

Inhalt

Microlepidoptera in salt marshes – Life history, effects of grazing, and their suitability as ecological indicators

By Corinna Rickert

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Summary

The aim of this thesis was to investigate the species richness of halobiontic moths of Schleswig-Holstein and to analyse their response to grazing management with sheep. Studies on the life history of specialised moth species were accomplished. Additionally, moth indicator species were named and proposed to be integrated in salt marsh monitoring programmes.

Study sites were located along the Western coast of Schleswig-Holstein. Between 2006 and 2009, differently managed salt marshes were sampled by net-sweeping, light-trapping photoelectors, and the collection of larval stages.

Altogether, 87 Microlepidoptera species were caught, of which 28 were considered halobiontic and occur mainly or only on salt marshes and inland saltings. In comparison to the occurrence of halobiontic moths before 1985 an increase in species richness was detectable, which was most likely associated with the cessation or extensification of grazing after the designation as National Park in 1985.

By standardised sampling on sites of an existing (25 years) grazing experiment on the Hamburger Hallig, the effects of grazing on the vegetation as well as on the species richness and abundance of moths could be determined. Comparisons to previous results on the reaction of invertebrate assemblages to grazing derived from an short-term grazing experiment (DIERBEN et al. 1994) enabled conclusions on underlying patterns and possible trends.

Moth communities were found to react highly sensitively to sheep grazing. With increasing grazing intensity a distinct shift in dominant species from Aster-feeding, halobiontic moths to often common species developing on grasses was evident. By tendency, a positive influence of extensive grazing on species richness was recognisable, though only minor differences towards the ungrazed sites was found. A comparative analysis of moth communities in short- and mid-term grazing experiments suggested a positive effect of extensive to moderate grazing intensities in long-term grazing management. Intensive grazing, however, led to an impoverished moths community.

In the short-term grazing experiment, moth assemblages were found to react more sensitively to grazing than spider, beetle and fly assemblages. Neither conclusions on the relationship of species richness between groups, nor a general pattern in the response of invertebrate communities to grazing could be derived.

Since the sampling and determination of invertebrate assemblages is time consuming and thus rarely feasible in nature monitoring, the identification of suitable indicators for salt marsh monitoring was aspired. To validate the results, data sets of four different study sites, two different sampling methods and two time periods were used as well as life histories of species considered.

The analysis resulted in the distinction of five suitable moth indicator species: *Eucosma catoptrana* and *Coleophora salicorniae* qualified as indicator species in ungrazed salt marshes, *Eucosma tripoliana* and *Phalonidia affinitana* in extensively grazed sites and *Eucosma lacteana* in moderately grazed plots. By contrast, overgrazing by sheep was indicated by eurytopic species feeding on grasses (*Crambus perlella*, *Chrysoteuchia culmella*, *Pediasia aridella*).

In conclusion, a combination of ungrazed, extensively and moderately grazed salt marshes would benefit moths diversity. The incorporation of moth indicator species in salt marsh monitoring programmes provides additional information on structural heterogeneity to results derived from regular vegetation and bird monitoring. However, the applicability of sole indicator species as surrogates for species richness needs to be verified in long-term grazing regimes. Till then, robustness of such proposed indicators remains questionable. Therefore, salt marsh monitoring should integrate moth indicator species in association with an assessment of invertebrate species richness.

Zusammenfassung

Die Microlepidoptera des Salzgrünlandes – Biologie, Beweidungseffekte und ihre Eignung als ökologische Indikatoren

Ziel dieser Arbeit war es, die Artenvielfalt halobionter Kleinschmetterlinge Schleswig-Holsteins zu untersuchen und ihre Reaktionen auf Beweidung mit Schafen zu analysieren. Untersuchungen zur Autökologie und Life History spezialisierter Kleinschmetterlinge wurden durchgeführt. Zusätzlich wurden Indikatoren benannt und es wurde vorgeschlagen, diese im Rahmen des Salzwiesen-Monitorings zu integrieren.

Die Untersuchungsflächen lagen entlang der Schleswig-Holsteinischen Westküste. Zwischen 2006 und 2009 wurden unterschiedlich beweidete Salzwiesen mittels Streifnetzfangen, Lichtfallen, Photoelektoren und der Sammlung von Larvalstadien beprobt.

Insgesamt wurden 87 Kleinschmetterlingsarten nachgewiesen, von denen 28 als halobiont gelten und ausschließlich oder überwiegend in Salzwiesen oder binnenländischen Salzstellen vorkommen. Im Vergleich zu Vorkommen von halobionten Kleinschmetterlingen vor 1985 konnte ein deutlicher Anstieg der Artenvielfalt festgestellt werden. Dieser steht sehr wahrscheinlich in Zusammenhang mit der Aufgabe bzw. Extensivierung der Beweidung in Teilen des 1985 gegründeten Nationalparks Wattenmeer.

Durch standardisierte Untersuchungen auf Flächen des seit 25 Jahren bestehenden Beweidungsexperiments auf der Hamburger Hallig konnten Auswirkungen von Beweidung sowohl auf die Vegetation als auch die Artenvielfalt und Individuenzahlen von Kleinschmetterlingen untersucht werden. Vergleiche mit früheren Ergebnissen zur Reaktion von Insektengemeinschaften auf Beweidung in kurzzeitigen Beweidungsexperimenten (DIERËN et al 1994) erlaubten Rückschlüsse auf zugrundeliegende Muster und mögliche Trends.

Kleinschmetterlings-Gemeinschaften reagierten sehr empfindlich auf Schaf-Beweidung. Mit zunehmender Beweidungsintensität war eine deutliche Verschiebung der dominanten Arten von Aster nutzenden, halobionten Kleinschmetterlingen hin zu sich an Gräsern entwickelnden, oft weit verbreiteten Arten ersichtlich. Tendenziell war ein positiver Einfluss von extensiver Beweidung auf die Artenvielfalt zu erkennen, wobei

nur geringe Unterschiede zur unbeweideten Salzwiese bestanden. Ein Vergleich der Ergebnisse für Kleinschmetterlings-Gesellschaften der früheren, kurzfristigen und der neuen Untersuchungen legte einen langfristig positiven Effekt von extensiver bis moderater Beweidung in Salzwiesen nahe. Intensive Beweidung dagegen führte zu einer verarmten Kleinschmetterlings-Gemeinschaft.

Auswertungen der Daten des kurzzeitigen Beweidungsexperiments ergaben, dass Kleinschmetterlings-Gesellschaften deutlich empfindlicher auf Beweidung reagierten als Spinnen-, Käfer- oder Fliegen-Gesellschaften. Es konnten jedoch weder Zusammenhänge zwischen den Artenzahlen verschiedener Insektengruppen noch ein generelles Muster in ihrer Reaktion auf Beweidung identifiziert werden.

Da die Erfassung und Bestimmung von Insektengemeinschaften zeitlich aufwendig ist und in Naturschutz-Monitorings selten zur Anwendung kommt, wurde versucht, geeignete Indikatoren für das Salzwiesen-Monitoring zu identifizieren. Zur Validierung der Ergebnisse wurden Datensätze von vier verschiedenen Standorten, zwei Fangmethoden und zwei Zeiträumen herangezogen sowie die spezifischen Life Histories der Arten berücksichtigt.

Hieraus ergaben sich fünf geeignete Kleinschmetterlings-Indikatoren: *Eucosma captoptrana* und *Coleophora salicorniae* waren als Indikatoren für unbeweidete Salzwiesen geeignet, *Eucosma tripoliana* und *Phalonidia affinitana* für extensiv beweidete Flächen und *Eucosma lacteana* für moderat beweidete Bereiche. Überweidung durch Schafe dagegen wurde durch eurytope, sich an Gräsern entwickelnde Arten angezeigt (*Crambus perlella*, *Chrysoteuchia culmella*).

Zusammenfassend kann festgestellt werden, dass eine Kombination von unbeweideten, extensiv und moderat beweideten Salzwiesen einer hohen Diversität von Kleinschmetterlingen zugute käme. Die Integration von Kleinschmetterlingen als Indikatoren im Salzwiesen-Monitoring würde zusätzliche Informationen über die strukturelle Vielfalt in Salzwiesen liefern, die nicht anhand des Vegetations- und Vogelmonitorings allein gewonnen werden können. Die Anwendbarkeit einzelner Indikatorarten stellvertretend für die Artenvielfalt von Insekten muss jedoch in Langzeit-Untersuchungen validiert werden. Bis dahin bleibt die Robustheit der vorgeschlagenen Indikatoren weiterhin fraglich. Die Anwendung der genannten Indikatoren sollte daher in Zusammenhang mit einer Erfassung der Insekten- und Spinnen-Gemeinschaften erfolgen.

1 Introduction

Salt marshes are narrow ecotones between terrestrial and marine systems, which are characterised by semi-terrestrial flora and fauna that are exposed to frequent tidal inundations. The Wadden Sea, which stretches from the peninsula of Skallingen in Denmark to Den Helder in the Netherlands, harbours a large area of partly natural, but mostly human-influenced salt marshes located on the sheltered landward coast of islands and Halligen and along the mainland coast.

Salt marshes have a high functional value for coastal protection and e.g. as a staging area for migratory birds and are therefore considered areas of high conservation value (DESENDER & MAELFAIT 1999, LEFEUVRE et al. 2000). Tidal inundations of salt water lead to moisture conditions varying from continuously waterlogged to temporarily moist soil and to the deposition of alluvial sediments on the shore (ADAM 1990). Only halo-tolerant plant communities and biocoenosis can cope with the varying chloride content of the soil (BEEFTINK 1992).

