade Bay did not exhibit abundance peaks at any depth. At Minsener Oog lowest sprat numbers were found in the top- and bottommost net chamber, respectively (Fig. 4.3).

Herring, sprat and smelt were encountered in the topmost two net chambers more frequently in 2007 than in 2006. This pattern was observed at both catch locations, but not in whiting and pipefish (Fig. 4.4). Among all five species examined, pipefish occurred most frequently



**Figure 4.4:** Presence of prey fish in all hauls carried out in 2006 (black bars) and 2007 (grey bars) in the Jade Bay (JB) and at Minsener Oog (MO) in the topmost 2 net chambers. The number of hauls (n) is given in brackets in the x-axis labels.

within the reach of the foraging terns. Differences in the frequency of occurrence in smelt, whiting and pipefish catches varied between the two catch locations, whereas herring (2006 and 2007) and sprat (only 2006) were caught with similar frequency in the top nets at both sampling sites (Fig. 4.4).

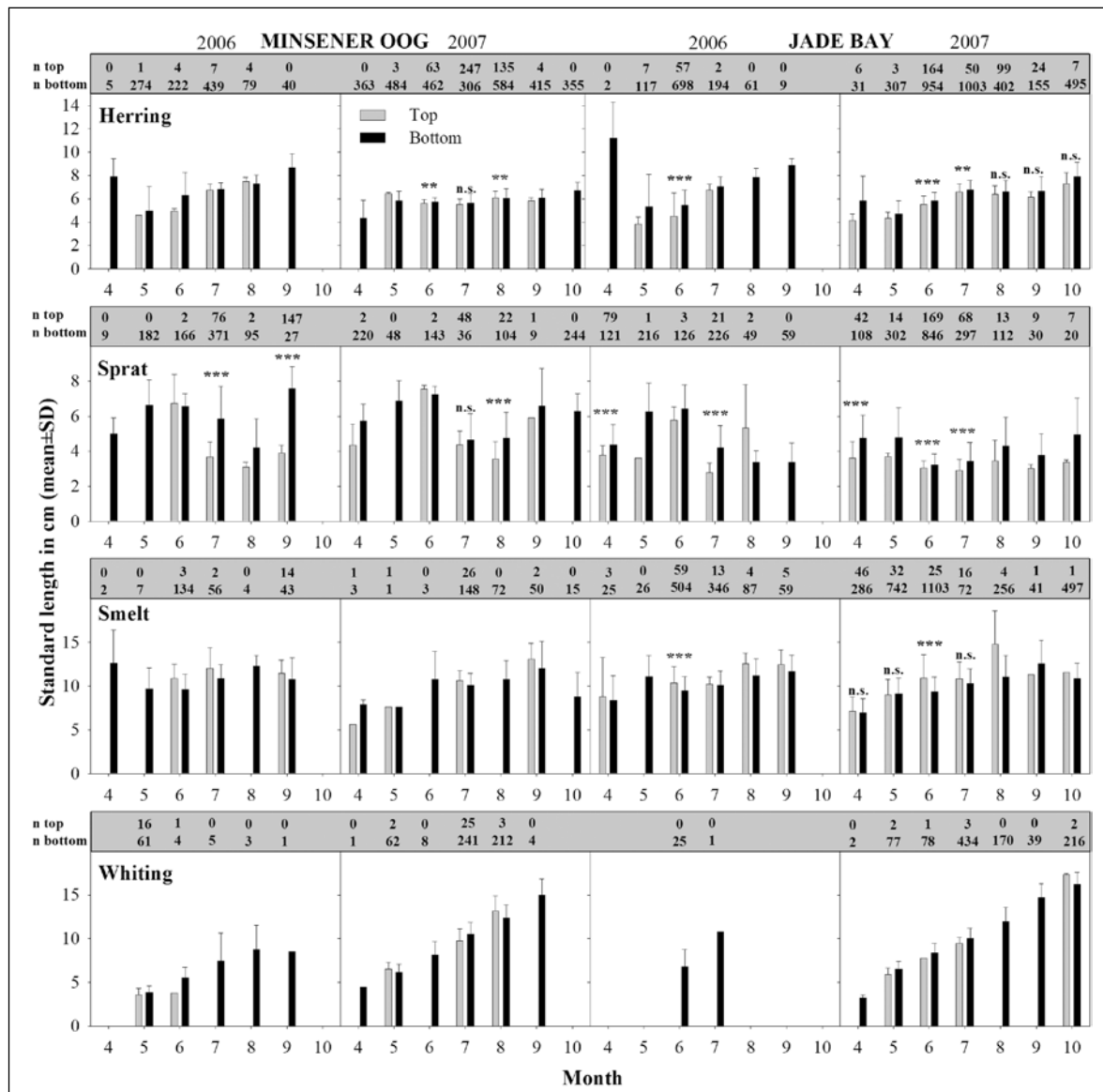
#### VERTICAL LENGTH DISTRIBUTION OF FISH

Herring obtained from the stow net catches were all juveniles. In the Jade Bay, herring caught in the top nets were significantly shorter than individuals caught in the bottom nets, both in 2006 and 2007. At Minsener Oog, herring caught in the top nets and in the bottom nets were of similar length in 2006; in 2007 individuals caught in the top nets were shorter than conspecifics obtained by the bottom nets (Table 4.1). This trend was seen, however less clearly, also throughout the season, with length differences between top- and bottom-caught herring successively decreasing in both years and at both sampling locations (Fig. 4.5).

**Table 4.1:** Standard length comparisons between herring, smelt, sprat and whiting caught in the two top-most (top) and at the three bottommost (bottom) net chambers in 2006 and 2007 in the central Jade Bay and at Minsener Oog. Sample size (n) and significance levels of Mann-Whitney-U-statistics and are given: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ , n. s. = not significant. In 2006, no whiting were caught near the surface of the Jade Bay. For Nilsson's pipefish length data were not available.

	Herring		Sprat		Smelt		Whiting	
	p	n top/bottom	p	n top/bottom	p	n top/bottom	p	n top/bottom
Minsener Oog								
2006	n. s.	16/615	***	106/592	*	84/826	—	0/0
2007	***	452/2834	***	322/1199	***	125/3154	***	8/983
Jade Bay								
2006	***	42/851	***	227/797	***	19/198	**	17/60
2007	***	353/2377	***	75/719	n. s.	29/220	***	30/362

Sprat sampled by the top nets were mostly very early juveniles that had just completed metamorphosis. Catches from the bottom nets were composed of late juveniles and young adults that were significantly longer. This pattern was observed in the Jade Bay in 2006 and at Minsener Oog in both years. In 2007, length differences between top- and bottom-caught sprat were subtle, yet still significant (Table 4.1). The pattern of sprat caught by the top nets being smaller than conspecifics caught in the bottom nets persisted throughout the season, despite the great seasonal variability in length composition. In eight out of nine cases with sufficient sample size, the top-bottom length differences were highly significant (Fig. 4.5). Smelt of all age classes from juveniles to large adults were represented in the catches. In 2006 individuals caught in the top nets in the Jade Bay were significantly longer than those caught in



**Figure 4.5:** Seasonal standard length development of herring, smelt, sprat and whiting caught between April 19<sup>th</sup> and September 5<sup>th</sup> 2006 and between April 24<sup>th</sup> and October 10<sup>th</sup> 2007 in the central Jade Bay and at Minsener Oog. Significance levels of Mann-Whitney-U-statistics and sample size (n top and n bottom) are given in the figures: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ , n. s. = not significant. Statistics could not be applied in all cases due to low sample size. In 2006, no whiting were caught near the surface of the Jade Bay. For Nilsson's pipefish length data were not available.

the bottom nets. Despite significant differences, the picture was less clear in 2007, when both shortest and longest smelt were caught in the top nets. Smelt caught at Minsener Oog in 2006 in the bottom nets were longer than those obtained from the top nets. In 2007, no length differences between top- and bottom-caught smelt were observed (Table 4.1). Resolved by month, the pattern of smelt caught at the top being longer than those caught at the bottom was also observed in the Jade Bay, but not significant in all cases. This was evident also at Minsener Oog, but could not be tested statistically due to very low catch numbers in the top nets (Fig. 4.5).

In both years and at both sampling sites only juvenile whiting were caught. In the Jade Bay the sample size from the top nets was too low to compare length distributions between depths in both years. At Minsener Oog, individuals caught in the bottom nets were significantly longer than those caught in the top nets, which was more obvious in 2007 than in 2006 (Fig. 4.5). In 2006, whiting were caught in the top nets only in April and May at Minsener Oog. In 2007, top-bottom length comparisons were also hampered by very low catch numbers in the top nets, prohibiting statistical comparisons between top- and bottom-caught whiting (Fig. 4.5). For pipefish no length data were available.

#### CORRELATIONS OF VERTICAL ABUNDANCE DISTRIBUTION

When all hauls from both years and both sampling sites were combined in one analysis, positive and significant correlations between fish abundance in the top nets and in the bottom nets (hereafter referred to as top-bottom correlations) appeared to be a common pattern across all species examined, except for sprat. This was also true for the catches obtained at Minsener Oog for the years 2006 and 2007 combined (Table 4.2).

**Table 4.2:** Correlation between abundance of herring, smelt, sprat, whiting and pipefish in the top net chambers (1 and 2) and the bottom net chambers (3, 4, and 5), representing the water strata accessible and inaccessible, respectively, to the terns. Pearson's product moment correlation coefficient (r), significance level (p, corrected for testwise type I error rate, for details see Methods section) and sample size (n) are given. \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ , n. s. = not significant. Significant correlations are in bold. MO = Minsener Oog, JB = Jade Bay.

	Herring	Sprat	Smelt	Whiting	Pipefish
	r <sup>p</sup> (n)				
MO + JB 2006 + 2007	<b>0.31** (120)</b>	0.21 <sup>n.s.</sup> (122)	<b>0.47** (111)</b>	<b>0.81** (66)</b>	<b>0.71** (124)</b>
MO 2006 + 2007	0.29 <sup>n.s.</sup> (51)	0.36 <sup>n.s.</sup> (48)	<b>0.76** (35)</b>	<b>0.95** (26)</b>	<b>0.91** (49)</b>
JB 2006 + 2007	<b>0.63** (69)</b>	0.09 <sup>n.s.</sup> (74)	<b>0.50* (76)</b>	0.28 <sup>n.s.</sup> (40)	0.15 <sup>n.s.</sup> (75)
MO + JB 2006	-0.01 <sup>n.s.</sup> (63)	0.29 <sup>n.s.</sup> (65)	<b>0.64** (62)</b>	-0.03 <sup>n.s.</sup> (19)	<b>0.73** (67)</b>
MO + JB 2007	0.30 <sup>n.s.</sup> (57)	0.08 <sup>n.s.</sup> (57)	<b>0.34* (49)</b>	<b>0.86** (47)</b>	<b>0.45* (57)</b>
MO 2006	0.01 <sup>n.s.</sup> (29)	0.34 <sup>n.s.</sup> (29)	<b>0.87** (24)</b>	0.21 <sup>n.s.</sup> (12)	<b>0.93** (29)</b>
MO 2007	0.23 <sup>n.s.</sup> (20)	<b>0.70** (19)</b>	<b>0.97* (11)</b>	<b>0.99* (14)</b>	0.42 <sup>n.s.</sup> (20)
JB 2006	<b>0.53** (34)</b>	0.17 <sup>n.s.</sup> (36)	<b>0.60* (38)</b>	<b>no data</b>	0.04 <sup>n.s.</sup> (38)
JB 2007	<b>0.64** (37)</b>	0.00 <sup>n.s.</sup> (38)	<b>0.39* (38)</b>	0.26 <sup>n.s.</sup> (33)	<b>0.44* (37)</b>

These correlations suggested that fish abundance in the depth strata accessible for the terns increases with the fish abundance across the entire depth range sampled. At a finer resolution, however, the relationships differed with regard to catch location, year and strength of the correlation within as well as between species (Table 4.2). The top-bottom correlations in herring

numbers were strong and highly significant in the Jade Bay in both years taken separately as well as combined. At Minsener Oog the top-bottom correlations were significant in neither case (Table 4.2). In sprat, the top-bottom correlations were usually weak and not significant, except for Minsener Oog in 2007 (Table 4.2). In smelt, the top-bottom correlations were strong and significant in all cases. Despite lower catch numbers at Minsener Oog than in the Jade Bay (Fig. 4.3), the top-bottom correlations were among the strongest found and highly significant (Table 4.2). Whiting numbers from the top nets were strongly and significantly correlated with the abundance in the bottom nets only in 2007 at Minsener Oog. This resulted in positive correlations in all other combinations containing these catch results (Table 4.2). In pipefish, the top-bottom correlations at Minsener Oog were significant in 2006 but not in 2007, whereas the opposite was observed for pipefish catches from the Jade Bay. Owing to the strength of the respective correlations of the single years, top-bottom correlations for the single sampling sites but with both years combined were significant in the case of Minsener Oog but not significant for the Jade Bay (Table 4.2).