For centuries these coastal habitats have been impacted by human activity and over-exploitation. Embankments, drainage and intensive grazing have led to a loss of biodiversity and ecological resilience (KIEHL 1997, LOTZE ET AL. 2006, PÉTILLON & GARBUTT 2008) and formed an almost entirely artificial landscape (STOCK et al. 1997). When establishing the Wadden Sea National Park (1985), cessation of grazing was believed to be favourable for diversity and the conservation of rare species (BALMER & EHRHARDT 2000) and the importance of natural development was emphasised. Other scientific studies revealed, however, that cessation of grazing is beneficial for plant species richness as well as the heterogeneity of vegetation structure during the first few years after intensive grazing (BAKKER 1985, JENSEN 1985, BAKKER 1987, DIERBEN et al. 1994a, KIEHL 1997, ESSELINK ET AL. 2000, GETTNER 2002, BAKKER ET AL. 2003, KIEHL ET AL. 2003), but that eventually plant species such as *Elymus athericus* and *Atriplex portulacoides* will gain dominance and out-compete other species mostly by competition for light (JENSEN 1985, ESSELINK ET AL. 2002, BAKKER ET AL. 2003). An impoverished plant community in late successional marshes (BAKKER 1985, ESSELINK ET AL. 2002, MAYER ET AL. 2009) would be the consequence.

Extensive grazing has been recognised as an important management option influencing plant and insect diversity, and has been a popular tool in nature conservation, especially in calcareous grasslands, for decades (WALLISDEVRIES et al. 1999, BALMER & EHRHARDT 2000, WOODCOCK et al. 2005). It can facilitate the creation of a patchy vegetation structure and enhance structural heterogeneity through selective grazing (BERG et al. 1997, ESSELINK et al. 2002), benefiting species diversity. But while extensive grazing management has become common practice in terrestrial grasslands and positive effects on plants as well as invertebrates are documented (GIBSON et al. 1987, DENNIS et al. 1998b, SWENGEL & SWENGEL 1999, DENNIS et al. 2001, ESSELINK et al. 2002, KRUESS & TSCHARNTKE 2002a, HENDRICKX et al. 2007), conclusive results especially on the invertebrate fauna in salt marshes remained scarce.

Most theories on invertebrates and their distribution patterns in response to grazing or mowing management were derived from studies in calcareous or fresh grasslands (SIEMANN ET AL. 1996, MORTIMER et al. 1998, SIEMANN 1998, MORTIMER et al. 2002, HUGHES et al. 2000, DENNIS et al. 2001, WALLISDEVRIES et al. 2002, HENDRICKX et al. 2007), limiting their applicability to salt marshes (LEWINSOHN et al. 2005).

Salt marshes harbour highly specialised biota dominated by halobiontic invertebrates (DESENDER & MAELFAIT 1999), living in close association with salt marsh halophytes. Early studies on the halobiontic Lepidoptera (HEYDEMANN 1938, STÜNING 1980) as well as spiders and beetles (HEYDEMANN 1960, HEYDEMANN 1961, HEYDEMANN 1979) focused on species richness, host plants and their distribution along an inundation gradient. Grazing as a detrimental factor was only mentioned shortly, although specialised moths as vegetation-associated insects could be expected to be vulnerable to anthropogenic stress (DEBANO 2006, SAMWAYS & LU 2007).

Only few studies focused on the distribution of salt marsh invertebrates and the impact of grazing of either cattle or sheep (IRMLER & HEYDEMANN, 1986, JANSEN & HEMMINGA 1988, ANDRESEN et al. 1990, DIERBEN et al. 1994b, MEYER & REINKE 1996, DIERBEN et al. 1998, JANSEN 2005, PÉTILLON et al. 2008). Moth communities remained unnoticed.

The few more recent studies on invertebrates in salt marshes either focused on microlepidopteran species and their life history (STÜNING 1988, JANSEN & HEMMINGA 1988, JANSEN 2005) or the impact of an increase of *Elymus athericus* on the spider community (PÉTILLON et al. 2005, PÉTILLON et al. 2005a, PÉTILLON et al. 2008). Effects of grazing management on invertebrates were largely disregarded (but see PÉTILLON 2007).

Results, however, consisted of only short-term management effects, and so far, comparisons to mid- or long-term grazing experiments in salt marshes are missing. The validity of patterns in community responses to grazing derived from these results is limited (LEWINSOHN et al. 2005) and many questions regarding long-term changes in the invertebrate fauna remained unanswered.

Invertebrate surveys are time-costly, sampling effort is high, expert knowledge often missing, and due to high inter-annual variation only studies of time series can provide meaningful results. Therefore, concepts on surrogate values of species groups are tempting.

The complexity of ecosystems has ever since forced scientists to use simple, easily obtained and interpreted surrogates (indicators) to predict and monitor future developments and conditions of their environment (NIEMI & McDONALD 2004, HILTY & MERENLANDER 2000). An indicator is a species, whose presence or abundance readily reflects some measure of the character of the habitat within which they are found (McGEOCH & CHOWN 1998), and is supposed to be an easily measured surrogate for underlying processes of a system that are difficult to measure directly (MURTAUGH 1996, LANDRES et al. 1988).

In the context of the Convention on Biological Diversity (CBD) (GLOWKA et al. 1994) the need for a rapid assessment method for ecological monitoring has been recognised (MCKENZIE et al. 1992, BALMFORD et al. 2005). The challenge with indicator taxa still lies in distinguishing responses due to human disturbances from variation in baseline conditions due to natural variability (KREMEN et al. 1993, MURTAUGH 1996, ANDERSEN 1999). Knowledge on the life history traits of indicators is a crucial factor in determining cause and effect relationships between indicators and the environment (NOSS 1990, NELSON 2007). Ideally, by the occurrence of a defined number of moderately common species (LANDRES et al. 1988, SAWCHIK et al. 2005), conclusions on the species richness and quality of a community in a habitat can be drawn, making elaborate research unnecessary (OOSTERMEIJER & VAN SWAAY 1998). Because it is unlikely that one single indicator will possess all of the desirable properties, a set of complementary indicators is required (NOSS 1990, KREMEN 1994, PEARSON 1994, DA MATA et al. 2008).

Unfortunately, in many studies the selection of indicators has been suggested rather by occasion or convenience and favoured taxa (WOIWOOD & THOMAS 1993) than by formal testing of their adequacy (McGEOCH 1998) and for some taxa, high diversity was associated with the presence of a biological field station (PEARSON 1994).

The use of invertebrates as indicator taxa remained largely neglected in terrestrial systems (MORTIMER et al. 1998, ANDERSEN et al. 2004), due to their excessive numbers and taxonomic challenges (ANDERSEN et al. 2002). Nevertheless, various studies described the value of ground beetles, spiders and butterflies as indicators for habitat quality and proposed their use for monitoring (ROSENBERG et al. 1986, PEARSON 1994, LUFF & WOIWOOD 1995, MEYER & REINKE 1996, RYKKEN et al. 1997, REINKE & MEYER 1999, VILLA-CASTILLO & WAGNER 2002, PÉTILLON et al. 2005, NELSON 2007), but so far, studies rarely include a verification of the proposed indicators and there is only a confined area for which reliable insect indicators have been established (ANDERSEN et al. 2004, McGEOCH 2007). To understand and interpret the reactions of invertebrates to environmental changes, the research on global phenomena needs to be supported by intensive studies of the life histories of organisms in local environments (NOSS 1990, LANDRES et al. 1988).

Lepidoptera are the best collected and studied group of insect orders (GASTON 1991). They are known to react sensitively to changes in habitat heterogeneity and plant diversity (ERHARDT & THOMAS 1991, SAMWAYS 2005, DEBANO et al. 2006, SAMWAYS & LU 2007)

and are very specialised regarding larval host plants and adult nectar sources (NELSON 2007). Their short life cycles lead to a fast response to changes in their habitat and make them suitable organisms for ecological monitoring (DA MATA et al. 2008). Therefore, Lepidoptera, and moths in particular, can be expected to be sensitive indicators of apparently minor changes in plant composition and the vegetational structure of grassland habitats.

Clearly, much effort is still required to identify robust arthropod ecological indicators for monitoring (LANGOR & SPENCE 2006). The detection and comprehension of repeatable patterns determining the distribution of species assemblages is crucial for a successful protection of threatened habitats and their overall diversity (LAWTON & GASTON 1989).

This thesis aims at answering the following questions:

i) Which Microlepidoptera occur in salt marshes of Schleswig-Holstein? We can not protect what we do not know. To evaluate the impact of disturbances and environmental conditions on species richness and abundances, it is crucial to know how many and which species to expect in a habitat. The last studies on Lepidoptera in salt marshes dated back to the 1970's, and changes in species richness could be expected after the cessation or extensification of intensive grazing after 1985. Therefore, a contemporary assessment of the species richness of Microlepidoptera in salt marshes of Schleswig-Holstein was accomplished, to build a sound scientific basis for further investigations.

ii) What is the life history of occurring halobiontic Lepidoptera and which environmental factors influence their occurrence? Knowledge on the life history of Microlepidoptera is a key component for understanding distribution patterns and the effect of environmental factors and disturbances such as grazing on species richness. But information on the life history of halobiontic Microlepidoptera was scattered throughout literature or missing. In the course of this research, accessible information on the life history of occurring halobiontic species has been compiled from literature. Additional information was obtained by breeding and observing occurring species in order to close existing knowledge gaps and give a complete overview on life history of halobiontic Microlepidoptera.

iii) Does grazing management of salt marshes have an impact on the species richness and abundance of Microlepidoptera? Do Microlepidoptera respond similarly to grazing like other invertebrate groups (Araneae, Coleoptera, Diptera), so that general patterns on the response to grazing can be derived? Microlepidoptera, as herbivorous insects, are often specialised to single host plants and were expected to react sensitively to disturbances. Grazing alters habitats due to trampling, defoliation and fertilisation. It is likely that moth communities display a reaction to these habitat changes, possibly even faster than plant communities. A positive effect of extensive grazing on species richness, but a decline of moth species richness and a change and impoverishment of moth communities with increasing grazing intensity was expected. To understand the effects of grazing on communities and to give recommendations for grazing management in salt marshes and possibly other grasslands, general patterns in the response to grazing need to be identified. Therefore, the response of spider, beetle and fly communities to grazing was compared to that of moths. It was hypothesised, that different invertebrate groups show a similar decline in species richness in response to intensive grazing and that moth species richness would enable conclusions on the species richness of other invertebrate communities.

iv) Are halobiontic Microlepidoptera suitable as ecological indicators for the impact of grazing on salt marshes? The identification of indicator species would facilitate a time efficient determination of species richness of invertebrates and deliver additional infor-

mation on habitat quality in combination with vegetation and bird monitoring. Since halobiontic moths are highly adapted to their habitat and often host plant-specific, a sensitive reaction to the impact of grazing was expected. It was hypothesised that specialised moth species can be identified as ecological indicators for the influence of grazing in salt marshes.