#### BREEDING PERFORMANCE AND CHICK GROWTH IN COMMON TERNS

In 2006 Common Tern pairs had no breeding success on Minsener Oog due to severe egg predation, and no further data could be collected. In 2007, flooding of large parts of the breeding colony prevented breeding success again (Table 4.3). Consequently, an inter-annual comparison of the breeding performance of Common Terns at Minsener Oog was not possible.

The inter-year comparison at Banter See colony revealed, that both reproductive performance as well as chick growth were superior in 2007: On average, eggs were laid about 5 days earlier, clutches were larger, chicks grew faster higher daily weight gain of almost 2 g and achieved higher peak and pre-fledging mass than in 2006. Only breeding success in 2007 was lower than in 2006. This was due to starvation of many older chicks, caused by food shortage as a result of adverse weather conditions during the late breeding season. The recession from peak- to pre-fledging mass which was higher in 2007 than in 2006 is an indicator of the poor feeding conditions (2006:  $-8.1 \pm 0.5$  g,  $n = 272$ ; 2007:  $-11.1 \pm 0.6$  g,  $n = 222$ ;  $t = -3.755$ ,  $p < 0.001$ , t-test; Table 4.3). In 2007, the median egg laying date of Common Terns breeding at Minsener Oog was about 5 days later than at Banter See. Growth rates of chicks which died tended to be lower than at Banter See (n. s., Table 4.3).

## 4.5 DISCUSSION

#### METHODOLOGICAL ASPECTS

Information on small-scale prey availability to seabirds has mostly been obtained by means of hydroacoustic methods (e. g. Safina and Burger, 1988; Zamon, 2003; Burger et al., 2004;

**Table 4.3:** Reproduction and chick growth parameters of Common Terns breeding at Minsener Oog and at Banter See, Wilhelmshaven, in 2006 and 2007 (mean  $\pm$  SE). Due to flooding and predation, no comparable data are available for Minsener Oog in 2006 and partly in 2007. In 2007 a bad weather period reduced the breeding success at Banter See despite otherwise favourable foraging conditions. Tests of inter-year differences at Banter See: <sup>A)</sup>Mann-Whitney-U-test, <sup>B)</sup>t-test. Test of inter-site differences in 2007: <sup>C)</sup>Mann-Whitney-U-test,  $p < 0.001$ .

	Minsener Oog	Banter See			
Parameter	2007	2006	2007	Statistics	
Reproduction <sup>A</sup>				z	p
N clutches studied	17	442	411		
Egg laying date [pentad]	29.1 $\pm$ 0.1 <sup>C</sup>	29.1 $\pm$ 0.1	28.2 $\pm$ 0.1	-6.427	<0.001
Clutch size [eggs * clutch <sup>-1</sup> ]	2.8 $\pm$ 0.1	2.3 $\pm$ 0.0	2.6 $\pm$ 0.0	-7.144	<0.001
Fledglings * pair <sup>-1</sup>	0.0 $\pm$ 0.0 <sup>C</sup>	0.57 $\pm$ 0.03	0.45 $\pm$ 0.03	-3.355	<0.001
Chick mass growth ( <i>N</i> ) <sup>B</sup>				t	p
Growth rate [g * day <sup>-1</sup> ]		3.2 $\pm$ 0.3 (71)		-5.607	<0.001
Chicks not fledged	4.6 $\pm$ 0.8 (31)		5.6 $\pm$ 0.3 (77)	-1.198	n. s.
Chicks fledged		5.3 $\pm$ 0.3 (76)	7.2 $\pm$ 0.2 (93)	-6.323	<0.001
Peak mass [g]		120.7 $\pm$ 0.6 (272)	127.8 $\pm$ 0.7 (222)	-7.917	<0.001
Pre-fledging mass [g]		112.6 $\pm$ 0.7 (272)	116.7 $\pm$ 0.7 (222)	-4.148	<0.001

Grémillet et al., 2004). In the Wadden Sea shallow water depth would have caused interference of the beam with the water-ground or the water-air interface and high turbulence increasing air bubbles, especially near the surface, i. e. in the foraging horizons of the terns. Moreover, in an environment with high species diversity echoes would be interpretable only after thorough calibration with net catches. Thus, sonars or echosounders were not considered appropriate to address the small-scale prey availability to the Common Terns in the area. Instead, a stow net specifically designed to address the small-scale vertical fish distribution was developed and employed. Stow nets are standard gear to sample pelagic fish, mostly because they cover the whole water column and, since it is a passive catch method being operated from an anchoring vessel, ship avoidance of the target species appears unlikely (Breckling and Neudecker, 1994). The vertical distribution of juvenile fish was investigated by Maes et al. (1999), who found highest proportions of herring and sprat in stow net catches carried out close to the surface. In their study, fish caught between the surface and 4 m depth were assigned “close to the surface”, allowing no conclusions about fish availability at depths relevant to foraging terns.

The low catch numbers in the two topmost net chambers reported here are not a methodological artefact, e. g. resulting from the upper beam causing turbulence and chasing fish away or the net symmetry inevitably guiding fish into the middle and away from the topmost net

chambers. The validity of the catch results became evident in the length differences between fish caught in the topmost and the bottommost nets. Furthermore, both sprat larvae with their limited ability to avoid gear and garfish (*Belone belone*), being highly mobile and perceptive, were mainly caught in the two topmost net chambers. In addition, vertical distribution patterns of clupeids and whiting similar to our study were reported from the Schleswig-Holstein Wadden Sea (Herrmann et al., 1998).

#### VERTICAL DISTRIBUTION AND PREDATOR AVOIDANCE

The vertical distribution of potential prey fish of the terns observed in the present study may be a compromise between predator avoidance and profitable feeding conditions occurring near the water surface (Neilson and Perry, 1990; Herrmann et al., 1998; Brown et al., 2006). Neither garfish, owing to its size, nor fish larvae, due to their lack of pigmentation, would be vulnerable to avian predation. In contrast, species and life stages susceptible to be preyed upon appeared to avoid the depth strata accessible to the terns. Especially herring and smelt, which are very profitable prey in terms of energy yield per unit foraging effort (Massias and Becker, 1990), were usually out of reach of the plunge-diving Common Terns, even at times of maximum abundance e. g. of herring at Minsener Oog in 2007.

The top-bottom correlations did not show a consistent pattern. They appeared to be both species- and site-specific rather than driven by overall fish abundance. In the light of these results, the hypothesis that fish abundance in reach of the terns generally increases with overall prey fish abundance has to be rejected. Alternatively, the vertical distribution of less profitable prey such as pipefish and small sprat compared to more profitable prey such as herring, larger sprat, smelt and whiting could be explained by the intensity of anti-predator behavior of prey matching the degree of threat posed by the predator. The theoretical framework of this mechanism is known as the threat-sensitive predator avoidance hypothesis (Helfman, 1989; Helfman and Winkelman, 1997), which may explain the observed patterns, including the top-bottom correlations. At times of high abundance the probability to catch at least one herring within the topmost water layers increases both at Minsener Oog and in the Jade Bay. However, the top-bottom correlations in herring being caught at Minsener Oog were much weaker than in the Jade Bay or not significant at all, despite a much higher herring abundance at Minsener Oog in both years. These findings are also in agreement with the threat-sensitive predator avoidance hypothesis in that herring may avoid surface-near water strata at Minsener Oog, where they are by far the most important prey fish to the terns. In the Jade Bay, predation pressure by seabirds is partly directed also at smelt.

In sprat, the vertical abundance distribution at Minsener Oog was quite different from that in the Jade Bay, and there was no clear pattern in the top-bottom correlations. But in all cases individuals caught in the topmost two net chambers were much smaller than in the bottommost net chambers. Anti-predator behavior in the form of schooling commences at the larval stage and persists throughout the whole lifespan (Fernö et al., 1998), but predator avoidance



by means of vertical distribution may not be fully developed in very young sprat that have just transformed from nearly transparent larvae into pigmented juveniles.

In smelt, top-bottom correlations were significant in all cases. Correlations were stronger and smelt were more evenly distributed over the water depths sampled at Minsener Oog, where smelt is only of marginal importance as tern food (Becker et al., 1987; Frank, 1992; Frick and Becker, 1995; Dänhardt and Becker, 2008), possibly due to the lower abundance of smelt using the waters around Minsener Oog as a transit area on their way into the Jade Bay. In the Jade Bay, where smelt is among the most frequently utilized prey fish of the Common Terns breeding at Banter See (Dänhardt and Becker, 2008), smelt were below the maximum diving depth of the terns and the top-bottom correlations were significant but much weaker than at Minsener Oog. This may be due to the presence of herring, another abundant and profitable prey resource, reducing the fish species-specific predation pressure.

Vertical distribution patterns of whiting were similar to that of herring. In addition to a possible anti-predator component, abundance peaks in the water column may also be attributed to spatial overlap with the whiting's benthic prey, chiefly brown shrimp *Crangon crangon* and gobies *Pomatoschistus spec.* (Berghahn, 1996; Jansen, 2002).

The availability of the fish species investigated in the upper water column is not sufficient to support large colonies of surface-feeding seabirds as encountered in the Wadden Sea. Nevertheless, they regularly occur in the diet of Common Terns in high proportions (Becker et al., 1987; Frank, 1992; Frank and Becker, 1992; Frick and Becker, 1995; Frank, 1998). Apart from their vertical distribution in the deep channels, prey fish may become available to their avian predators also through other mechanisms. Sub-surface foragers such as predatory fish, marine mammals or pursuit-diving seabirds chase potential prey fish to the surface (Camphuysen and Webb, 1999). Energy flow to piscivorous predators is also strongly associated with the tidal phase in habitats where physical forcing such as tidal fronts and jets, eddies and upwelling are present (Wolanski and Hamner, 1988; Hunt et al., 1999; Zamon, 2003). Fish may aggregate around an enhanced food density resulting from these hydrographic phenomena, which, in turn, may also compromise schooling behavior and avoidance of near-surface water strata.

These mechanisms potentially result in enhanced prey availability to the terns compared to "undisturbed" conditions in the tidal channels (Hunt et al., 1999). At foraging sites where the "undisturbed" vertical distribution is disrupted by hydrography or predators the energy return per unit foraging effort will likely be higher, because prey may be concentrated (Hunt et al., 1999). Furthermore, larger fish may be available that would otherwise be out of reach in the "undisturbed" situation. Despite the presumably lower prey availability the relative importance of tidal channels as foraging habitat may still be considerable, because foraging activity is positively related to current speed, which is enhanced in the tidal channels (Schwemmer et al., 2009). Small pelagic fish require sufficient water depth to form their schools, a behavior that commences already at the larval stage and persists throughout

the whole lifespan (Fernö et al., 1998). They are thus adapted to the deep tidal channels, as observed by Herrmann et al. (1998), who found herring and sprat in the Schleswig-Holstein Wadden Sea to be associated with tidal channels of 4–12 m depth. Since the tern prey with the highest energy density are schooling fish (Massias and Becker, 1990), the stow net catches from the tidal channels represent an important foraging habitat of the terns. In fact, terns use a wide variety of foraging habitats over the course of a tidal cycle (Becker et al., 1993; Stienen et al., 2000; Schwemmer et al., 2009), also including tidal channels where the stow net was employed.

Together with abundance, the size of the fish the terns can reach determines the potential energy return per unit foraging effort. Except for smelt, individual fish caught in the top nets were mostly smaller than conspecifics caught in the bottom nets, both integrated over the whole season and resolved by month. These vertical length differences may be either due to intra- or inter-cohort behavioural plasticity, i.e. the observed length differences may be the result of species-specific seasonal migration dynamics: Early in the season (April/May), 1-year-old herring overlap with the arriving 0-group that was presumably spawned in winter in the English Channel (Dickey-Collas et al., 2009). As larger herring leave the Wadden Sea, the top-bottom length differences change from inter- to intra-cohort and decrease but remain. This indicates behavioural differences between smaller and larger individuals also within a given cohort. This explanation is also supported by the large top-bottom length differences prevailing over the whole season in sprat, being a mixture of locally and externally spawned batches of individuals (Baumann et al., 2009). The gradual length progression seen in whiting indicates only one cohort being present in the Wadden Sea. Accordingly, top-bottom length differences were relatively small.

Reproductive performance of seabirds and growth of their chicks reflects food availability during the breeding season (e.g. Cairns, 1987; Monaghan et al., 1992; Greenstreet et al., 1999; Tasker and Furness, 2003; Vincx et al., 2007). The parameters of breeding performance of the Common Terns and of chick growth indicated more favorable foraging conditions in 2007 than in 2006, when eggs were laid later and clutches were smaller. The poor feeding conditions in 2006 as compared to 2007 were also reflected in the physiological state of the breeding birds as expressed by cholesterol and triglyceride levels (Bauch et al., 2010). Furthermore, their chicks showed reduced growth rates, peak- and pre-fledging mass. With regard to a long term comparison at Banter See colony (1992–2007; see Becker and Wink, 2003; Schaubroth and Becker 2008; Schaubroth and Becker unpublished data), growth rate in 2006 was among the two lowest annual values, and peak mass and pre-fledging mass among the three lowest values. On the other hand, peak-mass in 2007 was among the five highest values ever recorded in this colony. The seabird data correlate well with the information on food availability collected in this study: In 2006, herring and whiting abundance was lower and the chances to encounter herring, sprat or smelt within foraging range were reduced compared to 2007.

## CONCLUSIONS

Given the great diversity of potential foraging habitats in the Wadden Sea, prey availability in the tidal channels represented by the stow net catches can only be one factor determining food supply. Even though a clear relationship between prey fish abundance and prey availability at the surface could not be demonstrated in all species examined, overall fish abundance appears to be the main driver of prey availability, as chances of predator-prey encounter increase with increasing prey density at all foraging sites utilized by the terns. In conclusion, physical factors (Zamon, 2003; Schwemmer et al., 2009) and biological interactions (Camphuysen and Webb, 1999) can only work to enhance food availability to surface feeding seabirds when baseline food abundance is sufficient. In the case of the terns main prey this is mainly determined outside the Wadden Sea and may be subject to a variety of influences, both natural (e. g. climate driven recruitment failure of North Sea herring, Payne et al., 2009) and anthropogenic (e. g. connectivity of river passages for diadromous species such as smelt).

## ACKNOWLEDGEMENTS

We wish to thank Captain K.-H. Rostek, his crew and many volunteers who helped sorting the stow net catches. J.-P. Herrmann's contribution to the design of the stacked stow net and the valuable discussions are gratefully acknowledged. We also thank C. Bauch, V. Blum, A. Braasch, T. Ezard, T. Freseman, S. Kreutzer, M. Martínez Benito, A. Ostendorp, J. Riechert, L. Schmidt, J. Sprenger and G. Wagenknecht for their support in collecting the data on breeding performance and chick growth in Common Terns. The project received financial support from the Niedersächsische Wattenmeerstiftung (53-NWS-41/04).

## 4.6 REFERENCES

- Barrett RT and Krasnov YV (1996) Recent responses to changes in stocks of prey species by seabirds breeding in the southern Barents Sea. *ICES Journal of Marine Science* 53: 713–722.
- Barrett RT (2007) Food web interactions in the southwestern Barents Sea: black-legged kittiwakes *Rissa tridactyla* respond negatively to an increase in Herring *Clupea harengus*. *Marine Ecology Progress Series* 349: 269–276.
- Bauch C, Kreutzer S and Becker PH (2010) Breeding experience affects body condition: blood metabolite levels over the course of incubation in a seabird. *Journal of Comparative Physiology B* 180: 835–845.
- Baumann H, Mahlzahl AM, Voss R and Temming A (2009) The German Bight (North Sea) is a nursery area for both locally and externally produced Sprat juveniles. *Journal of Sea Research* 61: 234–243.
- Becker PH (1996) Flusseeeschwalben (*Sterna hirundo*) in Wilhelmshaven. *Oldenburger Jahrbuch* 96: 263–296.
- Becker PH (1998) Langzeittrends des Bruterfolgs der Flusseeeschwalbe und seiner Einflussgrößen im Wattenmeer. *Vogelwelt* 119: 223–234.
- Becker PH and Wink M (2003) Influences of sex, sex composition of brood and hatching order on mass growth in Common Terns (*Sterna hirundo*). *Behavioural Ecology and Sociobiology* 54: 136–146.
- Becker PH and Ludwig J-D (2004) *Sterna hirundo* Common Tern BWP Update Vol. 6 (1–2): 91–137.

- Becker PH, Frank D and Walter U (1987) Geografische und jährliche Variation der Ernährung der Flusseeeschwalbe (*Sterna hirundo*) an der Nordseeküste. *Journal für Ornithologie* 128: 457–475.
- Becker PH, Frank D and Sudmann SR (1993) Temporal and spatial pattern of Common Tern (*Sterna hirundo*) foraging in the Wadden Sea. *Oecologia* 93: 389–393.
- Berghahn R (1996) Episodic mass invasions of juvenile gadoids into the Wadden Sea and their consequences for the population dynamics of Brown Shrimp (*Crangon crangon*). *Marine Ecology* 17 (1–3): 251–260.
- Boyd IL, Wanless S, Camphuysen CJ (2006) *Top Predators in Marine Ecosystems*. Cambridge University Press, Cambridge 378 pp.
- Breckling P and Neudecker T (1994) Monitoring the fish fauna in the Wadden Sea with stow nets (part 1): A comparison of demersal and pelagic fish fauna in a deep channel. *Archive of Fisheries and Marine Research* 42: (1) 3–15.
- Brown GE, Rive AC, Ferrari MCO and Chivers DP (2006) The dynamic nature of antipredator behavior: prey fish integrate threat-sensitive anti-predator responses within background levels of predation risk. *Behavioural Ecology and Sociobiology* 61: 9–16.
- Burger AE, Hitchcock CL and Davoren GK (2004) Spatial aggregations of seabirds and their prey on the continental shelf off SW Vancouver Island. *Marine Ecology Progress Series* 283: 279–292.
- Cairns DK (1987) Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261–271.
- Cairns DK (1992) Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. *The Condor* 94: 811–824.
- Dänhardt A and Becker PH (2008) Die Bedeutung umweltbedingter Verteilungsmuster von Schwarmfischen für Seevögel im Ökosystem Niedersächsisches Wattenmeer. Final project report, 248 pp. (in German).
- Dickey-Collas M, Bolle LJ, Van Beek JKL and Erftemeijer PLA 2009 Variability in transport of fish eggs and larvae. II. Effects of hydrodynamics on the transport of down Herring larvae. *Marine Ecology Progress Series* 390: 183–194.
- Einoder LD (2009) A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research* 95: 6–13.
- Fauchald P and Erikstad KE (2002) Scale-dependent predator-prey interactions: the aggregative response of seabirds to prey under variable prey abundance and patchiness. *Marine Ecology Progress Series* 231: 279–291.
- Fernö A, Pitcher TJ, Melle W, Nøttestad L, Mackinson S, Hollingworth C and Misund OA (1998) The challenge of the Herring in the Norwegian Sea: making optimal collective spatial decisions. *Sarsia* 83: 149–162.
- 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.
- Frank D (1998) Bruterfolgsmonitoring an der Flusseeeschwalbe *Sterna hirundo* als Instrument ökologischer Begleituntersuchungen zu einer Pipeline-Verlegung im Wattenmeer. *Vogelwelt* 119: 235–241.
- Frank D and Becker PH (1992) Body mass and nest reliefs in Common Terns *Sterna hirundo* exposed to different feeding conditions. *Ardea* 80: 57–69.
- Frederiksen M, Wright PJ, Harris MP, Mavor RA, Heubeck M and Wanless S (2005) Regional patterns of kittiwake *Rissa tridactyla* breeding success are related to variability in sandeel recruitment. *Marine Ecology Progress Series* 300: 201–211.
- Frederiksen M, Furness RW and Wanless S (2007) Regional variation in the role of bottom-up and top-down processes in controlling sandeel abundance in the North Sea. *Marine Ecology Progress Series* 337: 279–286.
- Frick S and Becker PH (1995): Unterschiedliche Ernährungsstrategien von Fluss- und Küstenseeschwalbe (*Sterna hirundo* und *S. paradisaea*) im Wattenmeer. *Journal für Ornithologie* 136: 47–63.
- Furness RW and Tasker ML (1999) Diets of seabirds and consequences of changes in food supply. *ICES Cooperative Research Report* 232: 1–66.
- Furness RW and Tasker ML (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series* 202: 253–264.

- Greenstreet SPR, Becker PH, Barrett RT, Fossum P and Leopold MF (1999) Consumption of pre-recruit fish by seabirds and the possible use of this as an indicator of fish stock recruitment. In Furness RW and Tasker ML (Eds.): Diets of seabirds and consequences of changes in food supply. ICES Cooperative Research Report 232: 6–17.
- Grémillet D, Kuntz G, Delbart F, Mellet M, Kato A, Robin J-P, Chaillon P-E, Gendner J-P, Lorentsen S-H and Le Mayo Y (2004) Linking the foraging performance of a marine predator to local prey abundance. *Functional Ecology* 18: 793–801.
- Helfman GS (1989) Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behavioural Ecology and Sociobiology* 24: 47–58.
- Helfman GS and Winkelman DL (1997) Threat sensitivity in bicolor damselfish: effects of sociality and body size. *Ethology* 103: 369–383.
- Herrmann J-P, Jansen S and Temming A (1998) Fische und dekapode Krebse in der Sylt-Rømø-Bucht. In Gätje C and Reise K (Eds.): Ökosystem Wattenmeer – Austausch, Transport und Stoffumwandlungsprozesse. Springer Berlin, Heidelberg, New York: 81–88.
- Hunt GL, Montevecchi WA and Leopold MF (1999) A review of issues related to seabird consumption of fish and shellfish stocks discards and mariculture as well as the trophic role of seabirds and waders. In Furness R W and Tasker M L (Eds.) Diets of seabirds and consequences of changes in food supply. ICES Cooperative Research Report 232: 2–5.
- Jansen S (2002) Das Räuber-Beute-System juveniler Gadiden, Grundeln und Garnelen im Wattenmeer nördlich von Sylt. PhD thesis, University of Hamburg, 158 pp.
- Lewis S, Wanless S, Wright PJ, Harris MP, Bull J and Elston, DA (2001) Diet and breeding performance of black-legged kittiwakes *Rissa tridactyla* at a North Sea colony. *Marine Ecology Progress Series* 221: 277–284.
- Massias A and Becker PH (1990) Nutritive value of food and growth in Common Tern (*Sterna hirundo*) chicks. *Ornis Scandinavica* 21: 187–194.
- Mlody B and Becker PH (1991): Körpermasse-Entwicklung und Mortalität von Küken der Flussseseschwalbe (*Sterna hirundo* L.) unter ungünstigen Umweltbedingungen. *Vogelwarte* 36: 110–131.
- Montevecchi WA (1993) Birds as indicators of change in marine prey stocks. In Furness RW and Greenwood JJD (Eds.): Birds as monitors of environmental change. Chapman and Hall, London, pp. 217–266.
- Muus BJ and Nielsen J (1999) Die Meeresfische Europas in Nordsee, Ostsee und Atlantik. Kosmos guide, 336 pp.
- Neilson JD and Perry RI (1990) Diel vertical migrations of marine fishes: an obligate or facultative process. *Advances in Marine Biology* 26: 115–168.
- Payne MR, Hatfield EMC, Dickey-Collas M, Falkenhaus T, Gallego A, Gröger J, Licandro P, Llope M, Munk P, Röckmann C, Schmidt JO and Nash RDM (2009) Recruitment in a changing environment: The 2000s North Sea Herring recruitment failure. *ICES Journal of Marine Science* 66: 1–6.
- Piatt JF and Sydeman WJ (Eds.) (2007) Seabirds as indicators of marine ecosystems. *Marine Ecology Progress Series* 352: 199–309.
- Regehr HM and Rodway MS (1999) Seabird breeding performance during two years of delayed capelin arrival in the Northwest Atlantic: a multi-species comparison. *Waterbirds* 22 (1): 60–67.
- Rindorf A, Wanless S and Harris MP (2000) Effects of changes in sandeel availability on the reproductive output of seabirds. *Marine Ecology Progress Series* 202: 241–252.
- Safina C and Burger J (1988) Prey dynamics and the breeding phenology of Common Terns (*Sterna hirundo*). *The Auk* 105: 720–726.
- Schwemmer P, Adler S, Guse N, Markones N and Garthe S (2009) Influence of water flow velocity, water depth and colony distance on distribution and foraging patterns of terns in the Wadden Sea. *Fisheries Oceanography* 18: 161–172.
- Scott BE, Sharples J, Wanless S, Ross ON, Frederiksen M and Daunt F (2006) The use of biologically meaningful oceanographic indices to separate the effects of climate and fisheries on seabird breeding success. In Boyd IL, Wanless S and Camphuysen CJ (Eds.) Top predators in marine ecosystems. Their role in monitoring and management, pp. 46–62. Cambridge University Press, Cambridge.
- Sokal RR and Rohlf FJ (1995) Biometry. WH Freeman, New York, 887 pp.