2 Study sites

2.1 Climate and inundation

Schleswig-Holstein is situated in the temperate zone with a sub-oceanic climate regime. It is predominantly influenced by Western winds in combination with areas of low pressure. Northern Friesland and Dithmarschen are close to the North Sea and influenced by the Gulf Stream. This leads to a mild climate throughout the year with only rare cold winters or hot summers and rather humid weather with 800 mm to 850 mm average annual precipitation inland, whereas the annual average precipitation on exposed salt marshes is about 100 to 200 mm lower (TISCHLER 1985).

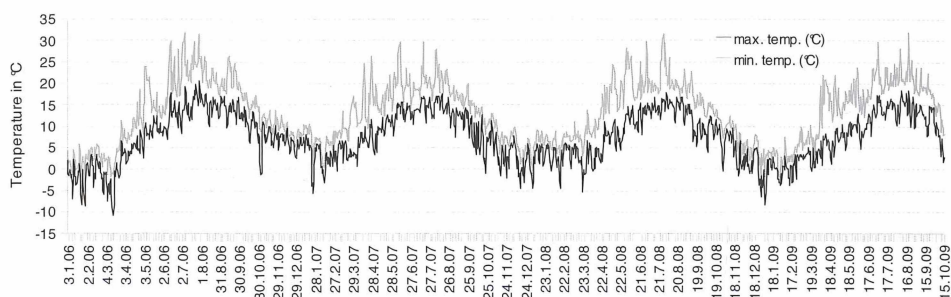


Fig. 1: Temperature profile of St. Peter-Ording in the years 2006 to 2009 (© DWD 2006-2009).

While the sample periods (2006 to 2009) did not differ greatly in mean high (between 13 and 13.3°C) and low (between 7.24 and 7.76°C) temperatures, 2006 stands out with an exceptionally cold winter in the beginning of the year and a following warm summer (Fig. 1). The years differed greatly, however, concerning annual precipitation rates. Compared to the long time mean precipitation (800-850 mm), 2006 was an exceptionally dry year with only 774.9 mm of rain, while 2008 was a very wet year (915.1 mm) (Fig. 2).

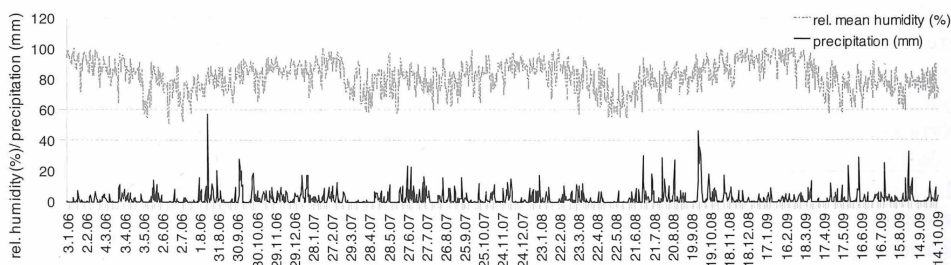


Fig. 2: Relative mean humidity and precipitation of the weather station in St. Peter-Ording Strand of the years 2006 to 2009 (© DWD 2006-2009).

The number of inundations of a salt marsh depends on its elevation compared to the Mean High Tide water level and climatic impacts such as wind, offshore storms, etc. Therefore, the number of inundations per year varies for the lower and higher parts of a salt marsh and between years.

For the calculation of the inundation frequency in the salt marshes of Westerhever, elevation measurements of 43 permanent plots distributed throughout the ungrazed, moderately grazed and intensively grazed salt marshes were used and aligned with the gauge data of Tümlauer Bucht. Figure 3 shows that in comparison, 2006 was a year with few high tides especially in the summer months, whereas the inundation frequency increased in 2007 with exceptionally high tides in autumn 2007 and spring 2008.

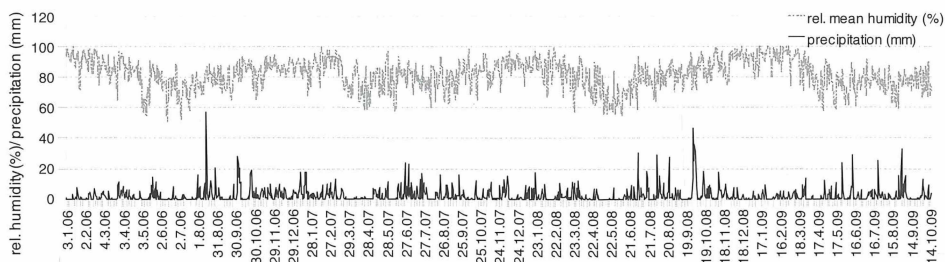


Fig. 3: Mean inundation levels of the salt marshes of Westerhever in the years 2006 to 2009. © Landesamt für Küsten- und Naturschutz Schleswig-Holstein, Husum.

2.2 Geographical location of the study sites

Focus of this study lies on the mainland salt marshes of Northern Friesland on the Hamburger Hallig, at Westerhever, in St. Peter-Ording and Schobüll as well as on Sylt and Langeness. Additionally, data of the Ecosystem Research Wadden Sea Project was analysed, which was sampled on the salt marshes of the Sönke-Nissen-Koog in Northern Friesland and the Friedrichskoog in Dithmarschen (Fig. 4).

For the studies on the development of Microlepidoptera in salt marshes under different grazing regimes, sites dominated by *Elymus athericus* were excluded from the study, since no Microlepidopteran species are known to feed and develop on it, and a very species poor community had to be expected.

The Hamburger Hallig

The salt marshes of the Hamburger Hallig cover 1050 ha and comprise the biggest coherent area of salt marshes in the Wadden Sea of Schleswig-Holstein. In 1991 a grazing experiment was initiated to determine the impact of cessation and extensification of grazing by sheep on the vegetation, and the utilisation by breeding birds (STOCK & KIEHL 2000). While in spring 1991 all parts were heavily grazed since 1994, 516 ha are ungrazed, nearly 200 ha extensively grazed with 1 to 2 sheep ha⁻¹, almost 100 ha are moderately grazed with 3 to 4 sheep ha⁻¹ and 256 ha intensively grazed with 10 sheep ha⁻¹.

While vegetation mappings every five years showed an increase in species richness in the first years after cessation or extensification of grazing (KIEHL 1997), recent vegetation mappings suggest an increase of sites dominated by *Elymus athericus* or *Artriplex portulacoides* especially in the ungrazed salt marsh (STOCK & PETERSEN 2008).

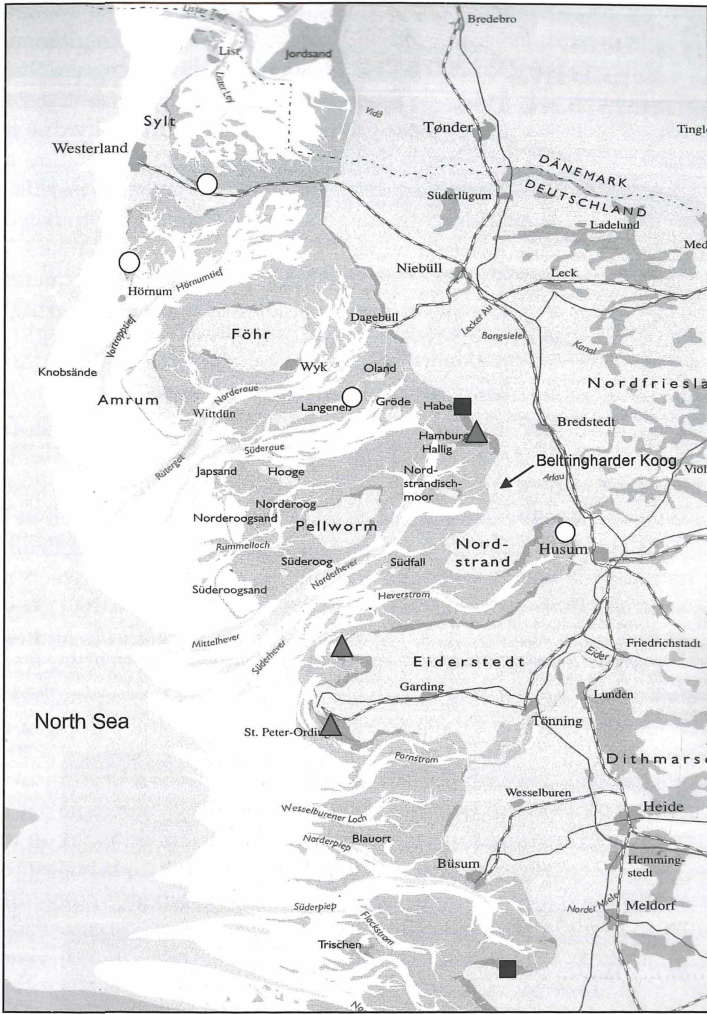


Fig. 4: West coast of Schleswig-Holstein and the position of main and additional working areas on the salt marshes (triangles: main working plots; squares: working plots of the Ecosystem Research Wadden Sea Project; circles: additional working plots; the location of the Beltringharder Koog is indicated) (altered according to KOHLUS & KÜPPER 1998).

Westerheversand

The foreland of Westerhever is located on the peninsula of Eiderstedt. The salt marshes cover an area of 260 ha and lie adjacent to the salt marshes of Tümlauer Bucht in the South and Norderheverkoog in the North, which together cover an area of 600 ha of uninterrupted salt marshes (STOCK et al. 2005). The salt marshes of Westerheversand are defined by an unusually high sand content compared to typically clayish mainland salt marshes especially in the seaward parts, which is due to a sandbank west of the salt marshes leading to a high content of suspended sand particles (PEITER 2004).

Since 1991, more than 70% of the salt marshes are ungrazed and only 31% of the salt marshes of Westerheversand located close to the seawall and along a path to the beach

remained intensively grazed by ten sheep per hectare (PEITER 2004). In the ungrazed sites grazing-sensitive plants such as *Atriplex portulacoides*, *Aster tripolium* and *Limonium vulgare* form a small scaled mosaic. An increase of *Elymus athericus* is recognisable and parts of the ungrazed salt marsh are already dominated by the grass (STOCK & PETERSEN 2008).

In the still intensively grazed area a clear gradient of grazing intensity due to grazing habits of sheep is recognisable. This leads to a highly differentiated structure of vegetation with short areas dominated mainly by *Festuca rubra* and *Puccinellia maritima* close to the seawall and along the pedestrian path, and a higher vegetation dominated by *Atriplex portulacoides* and *Puccinellia maritima* as well as *Festuca rubra*, and smaller shoots of *Aster tripolium* and *Armeria maritima* in less frequented parts. As a consequence, for the analysis, the salt marshes of Westerhever are considered a mid-term grazing management with moderate and intensive grazing intensity and an ungrazed control.

St. Peter-Ording

St. Peter-Ording is situated on the western tip of the Eiderstedt peninsula (Fig. 4) in Northern Friesland. The coastal area of St. Peter-Ording is characterised by wide and flat beaches stretching up to one to two km from the edge of the dunes to the sea. While parts close to the dunes have to be described as a low salt marsh dominated by *Salicornia europea*, *Suaeda maritima* and *Puccinellia maritima* and resemble a green beach, other localities display a natural salt marsh with meandering creeks, located between the beach dunes and the seawall. These salt marshes have been ungrazed for over 50 years and show a mosaic of *Limonium vulgare*, *Aster tripolium*, *Atriplex portulacoides* and other halophytes while an increase of *Elymus athericus* is detectable (STOCK & PETERSEN 2008).

The salt marshes of St. Peter-Ording have been sampled by net sweeping and in search for larval stages for researches on the species diversity of Microlepidoptera along the coast of Schleswig-Holstein.

Further salt marshes along the coast

In the years of 2006 to 2009, further salt marshes on the isle of Sylt close to the Morsum Cliff and Hörnum as well as salt marshes on the Hallig Langeness and in the Schobüll foreland were researched additionally, to consider topographical and habitat parameter differences to allow assumptions on the lepidopteran fauna along the West coast of Schleswig-Holstein (Fig. 4).

The Ecosystem Research Wadden Sea Project- comparison to a short-term grazing experiment

In the study carried out by DIERBEN et al. (1994) the grazing effects on microclimate, soil, vegetation and invertebrate fauna were studied in a lower salt marsh dominated by *Puccinellia maritima* (Sönke-Nissen-Koog) and an upper salt marsh dominated by *Festuca rubra* (Friedrichskoog) (DIERBEN et al. 1994, a, b, MEYER & REINKE 1997, REINKE & MEYER 1999). New statistical analyses of the data on Araneae, Coleoptera and Diptera as well as for the so far undetermined Lepidoptera were performed. These results were compared with the data on Lepidoptera obtained from 2006 to 2009 in present grazing experiments.

Because the grazing experiments on the Hamburger Hallig, in the Friedrichskoog and the Sönke-Nissen-Koog were controlled grazing managements with comparable stocking rates, the locations can be treated as replicates. Herein, the salt marshes of the Hamburger Hallig represent an intermediate successional stage of 20 to 25 years continuity, whereas Friedrichskoog and the Sönke-Nissen-Koog represent early successional stages after establishment of the grazing experiment (0 to 4 years duration). The data from the

salt marshes of Westerhever were treated as additional data for an intermediate successional stage in grazed salt marshes, though no controlled grazing management was implemented, since vegetation mappings of 1996, 2001 and 2006 as well as personal observations revealed a factual separation between moderate and intensive grazing.

3 Material and methods

3.1 Trapping methods

The use of different methods is important in ecological research, since species are influenced differently, e.g. by certain wavelengths of light, flight altitudes, temperatures, and wind. Additionally, methods which yield the best qualitative measurements and the highest number of species' are not necessarily suitable for statistical comparative studies. Contrarily, methods applied for analysis of comparability might not be adequate for a qualitative research on species richness due to an underestimation of rare species (WILLIAMS et al. 1955, OLDROYD 1970, Meier 1992, MEINEKE 1995, RAIMONDO et al. 2004, WIROOKS 2005).

Therefore, in this study five different methods were used with regard to the different research questions.

3.1.1 Light trapping with UV -lamps

Light traps are the most commonly used method in the research on Lepidoptera and have been used mainly with UV-lamps in all different types of habitats since the middle of the last century (DANIEL 1952, FROST 1958, HOLLINGSWORTH et al. 1968, CONRAD et al. 2004, HIRAO et al. 2008), most regularly in forests. Light traps with super actinic 12 Volt fluorescent tubes were used for the comparative studies on the response of moth communities to grazing as well as for overall species richness. The traps were run with a common rechargeable battery of 12 Volt and equipped with an automatic twilight switch. In nights with an expected low temperature above 10°C, without precipitation and a mean wind speed less than 4 bft one light trap was placed in each grazing regime.

By allurement of moths present in a habitat and supposedly distributed in a radius of about 25 m around the trap, light traps give an estimation of the species and their abundances present and active in an area (MCGEACHIE 1989, RICKETTS et al. 2002, WIROOKS 2005, WIROOKS 2006). But due to the effect of attraction towards light, no statement on the residency or development of species in an area can be made, and a high number of dispersing and non-resident species, so called 'tourist-species' are to be expected.

For further details on light-trapping please see DANIEL 1952, TAYLOR 1963, KURTZE 1974, BLOMBERG et al. 1978, MCGEACHIE 1989, STEINER 1994, WIROOKS 2005, STEWART et al. 1963, MIKKOLA 1972, STEINER 1994, DELISLE et al. 1998, NABLI et al. 1999, MEINEKE 1995.

3.1.2 Light- trapping with Mercury-Vapour-Lamps

In windless nights, light trapping with a Mercury-Vapour-Lamp was used as an additional trapping method for the study on the species richness of Microlepidoptera, because not all of the possibly occurring species are attracted by UV-light and further species could be expected (NABLI et al 1999). Effects of attraction of a Mercury-Vapour-Lamp are significantly higher than of a UV-lamp, but some species of moths avoid bright light. The lamp was set up irregularly during especially warm nights between June and September together with a white linen of about 5m² size, on which the attracted moths settled. It is a live-catch method

3.1.3 Photoeclector traps (PE)

For the analysis of the effect of grazing on species richness and abundance of moths, photoeclector traps (PE) (FUNKE 1971) were used. They are based on the principle of isolation of a defined area of vegetation and soil, and trap the imagines of various insects after hibernation and emergence in a trapping vessel due to positive phototropism of most insects and especially moths. The emergence-type traps consist of a square pyramidal construction of galvanised sheet steel of 1m² (MEYER & REINKE 1997, REINKE & MEYER 1999). Positioned on two sides of the trap were holes, covered with an opaque gauze for ventilation as a precaution against overheating. To prevent an escape of the emerging insects and immigration from surrounding plots, the trap was dug into the soil to a depth of approximately 5–10 cm. The photoeclector was equipped with a transparent trapping vessel on top of the trap, which contained an insecticide (DiChlorVos), dry beads against evaporation and a piece of egg carton to provide shelter.

From April to October in the years 2007–2009, three traps were randomly placed in each grazing regime on the Hamburger Hallig in the lower and upper salt marsh according to the last vegetation mapping of 2006 (STOCK & PETERSEN 2008). The elevational height of the paddocks (LANDESVERMESSUNGSAMT SCHLESWIG-HOLSTEIN 2007) was considered to allow highest possible comparability (Fig. 5). They were replaced every three weeks to avoid damage of plants underneath by absence of light and therewith also the damage of larvae. In total, for each grazing regime and year, 30m² of salt marsh were sampled. At each time of replacement, the vegetation was mapped and the percentage of coverage, the plant height, the thickness of the litter-layer and the area of bare soil were estimated.

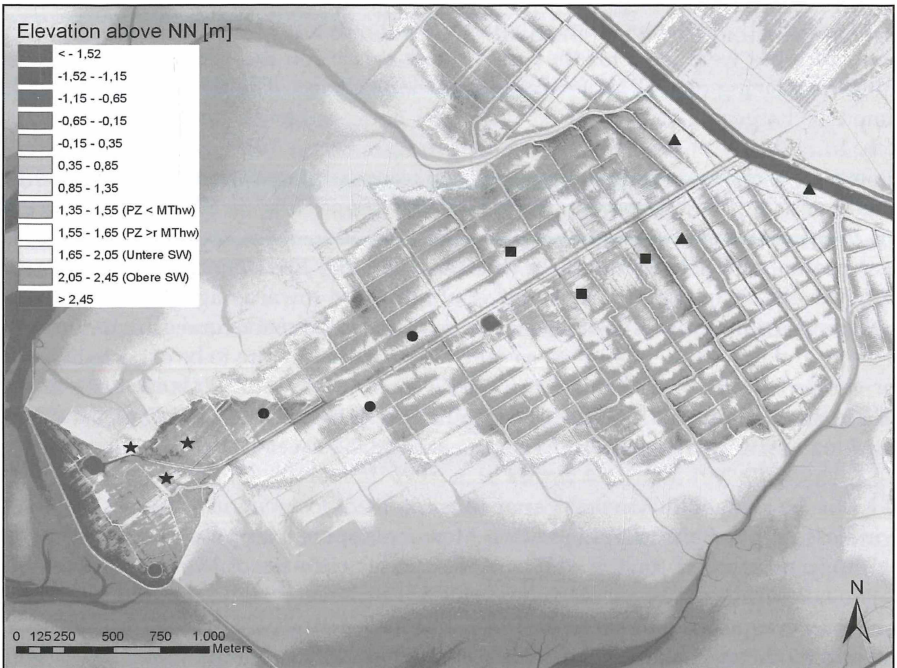


Fig. 5: Elevational model of the Hamburger Hallig © Landesvermessungsamt Schleswig-Holstein (2007). The position of the photoeclector traps is indicated (stars: moderate grazing, circles: ungrazed, square: extensively grazed, triangle: intensively grazed).