- Stearns SS (1992) The evolution of life histories. Oxford University Press, New York.
- Stienen EWM, van Beers PWM, Brenninkmeijer A, Habraken JMPM, Raaijmakers MHJE and van Tienen PGM (2000): Reflections of a specialist: patterns in food provisioning and foraging conditions in Sandwich Terns *Sterna sandvicensis*. *Ardea* 88: 33–49.
- Thyen S, Becker P H, Exo K-M, Hälterlein B, Hötter H and Südbeck P (1998) Monitoring Breeding Success of Coastal Birds. *Wadden Sea Ecosystem* 8: 1–55.
- Wagener M (1998): Praktische Hinweise für brutbiologische Untersuchungen an der Flussseseschwalbe (*Sterna hirundo*). *Vogelwelt* 119: 279–286.
- Wanless S, Harris MP, Redman P and Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294: 1–8.
- Wendeln H and Becker PH (1999): Effects of parental quality and effort on the reproduction of common terns. *Journal of Animal Ecology* 68: 205–214.
- Wolanski E and Hamner WM (1988) Topographically controlled fronts in the ocean and their biological influence. *Science* 241: 177–181.
- Vincx M, Kuijken E and Volckaert F (2007) Higher trophic levels in the southern North Sea. Final report EV/25, D/2007/1191/33, pp. 1–88.
- Zamon JE (2003) Mixed species aggregations feeding upon Herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. *Marine Ecology Progress Series* 261: 243–255.

## CHAPTER 5

TO EAT OR TO FEED? PREY UTILIZATION OF  
COMMON TERNS *STERNA HIRUNDO* IN THE WADDEN SEAAndreas Dänhardt<sup>1, 2\*</sup>, Tido Freseman<sup>3</sup> and Peter H. Becker<sup>1</sup>

<sup>1</sup> Institute of Avian Research “Vogelwarte Helgoland”,  
An der Vogelwarte 21, 26386 Wilhelmshaven, Germany.

\* Corresponding author  
present address:

<sup>2</sup> Suerhoper Brunnenweg 13 a, 21244 Buchholz/Nordheide, Germany,  
Phone: + (49) 1 79 / 5 17 15 36, E-mail: andreas@daenhardt.com

<sup>3</sup> Loitzer Straße 48, 17489 Greifswald, Germany,  
E-mail: tido.freseman@gmx.de

## 5.1 ABSTRACT

Prey availability to seabirds has a profound influence on individual decisions about allocating somatic and reproductive investment. These decisions can be expressed in foraging behaviour and prey utilization and have consequences for establishing relationships between changes in the fish populations and responses in seabird breeding performance. We report here results of an unusual opportunity to investigate the relationships between fish abundance and at-sea foraging behaviour, prey utilization and food provisioning of partners and chicks of Common Terns *Sterna hirundo* breeding in the German Wadden Sea. High quality prey was carried out of the foraging area disproportionately often, whereas almost all low quality prey items were ingested by the foraging adult bird itself. Proportions of prey being used for provisioning were more similar to prey being carried out of the foraging area than to prey caught. The preferential utilization of high quality food for provisioning suggests that large proportions of low quality food being delivered to the colony may indicate a shortage of high quality food and, consequently, poor prospects of good breeding performance. Moreover, seabirds feeding whole, undigested prey items may indicate a higher abundance of high quality fish in the sea, due to selecting high quality prey for provisioning. This may result in overestimating the abundance of high quality prey fish when calculated from colony-based diet studies of single-loading seabird species such as terns alone.

## KEYWORDS

*Foraging behaviour, prey utilization, central place foraging, Common Tern, Wadden Sea, prey quality, feeding observations*

## 5.2 INTRODUCTION

Seabirds have proven utility as indicators of change in their marine environment. This is due to their apical position in food webs and their colonial breeding, making it relatively easy to study their diet, demography, physiology and breeding performance (Cairns, 1987; Montevecchi, 1993; Becker, 2003; Boyd et al., 2006; Piatt and Sydeman, 2007). These favorable circumstances have stimulated a number of seabird diet studies drawing inferences about changes in fish populations (e.g. Aebischer et al., 1990; Davoren and Montevecchi, 2003; Barrett, 2007). Supplementing colony-based investigations (Duffy and Jackson, 1986; Barrett et al., 2007) with information on fish abundance (e.g. Grémillet et al., 2004; Barrett, 2007; Dänhardt and Becker, 2008) is required to establish a link between seabird responses and their food supply. Seabird characteristics can be reliably calibrated with the spatial and temporal changes in their fish populations, when only one or few fish species are utilized and when there are only few prey alternatives. For example, the diet and breeding success of Black-legged kittiwakes (*Rissa tridactyla*) breeding in the northern North Sea is closely correlated with sandeel (*Ammodytes marinus*) abundance (Furness, 2002, 2006; Frederiksen et al., 2004). This correlation is even the basis of the management rule in ICES sub-area IV, that the local sandeel fishery is closed when on average less than 0.5 kittiwake chicks fledge for three consecutive years (ICES, 2002).

The trophic levels of the fish populations in the sea and the seabirds in the colony are linked via the actual process of foraging, which may not always be proportional to prey abundance as in the example above. Seabirds forage beyond the colonies, and they adjust their foraging behaviour immediately to a changed food situation (Walter and Becker, 1998; Schwemmer et al., 2009), the presence of adequate prey alternatives provided. A behavioural response is thus regarded the most direct and useful indicator of food supply (Monaghan, 1996). At the same time, foraging behaviour is most difficult to study, because it requires predictable foraging events that can be accessed by the observer. These conditions are usually not met due to the foraging range of most seabird species being too large to be systematically surveyed. To meet these methodological challenges, techniques to obtain *indirect* measures of seabird behaviour while away from the colony have been developed and applied (Becker et al., 1993; Burness et al., 1994; Weimerskirch, 1998; Daunt et al., 2003; Elliott et al., 2008), whereas *direct* observations (Walter and Becker, 1998) of foraging behaviour at sea are still very rare (Davoren and Burger, 1999), especially in surface-feeding seabird species (Taylor, 1979).



Colony-breeding single loaders such as terns are predicted to bring only large and energy-rich prey items to their partners or chicks in order to maximize energetic investment in reproduction. This concept, known as the central place foraging theory (Orians and Pearson, 1979), implies that the relationship between prey abundance and a given seabird characteristic measured inside the colony may be biased due to individual decisions during foraging. This has been demonstrated by means of direct observations of Roseate Terns (*Sterna dougallii*) (Shealer, 1998) and Common Terns (*Sterna hirundo*) during courtship (Taylor, 1979). Terns are among the few seabird species that allow for direct observations at sea due to their limited foraging range around their breeding colonies (Taylor, 1979; Becker et al., 1993; Schwemmer et al., 2009).

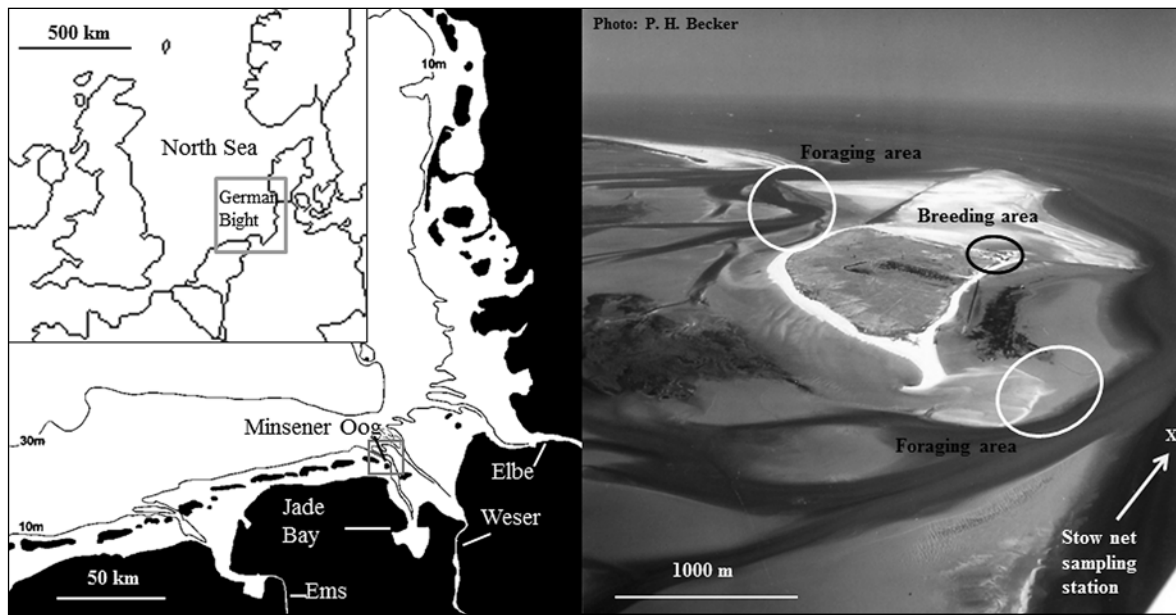
Using the conceptual framework of the central place foraging theory (Orians and Pearson, 1979), we present an integrated analysis of local fish abundance, foraging behaviour and prey utilization of Common Terns in their foraging areas at sea and, eventually, of the prey organisms being fed to partners or chicks in one of the largest breeding colonies in the German Wadden Sea.

### 5.3 MATERIAL AND METHODS

Between May and July 2007 foraging behaviour of Common Terns was observed around the island Minsener Oog (53°45' N 8°01' E) in the National Park Lower Saxon Wadden Sea in northern Germany. Minsener Oog is one of the most important breeding sites of terns and larid gulls in the German Wadden Sea, hosting 197 breeding pairs of Common Terns in 2007. Feedings of partners and chicks were observed in the breeding area in synchrony with the foraging observations. To provide information on the prey composition and abundance, stow net catches (Dänhardt and Becker 2010) were carried out close to the island (Fig. 5.1).

#### OBSERVATIONS OF FEEDING FLOCKS AND FORAGING BEHAVIOUR

In order to ensure successful foraging observations, the foraging locations of the terns had to be identified. Feeding aggregations were located from two elevated observation sites in the north and in the south of the island, respectively, using binoculars (Minox 10x42) and a scope (Leica 20x80). Feeding flocks could be reliably tracked within a range of  $\leq 3$  km around each observation point. Two locations close to the island turned out to be recurrently and predictably utilized for foraging by the Common Terns for at least 30 minutes: One at the southeast end at the confluence of two tidal channels, another off the northwest shore of the island, being confined to the north by a stony breakwater (Fig. 5.1). Common Terns breeding on Minsener Oog utilize a wide range of foraging areas, but these two locations represented one of two main foraging sites that had earlier been identified by means of radio-telemetry ("Wattengebiete", Becker et al., 1993). The feeding areas were easily accessed by the obser-



**Figure 5.1:** Study areas on and around the island of Minsener Oog in the Lower Saxon Wadden Sea, Northern Germany. The black circle denotes the colony location where feeding observations and egg and chick counts were carried out. White circles denote two preferred foraging areas of the Common Terns breeding on Minsener Oog. The white cross denotes the location where stow net catches were obtained.

ver either walking or by boat and could be approached close enough for reliable identification of behaviour and prey items ( $\leq 30$  m). Feeding flocks consisted of 15 individuals on average, below a minimum of 5 individuals observations were discontinued.

To ensure correct and consistent identification of prey items during the foraging and feeding observations at Minsener Oog, observers were trained at another Common Tern colony (Banter See, Wilhelmshaven, for details see Becker, 1996) with convenient observation conditions and with breeding phenology being two weeks ahead of Minsener Oog. At Minsener Oog, observations of foraging behaviour were carried out weekdays five times a week, using binoculars (Minox 10x42). Individual Common Terns were randomly selected from the foraging flock and their behaviour was tracked for exactly one minute. On any given observation day 25 observations of one minute each were carried out in each of the two foraging areas, unless weather conditions or breakup of foraging flocks terminated the observations before 25 minutes of individual tracking were completed. Between May 3<sup>rd</sup> and July 28<sup>th</sup> the observation effort amounted to 597 minutes and 935 minutes in the foraging areas northwest and southeast of Minsener Oog, respectively (Fig. 5.1).