3.1.4 Net sweeping

Additionally, for the qualitative estimation of species richness in salt marshes, during twilight at sunset and sunrise, sweep net samples were taken to catch those species occurring in salt marshes that are not attracted by light. No quantitative estimation of samples with sweep nets by standardised transect walks according to POLLARD (1977) was accomplished due to the small size of most halobiontic Microlepidoptera and difficult light conditions. Over- or underestimation of abundances as well as difficulties of determinations in the field would have lead to possible wrong identifications.

3.1.5 Collection and breeding of larval stages

Larval stages of halobiontic moths were collected from May 2006 to September 2009 and taken to the laboratory for research on their life history. Larvae were kept in a plastic box of 20 x 20 cm, fed with their known food plant or the plant they were found on and a sand/earth mixture to offer coarse material for pupation. Pupae were kept in the same plastic box under as natural conditions as possible and care was taken to avoid both desiccation and mould formation. After hibernation and pupation, pupa were kept in a warm place in the laboratory and checked every day for emerging moths, which were then either spread and determined or set up in a cage with their food plant for further breeding and research on life history traits.

For each obtainable developmental stage, photographs were taken and morphological as well as biological details described.

3.2 Statistical analysis

3.2.1 Impact of grazing on species richness and abundance

Prior to analysis, graphical exploratory techniques were used to check for outliers, influential data points and collinearity in species and matrix data. Since grazing showed strong collinearity to other predictor variables, such as plant height, plant cover, bare soil and plant species richness, grazing was preferred as a potential co-variate for further analysis to meet the study objectives. The influence of grazing on species richness, abundance and composition of invertebrates was analysed by different statistical methods. All statistical analysis was conducted with the statistical program R version 2.10.1 (R Development Core Team, <http://cran.r-project.org/> 2009).

To analyse the effect of grazing on vegetation structure (plant height, plant cover, plant species numbers, thickness of litter layer and bare soil), Kruskal-Wallis ANOVA followed by Wilcoxon-Mann-Whitney *U*-tests with a Bonferroni adjustment were applied, since the assumption of normality was violated.

Non-metrical multidimensional scaling (NMDS) using the *metaMDS* function, was applied to assess patterns of plant assemblage variation and the effects of environmental factors on plant distribution in four different grazing regimes on the Hamburger Hallig.

NMDS is an indirect gradient analysis (ordination) based on abundance data which uses similarity or dissimilarity matrices to establish a relation between objects. For the calculation of the distance matrix the Bray-Curtis dissimilarity measure was employed. Variations of patterns described in the ordination plot were analysed by a multivariate ANOVA (ADONIS) based on 999 permutations (OKSANEN 2010). The ADONIS allows the use of any semi-metric (e.g. Bray-Curtis, aka Steinhaus and Sørensen) or metric (e.g. Euclidean) distance matrix (MCARDLE & ANDERSON 2001). In this case, the Bray-Curtis measure of dissimilarity was applied, which is commonly used in ecological data analysis (CHAO et al. 2006).

Species are not distributed equally in habitats, but instead it is common that some species are highly abundant, others are moderately common, whereas often the majority of species is rare. THIENEMANN (1920) already stated that homogeneous habitats are dominated by few species which occur in high abundances, whereas highly heterogeneous habitats facilitate a high species density with low abundances per species. Therefore, in extreme habitats like salt marshes, comparably few species with high abundances were expected.

To analyse and compare the invertebrate communities in differently grazed parts of the salt marsh, dominance levels for each species of each grazing unit were calculated according to the logarithmic dominance classification of ENGELMANN (1978): eudominant: $> 32.0 \leq 100$ %, dominant: $> 10.0 \leq 32.0$ %, subdominant: $> 3.2 \leq 10.0$ %, recedent: $> 1.0 \leq 3.2$ %, subrecedent: $> 0.32 \leq 1.0$ %, sporadic: ≤ 0.32 %, missing: 0 %.

Studies based on trapping always raise the question, whether a representative part of the population in a habitat could be extracted to justify further analysis (GOTELLI & COLWELL 2001) and to assume that the results derived from the data give insight on distribution patterns of the communities and are not just a sampling artefact.

To compare species richness and diversity between different grazing regimes and to analyse completeness of sampling in each habitat (MACAGNO & PALESTRINI 2009), the number of total expected species in salt marsh communities of spiders, beetles, flies and moths under different grazing regimes was estimated using Kindt's exact accumulator (KINDT et al. 2006, UGLAND et al. 2003, COLWELL et al. 2004). Kindt's exact accumulator is a sample-based approach estimating the expected species richness of a habitat producing a smooth curve extremely close to classical algorithms but less prone to overestimation in the case of large areas or underestimation in the case of small areas (KINDT et al. 2006). For each type of grazing management and species group the expected species accumulation curve and its confidence interval were computed on the basis of the expected mean number of species with increasing number of sites. The analysis was done using the *specaccum* function of the *vegan* package in R (OKSANEN 2010).

The assumption of normality does not hold for the count data (data of photoelector and light-traps), therefore a generalised linear model would be appropriate (GLM). Since data represent repeated measures over time (12 to 14 sequential weeks), the temporal correlation structure must be considered. For this reason, the longitudinal data were analysed using generalised estimation equations (GEE), which represent an extension of a GLM. To adjust the model for not normally distributed and correlated data structures, GEE's model the mean response as a dependent on co-variables and not on random effects, and are therefore suitable to include a dependence structure of the response variable (ZUUR et al. 2009). Thus, the Generalised Estimation Equation model (GEE) measures the effect of different grazing regimes, while considering the time-dependent replication of measurements (LIANG & ZEGER 1986, ZUUR et al. 2009). The results allow an interpretation of the responses of insect and spider communities in their species richness and abundance, and, therefore, conclusions on the occurrences of species under different management regimes are possible.

Correlations between the 12 respectively 14 weeks sampling periods were taken into account using an auto-regressive correlation structure (AR-1). The GEE models were specified employing the log link function and a poisson distribution. Over-dispersion was corrected for using a quasipoisson or negative-binomial distribution (dispersion parameter > 20). Stepwise backwards elimination procedures were applied to identify non-significant co-variables ($\alpha = 0.05$). Statistical assumptions were assessed by different

residual validation plots (ZUUR et al. 2007). The regression models were fitted using the *geepack* R library (YAN et al. 2010).

3.2.2 Species composition and Indicator Species

To test for significant differences in species composition of invertebrates in varied grazing intensities an ADONIS (see chapter on plant species richness and vegetation parameters) using the Bray-Curtis measure of dissimilarity was computed.

To determine characteristic species for the impact of grazing in salt marshes, a compositional indicator species analysis was applied using the *indpsc* function of the *labdsv* package in R (ROBERTS 2010), which calculates the mean similarity of all samples a species occurs in and thus calculates an Indicator Species Value (ISV) for each species of a group. It combines a species' relative abundance with its relative frequency of occurrence in a group of sites. The analysis of indicator values is widely discussed in ecology and recommended for the identification of indicator taxa of animal or plant communities (MCGEOCH & CHOWN 1998, DAI et al. 2006, BAKKER 2008b). Indicator species values can vary between 0.0 and 1.0, where an indicator value of 1.0 indicates that a species occurred in all plots within a group but was absent in all other plots outside that group.

To test the significance of an observed indicator value, a comparison of 999 randomly generated values was conducted. The random values were generated with a random reallocation procedure, where the number of individuals per species per plot was randomly reshuffled over the plots (DUFRENE & LEGENDRE 1997). If the observed indicator value of a species in a cluster fell within the top 5 % of the random indicator value it was considered to deviate significantly from the expected random mean.

Since indicators for species richness must be common enough to be detected in a brief survey (SAHLÉN & EKKESTUBBE 2001) and to reduce the influence of inadequately sampled species or 'tourist species' (RICKETTS et al. 2002), species occurring with abundances below ten in the light trap samples and below five in the photoeclector samples were excluded from the analysis. These species yield little information on compositional species distribution and must be considered unsuitable as indicator species (LEYER & WESCHE 2007). The threshold value for suitable indicator species is considered to be 0.25 with a higher indication potential for higher values (BAKKER 2008b, DUFRENE & LEGENDRE 1997). Significant differences in species indicator values were comparable to the mean of the complete matrix.

3.3 Nomenclature

The reference of names of Microlepidoptera follows "The Lepidoptera of Europe" by KARSHOLT & RAZOWSKI (1996) and regarding plants the „Standardliste der Farn- und Blütenpflanzen Deutschlands“ by WISSKIRCHEN & HAEUPLER (1998).

4 Results

4.1 Life histories - comprehensive compilation and new results

Information on the life histories of halobiontic Microlepidoptera was compiled and is complemented by new results obtained during this study.

The term Microlepidoptera has long been employed to refer to small, often night active moths, though it is by no means a sound scientific distinction from the bigger so called Macrolepidoptera (PARENTI 2000). Nevertheless the term has acquired a common acknowledgement and is recognised by entomologists. Therefore, in the frame of this study it is used to refer to small moths, excluding (Sesiidae, Cossidae and Zygaenidae).

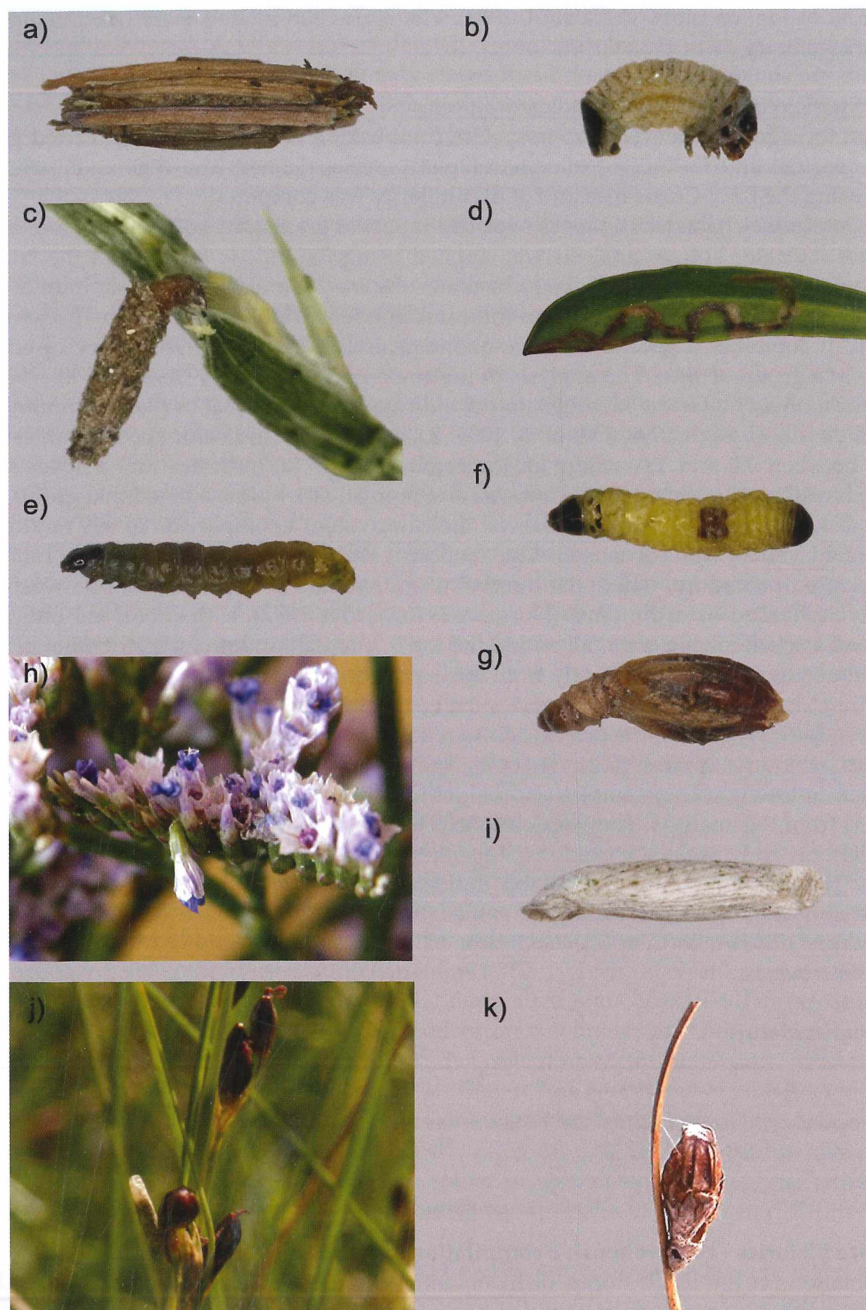


Plate 1 *Whittleia retiella*: larval case (5mm) (a), larva (3mm) (b), young larva with first case on *Puccinellia maritima* (c); *Bucculatrix maritima*: leafmines on *Aster tripolium* (d), larva (4mm) (e); *Goniodoma limoniella*: larva (4mm) (f), larval case on *Limonium vulgare* (h); *Coleophora adjunctella*: larva in case (4mm) (g), larval case on *Juncus gerardii* (3mm) (k); *Coleophora glaucicolella* (4mm): larval case (i), larval case on *Juncus gerardii* (j).

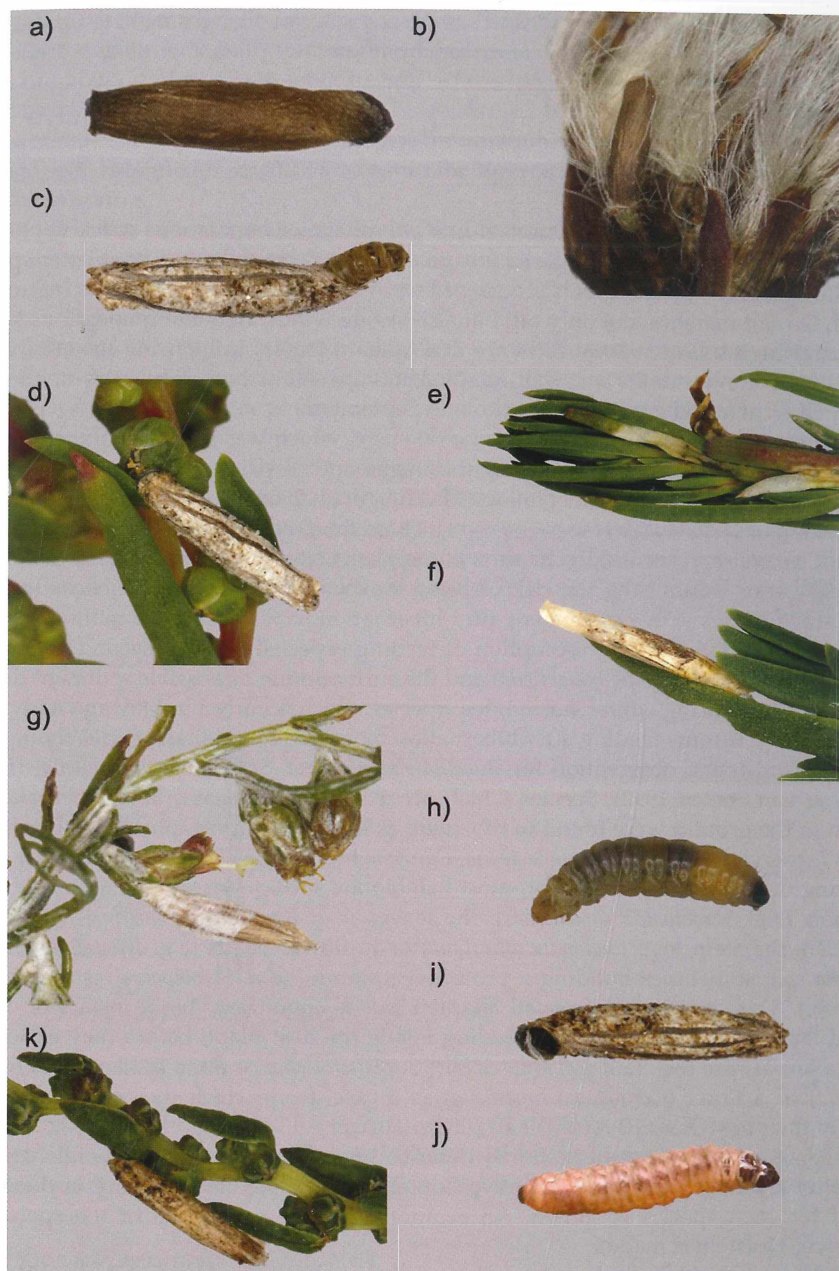


Plate 2 *Coleophora asteris*: larval case (5 mm) (a), larval case on *Aster tripolium* (b); *Coleophora atriplicis*: larval case and larva (4 mm) (c), larval case on *Suaeda maritima* (d), *Coleophora deviellei*: frass on *Suaeda maritima* (e), larval case on *Suaeda maritima* (5 mm) (f), *Coleophora artemisiella*: larval case on *Artemisia maritima* (g), larva (3 mm) (h), *Coleophora adspersella*: larval case (4 mm) (i), larval case on *Suaeda maritima* (4 mm) (k); *Coleophora salicorniae* larva (5 mm) (j).

The life history of a species is defined as the sequence of changes making up the span of an organism's life and can be described by its unique phenological appearances in different stages of its development, its size and its time of occurrence throughout the year.

Microlepidoptera, like all Lepidoptera, undergo a so-called complete metamorphosis including life stages as egg, larva, pupa and imago, which are distinguishable for most species.

While many species are eurytopic, feeding polyphagously on various species of plants, some species specialised on single or few halophytes as host plants. These latter species are called halobiontic, since their occurrence seems to be restricted to habitats influenced by salt. On salt marshes, not only salt but also strong winds, frequent inundations by sea water and high sedimentation rates are determinant factors influencing the survival of moths. Halobiontic moths are well adapted to cope with these intricacies of life and mainly fly in a period from early June to mid September.

Halobiontic moths hibernate in their larval stage, which was identified as more resistant to unpleasant climatic conditions than eggs and pupal stages and thus are well adapted to flooding and sedimentation (MATTILA et al. 2008). They are mostly sheltered by a cocoon or larval case close to the rootstock on the ground (e.g. *Eucosma* sp., *Whittleia retiella*, *Coleophora* sp.) or hidden in parts of the plants (e.g. *Phalonia affinitna*, *Goniodoma limoniella*), thus minimising the risk of being washed away. Possibly, hibernation in a larval stage allows active movement after hibernation to reach suitable mating sites (as observed in *W. retiella*), the resumption of feeding especially for the second generation (as observed for *Scrobipalpa instabilella*) and the surmounting of possible sediment deposits on the cases during winter storm tides. Species which occurred in May and early June were found to resume feeding after hibernation more frequently than species flying later in the season (pers. observation for *Bucculatrix maritima*, *Scrobipalpa instabilella*) (Hemminga & van Soelen 1992). Species which occur later in the season and hibernate in a cocoon in the ground were found to hibernate as last instar larvae, pupating after hibernation (observed e.g. for *Eucosma lacteana*, *Eucosma tripoliana*, *Coleophora artemisiella*).

During their larval development, most halobiontic species are endophagous either in the roots (e.g. *Scrobipalpa samadensis*), the leaves (e.g. *Bucculatrix maritima*, *Scrobipalpa nitentella*), the stem (e.g. *Phalonia affinitana*) or in flower heads (e.g. *Aristotelia brizella*, *Eucosma* sp.), sometimes building a protective spinning (e.g. *Scrobipalpa instabilella*, *Eucosma* sp.). They are, therefore, well adapted to site conditions. Early instars of coleophorid larvae were found to start feeding inside the host plant, before they either develop a larval case (e.g. *C. deviella*, *C. asteris*, *C. glaucicolella*) or use a seed capsule (*C. adjunctella*) or a floret (*Goniodoma limoniella*) as a case, from which they feed mostly on seeds of their host plant (BUCHELI et al. 2002).