During both foraging and feeding observations, prey items were identified to the lowest possible taxonomic level. Herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and twaite shad (*Alosa fallax*) could not be distinguished and were thus summarized as clupeids. Plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and sole (*Solea solea*) were noted as flatfish. Whiting (*Merlangius merlangius*) and cod (*Gadus morhua*) were recorded as ga-

dids; identification of squid, gobies (*Pomatoschistus spec.*), pipefish (*Syngnathus spec.*) and sandeel (*Ammodytes spec.* or *Hyperoplus spec.*) was also not possible down to species level. Judging from the stow net catches, where species identification was always carried out except for gobies, clupeids were mainly herring, flatfish were mainly plaice, gadids were mainly whiting, pipefish were mainly Nilsson's pipefish (*Syngnathus rostellatus*) and sandeel were mainly lesser sandeel (*Ammodytes tobianus*). Brown shrimp (*Crangon crangon*), eelpout (*Zoarces viviparus*), hooknose (*Agonus cataphractus*) and smelt (*Osmerus eperlanus*) could be identified to species level. If identification was not possible, prey items were recorded as "unidentified". In addition to the identification of the prey it was noted if the item was consumed by the successful forager itself or if the prey was carried away.

Prey group-specific length differences, as examined in earlier studies (e.g. Taylor, 1979), were not considered, because the length range of the majority of prey items observed was smaller than the potential bias inherent to length comparisons based on average bill length (Duffy and Jackson, 1986; Barrett et al., 2007).

#### OBSERVATIONS IN THE COLONY

Starting in the middle of May, clutches and eggs were counted every other day in a colony in the north of Minsener Oog, representing the majority of Common Tern breeding pairs on the island (Fig. 5.1). From the beginning of June chicks were regularly counted. Feeding observations were carried out during a total of 47 hours in May, 63 hours in June and 44 hours in July. Feeding observations were synchronized with the foraging observations described above. Feedings of partners and chicks were observed in units of two hours. Prey eaten by partners or chicks was identified as described above. Courtship feedings were observed between May 13<sup>th</sup> and June 13<sup>th</sup>. Eggs were present after May 22<sup>nd</sup>; first chicks were observed on June 11<sup>th</sup>. All chicks died during a storm flood on June 27<sup>th</sup>/28<sup>th</sup>. After that, partner feedings were again observed. Accordingly, observations of foraging (May 3<sup>rd</sup>–June 13<sup>th</sup>) and partner feedings (May 13<sup>th</sup>–June 13<sup>th</sup>) are subsequently referred to as "courtship 1", referring to both courtship feedings in the colony and provisioning of incubating females. The category courtship 1 also included prey caught and delivered to partners before colony formation. Prey captured and fed between June 14<sup>th</sup> and June 27<sup>th</sup> is labelled "chicks"; foraging and feeding observations were noted as "courtship 2" from June 28<sup>th</sup> until July 28<sup>th</sup>.

#### STOW NET FISHERIES

To account for the terns' prey supply, stow net catches were conducted at a fixed sampling station located in the immediate vicinity of both foraging areas and breeding sites of the Common Terns (Fig. 5.1). Stow nets are passive catching gear operated from an anchoring vessel, utilizing the water movement as encountered in rivers or in tidal marine areas such as the Wadden Sea. This gear is largely unselective and thus representative especially of pelagic fish (Breckling and Neudecker, 1994; Dänhardt and Becker, 2008), the terns' main

prey. Stow net catches were timed to represent prey composition during the breeding periods described above. The fishing campaigns took place on May 23<sup>rd</sup>, June 19<sup>th</sup> and July 9<sup>th</sup>/10<sup>th</sup> and were assumed to represent prey availability during the different periods within the terns' breeding season (see results). Haul duration was  $45 \pm 5$  minutes. The stretched mesh size decreased from 40 mm close to the mouth to 10 mm in the cod end. Water flow was recorded by means of four propeller flow meters (Hydrobios, Kiel). Absolute catch numbers were normalized to individuals caught per 10 000 m<sup>3</sup> filtered water volume by

$$\text{No}_{10000} = \text{No}_{\text{absolute}} / (\text{FC}_{\text{End}} - \text{FC}_{\text{Start}} \times 0.3 \times \text{Net}_{\text{Height}} \times \text{Net}_{\text{Width}}) \times 10000$$

with  $\text{No}_{10000}$  = fish numbers per 10 000 m<sup>3</sup> fished water volume,  $\text{No}_{\text{absolute}}$  = absolute fish numbers,  $\text{FC}_{\text{End}}$  = flowmeter count at the end of a haul,  $\text{FC}_{\text{Start}}$  = flowmeter count at the start of a haul, 0.3 = meters per rotation of the propeller flowmeter (value provided by manufacturer),  $\text{Net}_{\text{Height}}$  = net height in m (varying with the current pressure),  $\text{Net}_{\text{Width}}$  = net width in m (constant). The catches were sorted by species and individuals were counted. Species that occurred in the stow net catches but were not utilized by the terns were excluded from subsequent analyses.

#### STATISTICS

The approach of the present paper mostly required comparisons of proportions. Thus, only non-parametric tests were applied. The similarity between the composition of stow net catches, the prey items caught, eaten and carried away by the foraging terns and the feeding observations was quantified using Renkonen's percentage similarity coefficient (Renkonen, 1938; Wolda, 1981; Krebs, 1999), ranging from 0 (no similarity) to 100 (complete similarity). The index is expressed in percent (Krebs, 1999).

Prey items were classified to be of high or low quality according to their potential energy yield per unit foraging effort to the terns. This classification was based on information on specific energy content (Massias and Becker, 1990; Hislop et al., 1991; Pedersen and Hislop, 2001; Harris et al., 2008; Fischer, unpublished data), determining whether a prey item can be profitably utilized by the terns. Clupeids, gadids, gobies, sandeel and squid were classified high quality items, brown shrimp, pipefish, flatfish and hooknose were classified low quality items. Smelt and eelpout were not considered, because only single individuals were recorded. Differences in the distribution of proportions of high and low quality prey items were tested for significance using cross tables and subsequent chi<sup>2</sup>-tests. Test results were not considered, if more than 20% of the cells of the respective cross table were allocated an expected frequency of less than 5. A sequential Bonferroni test was performed to adjust significance levels according to an assumed experimentwise type I error rate of 5% (Sokal and Rohlf, 1995). All tests were carried out two-sided and were considered significant at  $p < 0.05$ .

## 5.4 RESULTS

### COMPOSITION OF STOW NET CATCHES AND TERN PREY

In the stow net samples all prey items could be identified. Herring was by far the most numerous species in all months, followed by Nilsson's pipefish in May and brown shrimp and gadids in July. All other items, including sandeel, were present in proportions of 1 % or less. Eleven classes of tern prey were identified. In order of decreasing percentage, clupeids, pipefish, brown shrimp, gadids and gobies were dominant integrated over the whole season but with variable weighting within the single breeding periods (Table 5.1). Despite their numerical dominance in the stow net catches, only one half to one third of prey caught by the terns was clupeids. Sandeel was not observed to be caught, but occurred in the feeding observations. The remaining five prey classes eelpout, flatfish, hooknose, smelt and squid were caught by the terns only occasionally and in low numbers. They were thus summarized as "others". Of all prey items caught 3–10 % could not be identified (Table 5.1).

### PREY UTILIZATION

The different prey classes were consumed in the same proportions as they were caught, both during the single breeding periods and integrated over the whole season. Of all consumed prey items 3–8 % could not be identified (Table 5.1).

Prey items carried away were made up mainly of clupeids, gadids and gobies. The exception was courtship 2, when no clupeids were carried away. The percentage of both caught and ingested clupeids decreased over the course of the breeding period from 44 % in courtship 1 to 8–9 % during the courtship 2 period. However, clupeids made up the largest part of the partner and chick feedings. Even though gadids were not among the most numerous species in the stow net catches, their share of prey caught, consumed and carried away increased over the course of the breeding period. This development was also seen in the feeding observations. Gobies were neither caught with the stow net in considerable numbers nor were they fed to partners (courtship) or chicks. They were observed to be caught, consumed and also carried away during both courtship periods, but not during the chick rearing period.

In all three periods, the percentage of both pipefish and brown shrimp utilized by the terns was higher than in the stow net catches. These two prey species were mostly eaten by the adult terns themselves, even during courtship 1 and chick rearing, when pipefish and brown shrimp, respectively, were caught by the terns in highest proportions of all prey (Table 5.1). During courtship 1, 20 % of the prey class "others" was carried away. This was attributed to squid, of which 70 % were carried away, even though this prey class was among the least numerous species in the stow net catches. Of all prey items carried away 7–33 % were not identified (Table 5.1).

Among all prey items recorded in the feeding observations, clupeids, gadids and sandeel were fed in highest proportions to both partners and chicks. Clupeids and gadids were also

**Table 5.1:** Proportions (%) of the Common Terns' main prey items. Results from the stow net catches, the foraging observations in the feeding areas (highlighted in grey) and the feeding observations in the colonies are given. All prey proportions are presented both by breeding period (courtship 1: May 3<sup>rd</sup>–June 13<sup>th</sup>, chicks: June 14<sup>th</sup>–June 27<sup>th</sup>, courtship 2: June 28<sup>th</sup>–July 28<sup>th</sup>) and integrated over the whole breeding season. The top four prey classes represent high quality food, the bottom two prey species represent low quality food. For definition of breeding periods and food quality see material and methods section. \*Feeding observations.

Prey class (%)	Courtship 1					Chicks					Courtship 2					Whole season				
	Stow net catches, May 23 <sup>rd</sup>	Caught	Consumed	Carried away	Feed. obs.*, May 13 <sup>th</sup> –June 13 <sup>th</sup>	Stow net catches, June 8 <sup>th</sup> & 19 <sup>th</sup>	Caught	Consumed	Carried away	Feed. obs.*, June 13 <sup>th</sup> –28 <sup>th</sup>	Stow net catches, July 9 <sup>th</sup> /10 <sup>th</sup>	Caught	Consumed	Carried away	Feed. obs.*, June 29 <sup>th</sup> –July 28 <sup>th</sup>	Stow net catches, all dates	Caught	Consumed	Carried away	Feed. obs.*, whole season
Clupeids	84	44	44	49	36	97	23	20	50	70	84	8	9	0	46	86	34	33	44	50
Gadids	1	3	2	11	12	0	4	3	17	15	4	12	9	67	36	3	5	4	18	20
Gobies	0	3	2	9	3	0	0	0	0	0	0	1	0	17	0	0	2	1	9	1
Sandeel	1	0	0	0	19	0	0	0	0	3	0	0	0	0	2	0	0	0	0	9
Brown shrimp	0	14	16	0	1	0	10	11	0	0	8	62	65	0	0	6	23	26	0	0
Pipefish	13	28	32	4	0	2	52	57	0	1	3	10	11	0	0	4	28	31	4	0
others	2	3	1	20	5	1	1	2	0	0	2	2	2	0	0	1	3	1	16	2
unidentified	0	3	3	7	25	0	10	8	33	10	0	5	5	17	14	0	5	4	11	17
n	533	344	299	45	530	726	71	65	6	430	3086	110	104	6	412	4345	525	468	57	1372

caught, ingested and carried away by the terns from the foraging areas observed, whereas sandeels were never seen during the foraging observations and only rarely caught by the stow net. Pipefish and brown shrimp were hardly recorded in the feeding observations, which is in agreement with these species being hardly carried away from the foraging area. “Other” prey items were usually not seen in the feeding observations, except for squid, which made up 4% of prey fed to partners during courtship 1. The percentage of unidentified prey ranged from 10 to 25 % (Table 5.1).

#### SELECTION RATES

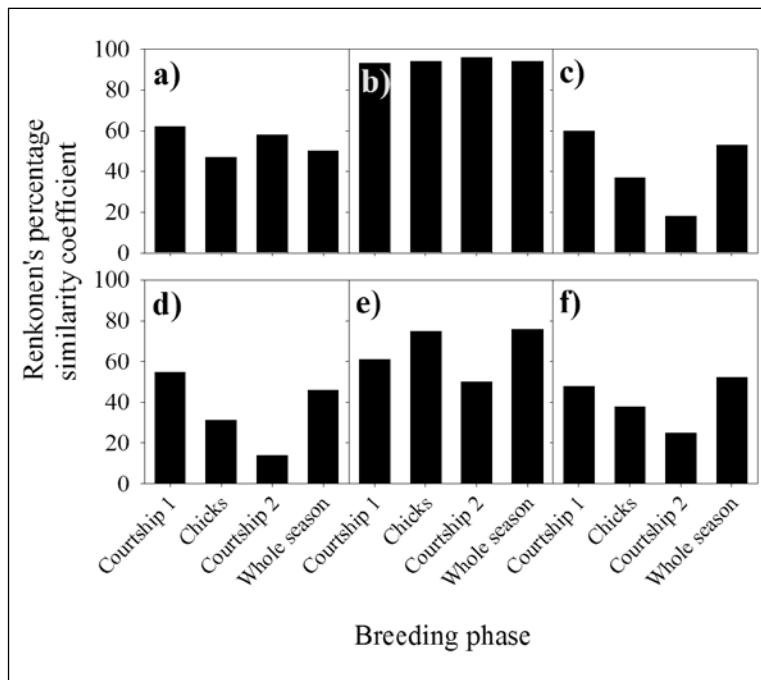
Integrated over the whole season, gobies, gadids and clupeids were transported off the foraging area most often, whereas brown shrimp and pipefish were hardly ever seen to be carried away, both within the single breeding periods and integrated over the whole season. Among the three prey items carried away most often, only the share of gadids remained relatively constant throughout the season. In gobies and clupeids there were marked fluctuations in selection rates with periods when they were not carried out of the foraging area at all. Of all unidentified prey items, 17–29% were carried away (Table 5.2).

**Table 5.2:** Number of prey items selected to be carried away expressed as percentage of prey caught. The selection rates are presented both by breeding period (courtship 1, chicks and courtship 2) and integrated over the whole breeding season. The top three prey classes represent high quality food, the bottom two prey species represent low quality food. Note that sandeel, though present in courtship and chick feedings, has not been observed to be caught in the foraging areas. For definition of breeding periods and food quality see material and methods.

	Courtship 1	Chicks	Courtship 2	Whole season
Clupeids	14	19	0	14
Gadids	42	33	31	36
Gobies	44	0	100	50
Brown shrimp	0	0	0	0
Pipefish	2	0	0	1
Unidentified	25	29	17	24

#### SIMILARITY IN PREY COMPOSITION

Stow net catches did not match the composition of prey caught by the terns very closely, which was the case in all three periods and integrated over the entire breeding season (Fig. 5.2a). The terns consumed prey in the same proportions as they caught it, being expressed in >90% similarity. This very high agreement remained constant throughout the breeding season



**Figure 5.2:** Renkonen's percentage similarity index of prey proportions in the stow net catches (stow net), of prey caught by the terns in the foraging areas (prey caught), prey eaten by the successful forager itself (prey consumed), prey carried out of the foraging area (prey carried away) and prey fed to partners or chicks. Values range from 0 (no similarity) to 100 (complete similarity). For definitions of breeding phases see text. A) stow net vs. prey caught, b) prey caught vs. prey consumed, c) prey caught vs. prey carried away, d) prey consumed vs. prey carried away, e) prey carried away vs. prey fed to chicks and partners, f) prey caught vs. prey fed to chicks and partners.

(Fig. 5.2 b). In contrast, similarity coefficients of prey caught vs. prey carried away were decreasing as the season progressed (Fig. 5.2 c). A decline over the course of the season was also noted in the similarity between prey consumed and prey carried away, reaching a minimum of less than 20% during the courtship 2 period (Fig. 5.2 d). The composition of prey carried away vs. prey fed to partners and chicks revealed the second-best match of all comparisons (Fig. 5.2 e). The similarity between prey caught in the foraging areas and fed to partners and chicks decreased from 50% during courtship 1 to 30% during courtship 2 (Fig. 5.2 f). In four out of six comparisons there was a tendency towards lower similarity as the season progressed with lowest similarity coefficients during the courtship 2 period (Fig. 5.2).

#### PROPORTION OF HIGH AND LOW QUALITY FOOD

The share of high quality food was significantly greater in the stow net catches than in the prey caught by the terns in all breeding periods examined (Table 5.3). This was mainly attributed to the large proportion of herring (Table 5.1). The relative contribution of high and low quality items to prey caught and prey consumed did not differ.

A significantly greater percentage of high quality prey organisms was carried out of the foraging area compared to both prey caught and prey consumed by the forager itself (Table 5.3). As already indicated by the comparatively large proportions of high quality prey being carried out of the foraging area (Tables 5.1 and 5.2), prey fed to partners and chicks contained significantly more high quality items than prey caught in the foraging area (Table 5.3). The composition of prey carried out of the foraging area did not match that of prey fed to partners and chicks. During courtship 1, slightly less high quality items were fed than carried



away and almost one quarter of all prey items fed was not identified. During the chicks and courtship 2 periods, statistical comparisons were not possible due to the low number of observations of prey being carried out of the foraging area (Table 5.3).

Throughout the season, the share of high quality items remained fairly constant in the stow net catches, the prey carried away and fed to partners and chicks. In contrast, there was a seasonal decline in the proportions of high quality prey caught and consumed (Table 5.3).

**Table 5.3:** Relative contribution of high quality food (clupeids, gadids, gobies, sandeel and squid), low quality food (brown shrimp, flatfish, hooknose and pipefish) and unidentified prey (unid.) to prey composition during courtship and chick periods. Percentage of high quality, low quality and unidentified prey and sample size are given. Largest proportions are highlighted in bold. Results of chi<sup>2</sup>-tests (chi<sup>2</sup>-values and Bonferroni-corrected significance levels) are given. n. s. = not significant, \*\*\* =  $p < 0.001$  (bold). Degrees of freedom = 2 in all cases. \*Results were not considered in cross tables where the expected frequency was less than 5 in more than 20% of the cells (indicated as e. g. 33.3% < 5).

	Courtship 1 high/low/unid. (n)	Chicks high/low/unid. (n)	Courtship 2 high/low/unid. (n)	Whole season high/low/unid. (n)
Stow net	<b>87.2</b> /12.8/0.0 (533)	<b>97.9</b> /2.1/0.0 (726)	<b>89.0</b> /11.0/0.0 (3055)	<b>90.3</b> /9.7/0.0 (8690)
vs. caught	52.9/43.6/3.5 (344)	26.8/ <b>63.4</b> /9.9 (71)	22.2/ <b>74.1</b> /3.7 (108)	42.9/ <b>52.4</b> /4.8 (5259)
Chi <sup>2</sup> /p	132.03/***	430.32/***	33.3% < 5 <sup>a</sup>	1285.48/***
Caught	<b>52.9</b> /43.6/3.5 (344)	26.8/ <b>63.4</b> /9.9 (71)	22.2/ <b>74.1</b> /3.7 (108)	42.9/ <b>52.4</b> /4.8 (525)
vs. consumed	48.2/ <b>48.8</b> /3.0 (299)	23.1/ <b>69.2</b> /7.7 (65)	18.6/ <b>78.4</b> /2.9 (102)	38.0/ <b>57.9</b> /4.1 (468)
Chi <sup>2</sup> /p	1.77/n. s.	0.54/n. s.	33.3% < 5 <sup>a</sup>	3.07/n. s.
Caught	<b>52.9</b> /43.6/3.5 (344)	26.8/ <b>63.4</b> /9.9 (71)	22.2/ <b>74.1</b> /3.7 (108)	42.9/ <b>52.4</b> /4.8 (525)
vs. carried away	<b>84.4</b> /8.9/6.7 (45)	<b>66.7</b> /0.0/33.3 (6)	<b>83.3</b> /0.0/16.7 (6)	<b>82.5</b> /7.0/10.5 (57)
Chi <sup>2</sup> /p	20.16/***	50% < 5 <sup>a</sup>	67% < 5 <sup>a</sup>	42.53/***
Consumed	48.2/ <b>48.8</b> /3.0 (299)	23.1/ <b>69.2</b> /7.7 (65)	18.6/ <b>78.4</b> /2.9 (102)	38.0/ <b>57.9</b> /4.1 (468)
vs. carried away	<b>84.4</b> /8.9/6.7 (45)	<b>66.7</b> /0.0/33.3 (6)	<b>83.3</b> /0.0/16.7 (6)	<b>82.5</b> /7.0/10.5 (57)
Chi <sup>2</sup> /p	25.54/***	50% < 5 <sup>a</sup>	67% < 5 <sup>a</sup>	52.98/***
Caught	<b>52.9</b> /43.6/3.5 (344)	26.8/ <b>63.4</b> /9.9 (71)	22.2/ <b>74.1</b> /3.7 (108)	42.9/ <b>52.4</b> /4.8 (525)
vs. fed	<b>74.3</b> /1.1/24.5 (530)	<b>89.1</b> /1.2/9.8 (430)	<b>85.2</b> /0.7/14.1 (412)	<b>82.2</b> /1.0/16.8 (1372)
Chi <sup>2</sup> /p	282.20/***	265.85/***	343.18/***	780.63/***
Carried away	<b>84.4</b> /8.9/6.7 (45)	<b>66.7</b> /0.0/33.3 (6)	<b>83.3</b> /0.0/16.7 (6)	<b>82.5</b> /7.0/10.5 (57)
vs. fed	<b>74.3</b> /1.1/24.5 (530)	<b>89.1</b> /1.2/9.8 (430)	<b>85.2</b> /0.7/14.1 (412)	<b>82.2</b> /1.0/16.8 (1372)
Chi <sup>2</sup> /p	20.63/***	50% < 5 <sup>a</sup>	50% < 5 <sup>a</sup>	16.92/***

The impact of unidentified prey items on  $\chi^2$ -test results was subtle. After leaving them out (not shown), the expected frequency in the cells of the cross tables “stow net vs. prey caught” and “prey caught vs. prey consumed” did not go below 5 anymore (see material and methods) and the tests revealed highly significant differences in the respective proportions of high and low quality food. In all other test results, significance patterns did not change.

## 5.5 DISCUSSION

### METHODOLOGICAL ASPECTS

The division of the study period into courtship 1, chicks and courtship 2 was more or less arbitrary, because the foraging and feeding observations were not individual-based, e. g. by marking birds or by direct and uninterrupted observations between prey capture and subsequent feeding to partners (Taylor, 1979) or chicks. Thus, it could not be decided, if a prey item carried away from the foraging area would be fed to the mate or to a chick. However, towards the end of courtship 1, there was only a short temporal overlap in which prey carried out of the foraging areas could have been fed to both incubating partners and chicks. Moreover, due to the abrupt termination of the chick rearing period on June 27<sup>th</sup>/28<sup>th</sup>, the periods chicks and courtship 2 could be reliably distinguished. The actual recipients of food carried out of the foraging area were thus likely to be correctly represented by the classification of the breeding periods.

The percentage of unidentified items was usually <10%, except for those carried away during the periods chicks and courtship 2 and during the feeding observations (Table 5.1). The high proportions of unidentified prey being carried away suggest that it may have been mostly high quality items. Moreover, low quality prey items, such as brown shrimp and pipefish, would have been more easily identified. Nevertheless, the uncertainty about the bias brought about by unidentified prey organisms remains, which is one major disadvantage of foraging and feeding observations in the field (Barrett et al., 2007).

### FORAGING OBSERVATIONS

The finding of the present study that profitable prey is carried away and fed to partners or chicks at much higher rates than low quality prey items agrees both with the literature (Taylor, 1979; Shealer, 1998; McLeay et al., 2009) and the predictions of the central place foraging theory (Orians and Pearson, 1979). Even though fish being caught could not be followed to its final destination, e. g. in the colony, there is support for assuming that fish seen being carried away was indeed brought into the colony to be fed to chicks or mates. Following radio-tracked Common Terns revealed that their flight course to and especially from the foraging areas was rectilinear and performed at high speed (Becker et al., 1991; 1993), indicating that the birds fly straight back to the colony. This is further supported by own observations during the field work of the present study (Freseman, unpublished data), that terns left the foraging

area in the majority of cases in the direction of the breeding colony. Those terns not leaving towards the colony on Minsener Oog headed either west or east, where other small colonies are located on neighboring islands (Wangerooge and Mellum). These birds may use the same foraging areas as their conspecifics breeding on Minsener Oog.

The rate at which prey was carried away during the periods chicks and courtship 2 must be interpreted with caution, since only six observations were available during each period. However, the results matched those of the courtship 1 period as well as the literature (e.g. Taylor, 1979; McLeay et al., 2009).