Each stage of development is shortly described for all on the west coast of Schleswig-Holstein occurring halobiontic Microlepidoptera, and, if possible, a figure of the flight period for each species is shown. An evaluation of the occurrence of the species in Schleswig-Holstein is made.

Pictures of imagines displayed on plates 5-7 were taken by Mona Dahmen, pictures displayed on plates 1-4 were taken by C. Rickert if not stated otherwise.

937 *Whittleia retiella* Newman, 1847

Host plant: *Puccinellia maritima* and other grasses of salt marshes.

Ovum: Oviposition takes place in the pupal skin in May.

Larva: The case is made with longitudinally attached pieces of grass, some of which project over the silken tube at the rear end and has a total length off 8-12 mm (Plate 1a). The cases can be found from September to April at the base of the host plant. These descriptions by HÄTTENSWILER (1985) could be confirmed by examinations of more than 50 larval cases. Young larvae have been found feeding on *Puccinellia maritima* in early June (Plate 1b, c), indicated by small damages at the base of the plant. Larvae do not resume feeding in spring.

Pupation: In the case affixed to grasses, where male pupa can be found near the roots while females are located higher up on the grass blade (BENGTON & PALMQVIST 2008). The cases can be found from the end of April to the beginning of May before hatching.

Imago: Wingspan: 8-10 mm.

Descriptions (following HÄTTENSWILER 1985) were validated examining more than 100 male (Plate 5a) and 27 female (Plate 5b) specimens. The species is univoltine and males were seen flying in sunshine at noon in the beginning of May, sometimes until the end of May, depending on the weather. In 2007, 2008 and 2009 a very warm and dry spring led to male moths occurring only for a very short period between the 1st and the 7th of May on warm and windless days (Fig. 6). In 2010 after a long and cold winter and spring, few males could only be seen flying in late May. Females could be found in the case attached to a blade of grass attracting males through pheromones. This could be shown in an attraction experiment with two females positioned in a cage which was deposited in the salt marsh (RICKERT et al. 2009).

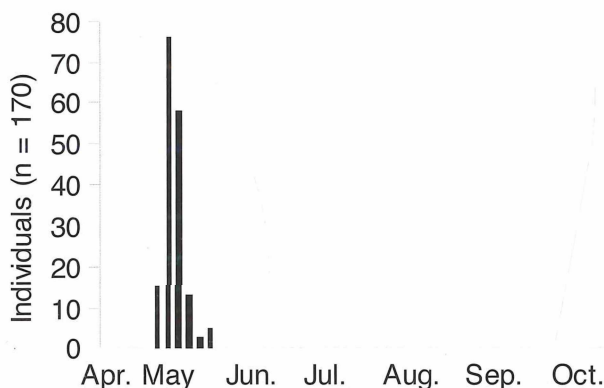


Fig. 6: Flight period of *W. retiella* in Schleswig-Holstein

W. retiella was first recorded for Germany in 2007 (RICKERT et al. 2009) and was found in high abundances on all investigated salt marshes except heavily grazed plots, where its food plants *Puccinellia maritima* and *Festuca rubra* occurred. The species can be very abundant in salt marshes.

1081 *Bucculatrix maritima* Stainton, 1851

Host plant: *Aster tripolium*.

Ovum: The eggs are placed on the underside of leaves in June and August.

Larva: Larvae mine at first in a long, narrow gallery, showing linear frass which is black or reddish. When the larva is leaving the primary mine, they make a series of shorter, full-depth mines (Plate 1d) and may continue feeding in this manner until fully grown (JANSEN & HEMMINGA 1988). Occasionally, the mines were found in the epidermis of

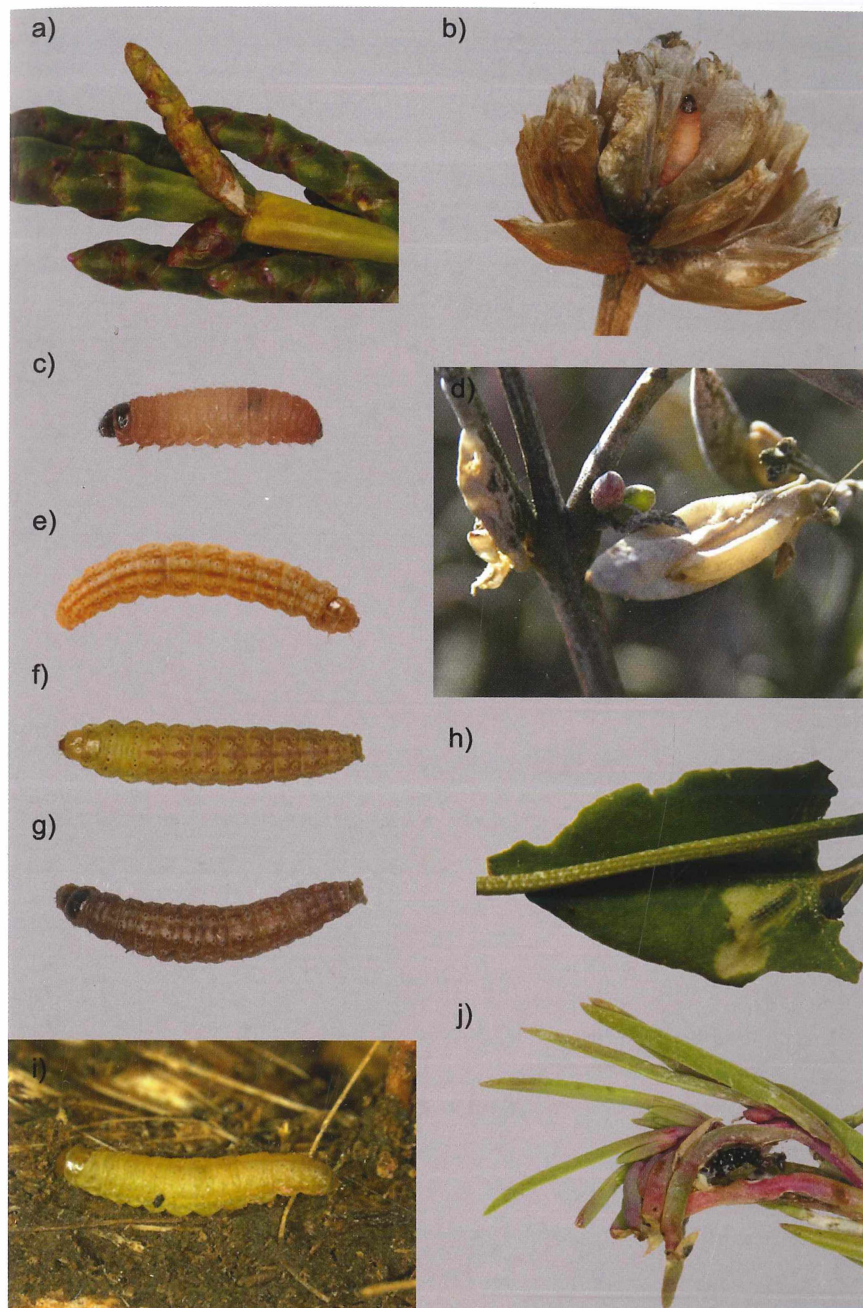


Plate 3 *Coleophora salicorniae*: larval case on *Salicornia europaea* (a); *Aristotelia brizella*: larva on *Armeria maritima* (b), larva (7 mm) (c); *Scrobipalpa instabilella*: mine on *Atriplex portulacoides* (d), larva (10 mm) (e) (photo Smith); *Scrobipalpa nitentella*: larva (9 mm) (f), mine on *Atriplex prostrata* (h); *Scrobipalpa salinella* larva (11 mm) (g), mine and spinning on *Suaeda maritima* (j); *Phalonidia vectisana*: larva of (4 mm) (i) (photo: M. Jansen).