The two foraging locations examined in the present study represent two out of five foraging sites identified by means of radio-telemetry: “Wattengebiete” and “Oldeoogrinne”, which have been the destination of 28.5% and 18.4% of foraging flights, respectively (Becker et al., 1991, 1993). Nevertheless, Common Terns have been found to utilize a wide variety of habitats within their foraging range around Minsener Oog which were located outside the area of investigation (Becker et al., 1991, 1993). However, the finding that Common Terns select high quality prey for provisioning and tend to eat low quality prey themselves is largely independent of the overall relevance of a given foraging site. Thus it remains valid even if an area is only secondarily used for foraging. Delivering high quality prey to partners or chicks appears to be a general behavioural pattern in the Common Tern not confined to a single breeding period such as courtship (Taylor, 1979), as indicated by high quality items preferentially being carried away in all three periods. Similar results have been reported for auks (Davoren and Burger, 1999) and other tern species (Shealer, 1998; McLeay et al., 2009). Even when utilizing anthropogenic food sources, this pattern becomes evident, as reported by Dänhardt and Becker (2008), who found that Common Terns foraging at a cooling water outlet of a power plant carried away 28% of clupeids, 50% of smelt and 17% of gobies (high quality food; Massias and Becker, 1990) as compared to 0% of flatfish, pipefish and brown shrimp, respectively (low quality food; Massias and Becker, 1990).

Individual decisions what to do with a given prey item after having caught it are a trade-off between somatic (eating the prey) and reproductive (feeding the prey to partners or chicks) investment (Swihart and Johnson, 1986). Despite the relatively large proportions of high quality food being carried away and fed to partners or chicks, the bulk of both high and low quality prey was eaten by the foraging tern itself. This may have been indicative of a favorable food situation in 2007, providing a surplus of profitable food items also to the adult forager. Nevertheless, clupeids were not utilized in proportions similar to those found in the stow net catches. This may be due to prey species-specific availability changing with the tide (e.g. Becker and Specht, 1991; Becker et al., 1993; Wendeln et al., 1994). Unfortunately, this aspect could not be covered by the stow net fisheries. The proportions of clupeids decreased after the courtship 1 period despite consistently high herring abundance throughout the whole breeding season. Starting in the last quarter of June, average wind speed increased causing turbulent water surfaces, most likely exacerbating foraging conditions. In addition to

a hampered visibility brought about by turbulent water surfaces (Dunn, 1973), pelagic schooling fish such as clupeids may avoid too turbulent water strata. Accordingly, the foraging success of the Common Terns was highest at low wind speeds with e.g. 74% of clupeids being caught at wind speeds of 1–2 Beaufort, but reduced at >6 Beaufort (Frank, 1992; Freseemann, unpublished data).

During the study period, high quality prey species were more abundant than low quality prey, but large proportions of low quality food were caught and consumed by the foraging terns in all three periods. As with the proportions of clupeids described above, this may also be due to prey species-specific availability changing within the tidal cycle. However, the most abundant low quality prey, the pipefish, is a pelagic species and its availability to the terns is probably equal to that of clupeids. Still 10 to 60% of tern prey was pipefish. Alternatively, utilizing low quality prey when high quality prey is available could indicate that selective foraging does not occur. Following the idea that foraging should generally be aimed at maximizing energy yield per unit foraging effort (Pyke, 1984; Ydenberg et al., 1994), choosing to consume low quality prey in the presence of high quality prey suggests that Common Terns do not select prey items prior to catching them. A certain amount of energy available for foraging would go into catching low quality food, which may be energetically justified given the lower effort required to self-feed. The probability of catching high quality food could be increased by choosing foraging sites where encounter with high quality food is more likely (e.g. Becker et al., 1993; Camphuysen and Webb, 1999), but the catch frequency of low quality prey may provide information to the foraging tern about the overall food situation and, as a consequence, influence its partitioning between somatic and reproductive investment.

#### FEEDING OBSERVATIONS

In years of poor food supply foraging trips may be longer due to lower rates of successful foraging attempts or lower rates of catching high quality food being worthwhile delivering to partners or chicks (Frank and Becker, 1992; Monaghan, 1996). Based on our results, it can be assumed that high quality prey will be used for provisioning disproportionately often, suggesting that the share of low quality food ending up the colony is in turn indicative of the availability of high quality food in the sea. In 2007, the overall food situation was obviously sufficient for low quality food not to be used for provisioning. In other years, even low quality food was utilized to provision mates or chicks (Becker et al., 1987; Frick and Becker, 1995; Schreiber, unpublished data).

The prey being used for provisioning was best reflected by the prey being carried out of the foraging area. Prey compositions would have been even more similar when sandeel was not considered. Sandeel was frequently noted in the feeding observations, but it was not caught with the stow net and it was also not observed to be caught in the foraging areas. Sandeel inhabits the shallow sandbanks north of Minsener Oog that were neither covered by the stow net catches nor by the foraging observations. These areas are however frequented for foraging.

ging by the Common Terns (Becker et al., 1991, 1993). The increase in gadid proportions in the courtship 2 period was attributed to a whiting invasion into the Wadden Sea, reaching its maximum in the beginning of July when partner feedings were again observed (Dänhardt and Becker, 2008).

#### CONCLUSIONS

The data presented here support the framework of the central place foraging theory. Below an (unknown) threshold when adult survival would be compromised, individual decisions by the adult terns can be viewed as a mechanism to buffer their reproductive success against environmental variability, including varying food supplies and impaired prey availability. The finding that high quality prey items are preferentially carried out of the foraging area suggests that in turn large proportions of low quality food items such as pipefish or brown shrimp being observed to be fed to partners or chicks may indicate a confined availability of high quality food and, consequently, poor prospects of good breeding performance.

The terns' phenotypic plasticity may also be a crucial aspect to consider when colony-based diet data are to be used to draw inferences about the state and abundance of fish populations being utilized by a given seabird species. Given the preferential delivery of high quality items to partners and chicks, the abundance of high quality fish in the sea would be overestimated when calculated from colony-based seabird diet studies. However, this bias due to preferring high quality prey for provisioning applies only to seabird species delivering whole and undigested prey to partners and chicks, but not to species swallowing their prey at sea and regurgitating stomach contents to partners and chicks at the colony. In these species, bias may emerge from differential digestion of body parts and tissue (Barrett et al., 2007) and prey selecting prey before catching it.

#### ACKNOWLEDGMENTS

We wish to thank Mellumrat e.V. and Wasser- und Schifffahrtsamt Wilhelmshaven for supporting field work on Minsener Oog and Captain K.-H. Rostek and his crew for their professionalism during the fish sampling. We also thank H. Mühlichen for carrying out the feeding observations, G. Wagenknecht for his support in collecting the data on breeding performance of the Common Terns and J. Schreiber for providing additional information on food quality used for provisioning in 2006. The project received financial support from the Niedersächsische Wattenmeerstiftung (53-NWS-41/04).

## 5.6 REFERENCES

- Aebischer NJ, Coulson JC and Colebrooke JM (1990) Parallel long-term trends across four marine trophic levels and weather. *Nature* 347: 753–755.
- Barrett RT (2007) Food web interactions in the southwestern barents sea: Black-legged kittiwakes *Rissa tridactyla* respond negatively to an increase in herring *Clupea harengus*. *Marine Ecology Progress Series* 349: 269–276.
- Barrett RT, Camphuysen CJ, Anker-Nilssen T, Chardine JW, Furness RW, Garthe S, Hüppop O, Leopold MF, Montevecchi WA and Veit RR (2007) Diet studies of seabirds: A review and recommendations. *ICES Journal of Marine Science* 64: 1675–1691.
- Becker PH (2003) Biomonitoring with birds. In Markert B., Breure T and Zechmeister H (Eds.) *Bioindicators and biomonitors – principles, concepts and applications (trace metals and other contaminants in the environment)*. Elsevier, Amsterdam, pp. 677–737.
- Becker PH and Specht R (1991) Body mass fluctuations and mortality in Common Tern *Sterna hirundo* chicks dependent on weather and tide in the Wadden Sea. *Ardea* 79: 45–56.
- Becker PH, Frank D and Walter U (1987) Geografische und jährliche Variation der Ernährung der Flusseeeschwalbe (*Sterna hirundo*) an der Nordseeküste. *Journal für Ornithologie* 128: 457–475.
- Becker PH, Frank D and Sudmann SR (1993) Temporal and spatial pattern of Common Tern (*Sterna hirundo*) foraging in the Wadden Sea. *Oecologia* 93: 389–393.
- Becker PH, Frank D, Sudmann S R and Wagener M (1991) Funkpeilung von Flusseeeschwalben (*Sterna hirundo*) bei der Nahrungssuche im Wattenmeer. *Seevögel* 12 (3): 52–61.
- Boyd IL, Wanless S and Camphuysen CJ (2006) *Top predators in marine ecosystems*. Cambridge University Press, Cambridge. 378 pp.
- Breckling P and Neudecker T (1994) Monitoring the fish fauna in the Wadden Sea with stow nets (part 1): A comparison of demersal and pelagic fish fauna in a deep channel. *Archive of Fisheries and Marine Research* 42: 3–15.
- Burness GP, Morris RD and Bruce JP (1994) Seasonal and annual variation in brood attendance, prey type delivered to chicks, and foraging patterns of male Common Terns *Sterna hirundo*. *Canadian Journal of Zoology* 72: 1243–1251.
- Cairns DK (1987) Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261–271.
- Camphuysen CJ and Webb A (1999) Multi-species feeding associations in North Sea seabirds: Jointly exploiting a patchy environment. *Ardea* 87: 177–197.
- Dänhardt A and Becker PH (2008) Die Bedeutung umweltbedingter Verteilungsmuster von Schwarmfischen für Seevögel im Ökosystem Niedersächsisches Wattenmeer. Institute of Avian Research, Wilhelmshaven. Final project report, 248 pp. (in German).
- Dänhardt A and Becker PH (2010) Does small-scale vertical distribution of juvenile schooling fish affect prey availability to surface-feeding seabirds in the Wadden Sea? *Journal of Sea Research in press*.
- Daunt F, Peters G, Scott B, Grémillet D and Wanless S (2003) Rapid-response recorders reveal interplay between marine physics and seabird behaviour. *Marine Ecology Progress Series* 55: 283–288.
- Davoren GK and Burger AE (1999) Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets *Animal Behaviour* 58: 853–863.
- Davoren GK and Montevecchi WA (2003) Signals from seabirds indicate changing biology of capelin stocks. *Marine Ecology Progress Series* 258: 253–261.
- Duffy DC and Jackson S (1986) Diet studies of seabirds: A review of methods. *Colonial Waterbirds* 9: 1–17.
- Dunn EK (1973) Changes in fishing ability of terns associated with windspeed and sea surface conditions. *Nature* 244: 520–521.
- Einoder LD (2009) A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research* 95: 6–13.
- Elliott KH, Woo K, Gaston AJ, Benvenuti S, Dall'antonia L and Davoren GK (2008) Seabird foraging behaviour indicates prey type. *Marine Ecology Progress Series* 354: 289–303.

- 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.
- Frank D and Becker PH (1992) Body mass and nest reliefs in Common Terns *Sterna hirundo* exposed to different feeding conditions. *Ardea* 80: 57–69.
- Frederiksen M, Wanless S, Harris MP, Rothery P and Wilson LJ (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology* 41: 1129–1139.
- Frick S and Becker PH (1995) Unterschiedliche Ernährungsstrategien von Fluss- und Küstenseeschwalbe (*Sterna hirundo* und *S. paradisaea*) im Wattenmeer. *Journal für Ornithologie* 136: 47–63.
- Furness RW (2002) Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. *ICES Journal of Marine Science* 59: 261–269.
- Furness RW (2006) Responses of seabirds to depletion of food fish stocks. *Journal of Ornithology* 148 (Supplement 2): 247–252.
- Garthe S, Grémillet D and Furness RW (1999) At-sea activity and foraging efficiency in chick-rearing northern gannets *Sula bassana*: A case study in Shetland. *Marine Ecology Progress Series* 185: 93–99.
- Greenstreet SPR, Becker PH, Barrett RT, Fossum P and Leopold MF (1999) Consumption of pre-recruit fish by seabirds and the possible use of this as an indicator of fish stock recruitment. In Furness RW and Tasker ML (Eds.) *Diets of seabirds and consequences of changes in food supply*. ICES Cooperative Research Report 232: 6–17.
- Grémillet D, Kuntz G, Delbart F, Mellet M, Kato A, Robin J-P, Chaillon P-E, Gendner J-P, Lorentsen S-H and Le Mayo Y (2004) Linking the foraging performance of a marine predator to local prey abundance. *Functional Ecology* 18: 793–801.
- Hamer KC, Humphreys EM, Garthe S, Hennicke J, Peters G, Grémillet D, Phillips RA, Harris MP and Wanless S (2007) Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: Flexibility, consistency and constraint. *Marine Ecology Progress Series* 338: 295–305.
- Harris MP, Newell M, Daunt F and Spe JR (2008) Snake pipefish *Entelurus aequoreus* are poor food for seabirds. *Ibis* 150: 413–415.
- Hislop JRG, Harris MP and Smith JGM (1991) Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *Journal of Zoology* 224: 501–517.
- ICES (2002) Report of the ICES advisory committee on ecosystems. ICES Cooperative Research Report 254. 129 pp.
- Krebs CJ (1999) *Ecological methodology*, Addison Wesley Longman, Menlo Park, Reading, New York, Harlow, Don Mills, Amsterdam, Madrid, Sidney, Mexico City.
- Massias A and Becker PH (1990) Nutritive value of food and growth in Common Tern (*Sterna hirundo*) chicks. *Ornis Scandinavica* 21: 187–194.
- McLeay LJ, Page B, Goldsworthy SD, Ward TM and Paton DC (2009) Size matters: Variation in the diet of chick and adult crested terns. *Marine Biology* 156: 1765–1780.
- Monaghan P (1996) Relevance of the behaviour of seabirds to the conservation of marine environments. *Oikos* 77: 227–237.
- Montevocchi WA (1993) Birds as indicators of change in marine prey stocks. In Furness RW and Greenwood JJD (Eds.): *Birds as monitors of environmental change*, p. 217–266, Chapman and Hall, London.
- Orians GH and Pearson NE (1979) On the theory of central place foraging. In Horn DJ, Mitchell RD and Stairs GR (Eds.): *Analysis of Ecological Systems*, pp. 154–177. Ohio State University Press., Columbus, Ohio.
- Pedersen J and Hislop JRG (2001) Seasonal variations in the energy density of fishes in the North Sea. *Journal of Fish Biology* 59: 380–389.
- Piatt JF and Sydeman WJ (2007) Seabirds as indicators of marine ecosystems. *Marine Ecology Progress Series* 352: 199–309.
- Pyke GH (1984) Optimal foraging theory: A critical review. *Annual Review of Ecological Systems* 15: 523–575.

- Renkonen O (1938) Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. Ann Zoo Soc Fenn Vanamo 6: 1–231.
- Schwemmer P, Adler S, Guse N, Markones N and Garthe S (2009) Influence of water flow velocity, water depth and colony distance on distribution and foraging patterns of terns in the Wadden Sea. Fisheries Oceanography 18: 161–172.
- Shealer DA (1998) Size-selective predation by a specialist forager, the Roseate tern. The Auk, 115: 519–525.
- Sokal RR and Rohlf FJ (1995) Biometry, WH Freeman, New York.
- Swihart RK and Johnson SG (1986) Foraging decision of American robins: Somatic and reproductive tradeoffs. Behavioural Ecology and Sociobiology 19: 275–282.
- Taylor I (1979) Prey selection during courtship feeding in the Common Tern. Ornis Scandinavica 10: 142–144.
- Walter U and Becker PH (1998) Influence of physical factors and fishing activity on the occurrence of seabirds scavenging around shrimpers in the Wadden Sea. Senckenbergiana maritima 29: 155–162.
- Weimerskirch H (1998) Can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. Journal of Animal Ecology 67: 99–109.
- Weimerskirch H, Mougey T and Hindermeyerx (1997) Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: Natural variation and experimental study. Behavioural Ecology 8: 635–643.
- Wendeln H, Mickstein S and Becker PH (1994) Auswirkungen individueller Ernährungsstrategien von Flusseeschwalben (*Sterna hirundo*) auf die Anwesenheit am Koloniestandort. Vogelwarte 37: 290–303.
- Wolda H (1981) Similarity indices, sample size and diversity. Oecologia 50: 296–302.
- Ydenberg RC, Welham CVJ, Schmid-Hempel R, Schmid-Hempel P and Beauchamp G (1994) Time and energy constraints and the relationships between currencies in foraging theory. Behavioural Ecology 5: 28–34.



## DANKSAGUNG

Der erste und herzlichste Dank gebührt Herrn Prof. Dr. Peter H. Becker für die Betreuung dieser Arbeit sowie für seine zuverlässige und professionelle Unterstützung bei allen Belangen der Forschungsarbeiten. Frau PD Dr. Ingrid Kröncke sei für das Zweitgutachten herzlich gedankt. Die erfolgreiche Bearbeitung komplexer wissenschaftlicher Fragestellungen ist ohne weitreichende Kooperationen, Synergien und die Unterstützung einer Vielzahl von Menschen und Institutionen kaum vorstellbar. Ein besonderer Dank gilt daher den Kooperationspartnern, die durch ihre vielfältige fachliche und logistische Unterstützung die Arbeiten für diese Promotion erst ermöglicht haben: Prof. Dr. Gerd Liebezeit (Universität Oldenburg, ICBM Terramare), Dipl. Biol. Jens-Peter Herrmann und Prof. Dr. Axel Temming (Universität Hamburg, Institut für Hydrobiologie und Fischereiwissenschaft), Dr. Gerald Millat und Dipl. Biol. Peter Südbeck (Nationalparkverwaltung Niedersächsisches Wattenmeer) sowie Dr. Alexander Bartholomä und Prof. Dr. Burghard Flemming (Forschungsinstitut Senckenberg, Abteilung für Meeresforschung).

Die logistische Unterstützung erfolgte ganz wesentlich durch Gunda Blödown und Monika Scholl von der Terramare Bibliothek, Helmo Nicolai, Rudolf Ellen, Waldemar Siewert und Ilja Gorgiev von der Terramare Werkstatt, Dörthe Zilian und Heike Scheele vom Sekretariat/Finanzbuchhaltung, Elke Ahrensfeld für Laborangelegenheiten und den netten Plausch am Kaffeeautomaten und Bernhard Seidler für gelegentliche Schiffsfahrten.

Die Kapitäne Karl-Heinz Rostek (MS „Conger“, Varel) und Jens Tattje (MS „Marion Albrecht“, Harlesiel) haben durch ihre hoch flexible Einsatzbereitschaft, die ein Untersuchungsgebiet wie das Wattenmeer erfordert, die Voraussetzung für diese Dissertation geschaffen.

Die fleißigen Hände bei der Fangaufarbeitung an Bord der MS „Conger“ gehörten Alexander Braasch, Sebastian Broders, Tanja Dänhardt, Henriette Dries, Ariane Duse, Volkert Erdwiens, Axel Ernst, Viola Fischer, Tido Freseman, Marc Hufnagl, Rudi Jenderze, Horst Kuhlmann, Ansgar Meyer, Jesko Peschutter, Kevin Schneider, Rolf Schneider, Andreas Wilken und Johann Wilken. Ein besonderer Dank gilt dem „wichtigsten Besatzungsmitglied“ der MS „Conger“, Liesbeth Rostek, die für das leibliche Wohl an Bord sorgte. Bei den Hamen- (2005) und Schleppnetzfishereien (2007) mit MS „Marion Albrecht“ halfen Christian Dethleffsen, Tido Freseman, Daphne Joost, Stefan Natterer, Rainer und Heinzl. Ihnen allen sei herzlich für die tatkräftige Unterstützung und die schönen wenn auch anstrengenden Stunden auf See gedankt.

Die Wissenschaftler vom Banter See (Alexander Braasch, Anna Ostendorp und Jana Sprenger) und von Minsener Oog (Tido Freseman, Henrike Mühlichen und Jochen Schreiber) widmeten sich sehr professionell der anspruchsvollen Aufgabe der Fütterungsbeobachtung und fügten der Dissertation dadurch einen weiteren essentiellen Datenbaustein hinzu.

Das Wasser- und Schifffahrtsamt Wilhelmshaven gewährte logistische Unterstützung bei der Unterbringung auf Minsener Oog sowie beim Transport von Forschern, Geräten und Verpflegung dorthin.

Dem Mellumrat e.V. und seinem Schutzgebietsreferenten für Minsener Oog, Dr. Dietrich Frank, sei für die Unterbringung auf Minsener Oog und die Unterstützung vor Ort herzlich gedankt.

Die fachlichen Diskussionen mit Dr. Loes Bolle (TMAP Fish expert group, IMARES, Wageningen), Dipl. Biol. Thorsten Brandt (Staatliches Fischereiamt Bremerhaven), Dr. Peter Breckling (Bundesfischereiverband), Dipl. Biol. Britta Diederichs (TMAP Fish expert group, Nationalparkamt Schleswig-Holsteinisches Wattenmeer, Tönning), Dr. Marc Hufnagl (Universität Hamburg, Institut für Hydrobiologie und Fischereiwissenschaft), Dr. Zwanette Jäger (TMAP Fish expert group, Ziltwater Advies, Holwjerde), Dr. Harald Marencic (TMAP Fish expert group, Common Wadden Sea Secretariat), Dr. Tom Neudecker (TMAP Fish expert group, vTI, Institut für Seefischerei, Hamburg), Dipl. Biol. Philip Oberdörffer (Landwirtschaftskammer Weser-Ems), Dipl. Biol. Jörg Scholle (TMAP Fish expert group, BioConsult), Dr. Daniel Stepputtis (vTI, Institut für Ostseefischerei, Rostock), Dr. Ralf Vorberg (TMAP Fish expert group, Marine Science Service) und Dr. Christopher Zimmermann (vTI, Institut für Ostseefischerei, Rostock) haben sehr zum Erkenntnisgewinn und der kritischen Betrachtung der Forschungsergebnisse beigetragen.

Danken möchte ich von Herzen meiner Frau Tanja und meiner Tochter Amanda, deren Rücksicht aber auch deren Anwesenheit mir gezeigt hat, dass Familie und Wissenschaft durchaus miteinander vereinbar sein können.

Die finanzielle Unterstützung der Niedersächsischen Wattenmeerstiftung (53-NWS-41/04) sei zu guter Letzt ausdrücklich gewürdigt.

## LEBENS LAUF ANDREAS DÄNHARDT

---

Suerhoper Brunnenweg 13 a  
 21244 Buchholz in der Nordheide  
 Tel.: 041 86/89 16 14  
 Mobil: 01 79/5 17 15 36  
 E-mail: andreas@daenhardt.com

**Staatsangehörigkeit** Deutsch  
**Geburtsdatum** 18. März 1973 in Hamburg  
**Familienstand** Verheiratet, 1 Kind

### Universitätsausbildung

**1996–1998** Grundstudium Biologie an der Universität Hamburg  
**1998–2003** Hauptstudium an der Universität Hamburg  
 Hauptfach: Hydrobiologie und Fischereiwissenschaft  
 1. Nebenfach: Angewandte Botanik  
 2. Nebenfach: Naturschutz  
 3. Nebenfach (freiwillig, ohne Prüfung): Biochemie  
**2003** Abschluss Diplom-Biologe an der Universität Hamburg,  
 Diplomarbeit: „Ernährungskondition von Sprottenlarven im Bornholmbecken“,  
 betreut von Prof. Dr. Axel Temming  
**2005–2008** Promotion am Institut für Vogelforschung „Vogelwarte Helgoland“  
 in Wilhelmshaven bei Prof. Dr. Peter H. Becker im Drittmittelprojekt  
 „Die Bedeutung umweltbedingter Verteilungsmuster von Schwarmfischen  
 für Seevögel im Niedersächsischen Wattenmeer“

### Berufliche Tätigkeiten

**08.–10.2003** Wissenschaftlicher Mitarbeiter am Johann Heinrich von Thünen-Institut,  
 Institut für Seefischerei, Hamburg  
**09.2003–12.2004** Freiberufliche Mitarbeit an Umweltverträglichkeitsstudien für  
 Offshore-Windparks in der deutschen AWZ  
**02.–08.2004 &  
 01.–02.2005** Wissenschaftlicher Mitarbeiter am Institut für Hydrobiologie  
 und Fischereiwissenschaft in Hamburg  
**01.05.2005–  
 30.06.2008** Wissenschaftlicher Mitarbeiter am Institut für Vogelforschung  
 „Vogelwarte Helgoland“ in Wilhelmshaven  
**15.08.2008–  
 31.12.2009** Wissenschaftlicher Mitarbeiter am Johann Heinrich von Thünen  
 Institut, Institut für Ostseefischerei, Rostock  
**Seit 01.01.2010** Selbstständiger Fachgutachter,  
 Schwerpunkt Fische und Vögel



## ERKLÄRUNG

---

Hiermit erkläre ich, Andreas Dänhardt, geboren am 18. März 1973 in Hamburg, dass ich die vorliegende Dissertation selbständig verfasst und nur die angegebenen Hilfsmittel verwendet habe.

---

Buchholz, den 1. September 2010