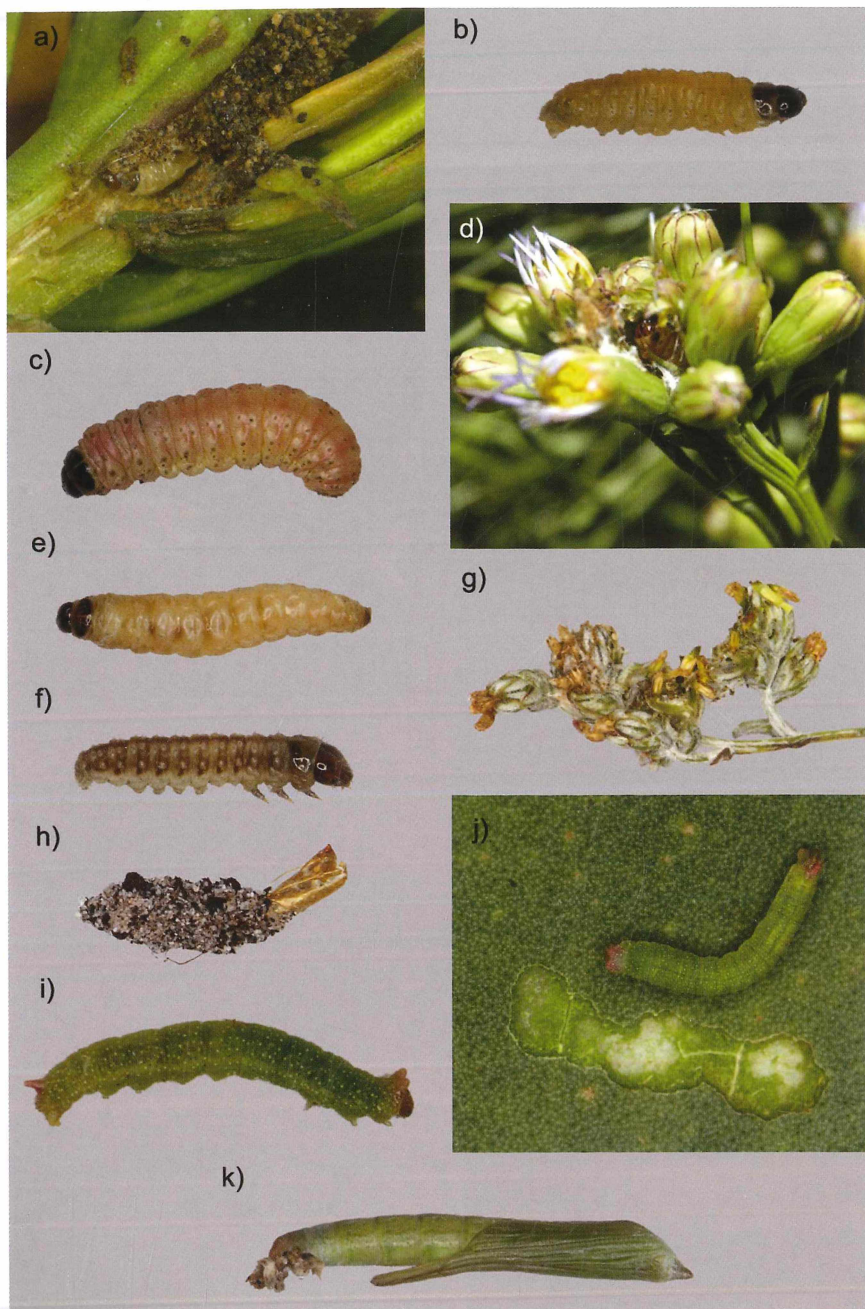


Plate 4 *Phalonidia affinitana*: larva of in stem of *Aster tripolium* (a) (photo M. Jansen), larva (4 mm) (b); *Eucosma catoptrana*: larva (13 mm) (c), larva spinning on *Aster tripolium* (d); *Eucosma tripoliana*: larva (12 mm) (e); *Eucosma lacteana*: larva (11 mm) (f); spinning on *Artemisia maritima* (g), pupa case made of sand (h); *Agdistis bennetii*: larva (17 mm) (i), feeding larva on *Limonium vulgare* leaf (j), young pupa (20 mm) (k).

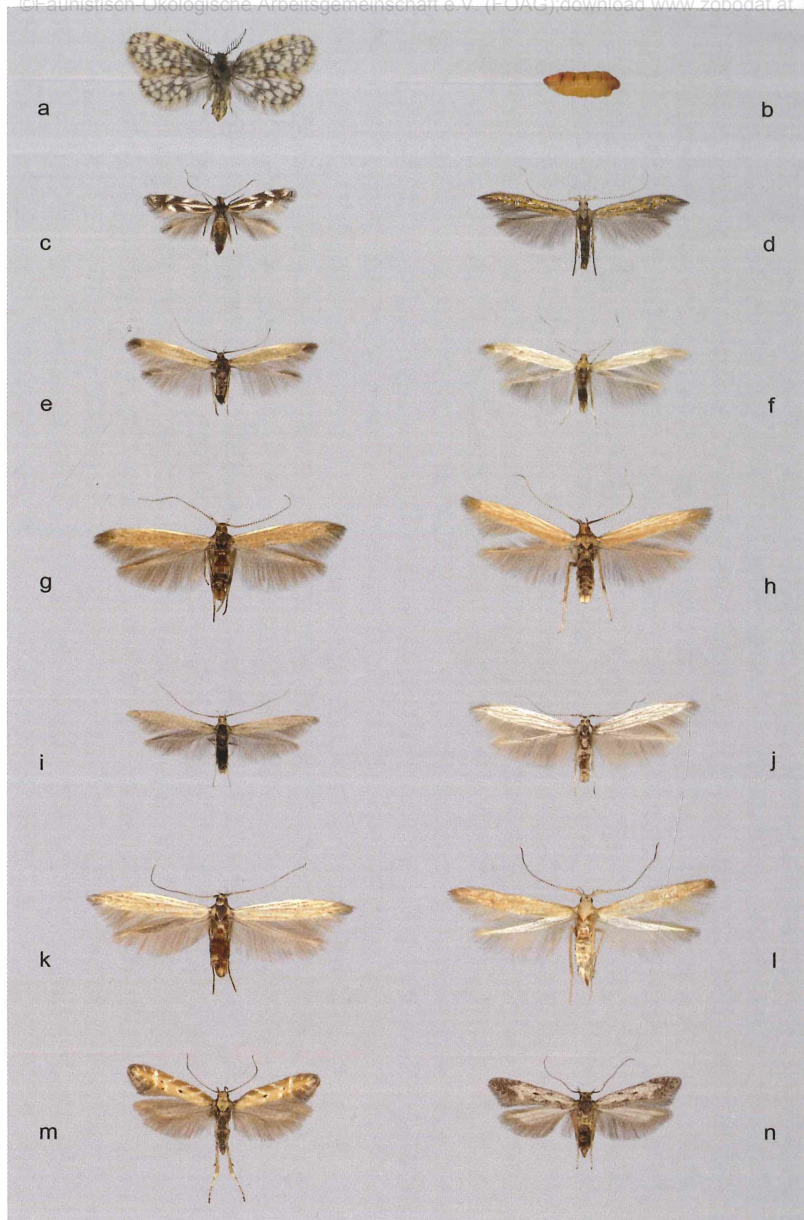


Plate 5: *Whittleia retiella* Newman, 1847: male (10mm) (a), female (4mm) (b); *Bucculatrix maritima* Stainton, 1851 (8mm) (c), *Goniodoma limoniella* Stainton, 1884 (11mm) (d), *Coleophora adjunctella* Hodgkinson, 1882 (10mm) (e), *Coleophora glaucicolella* Wood, 1892 (11mm) (f), *Coleophora asteris* Mühlig, 1864 (13mm) (g), *Coleophora atriplicis* Meyrick, 1928 (13mm) (h), *Coleophora deviella* Zeller, 1847 (10mm) (i), *Coleophora artemisiella* Scott, 1861 (12mm), k) *Coleophora adpersella* Benander, 1939 (14mm) (j), *Coleophora salicorniae* Heinemann & Wocke, 1876 (14mm) (l), *Aristotelia brizella* (Treitschke, 1833) (10mm) (m), *Monochroa tetragonella* (Stainton, 1885) (10mm) (n).; wingspan in brackets.

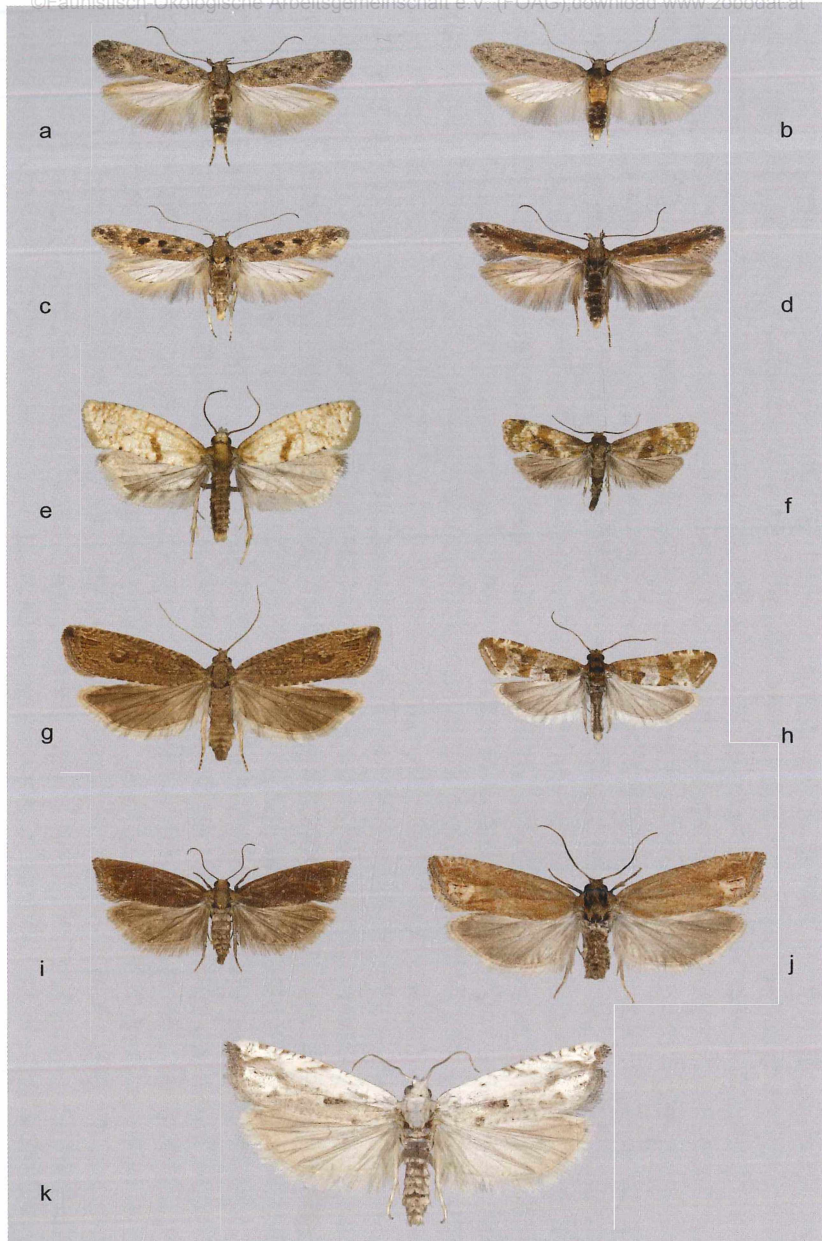


Plate 6: *Scrobipalpa instabilella* (Douglas, 1846) (13mm) (a), *Scrobipalpa nitentella* (Fuchs, 1902) (13mm) (b), *Scrobipalpa salinella* (Zeller, 1847) (13mm) (c), *Scrobipalpa samadensis* (Pfaffenzeller, 1870) (13mm) (d), *Phalonidia affinitana* (Douglas, 1846) (14mm) (e), *Phalonidia vectisana* (Humphreys & Westwood, 1845) (10mm) (f), *Bactra robustana* (Christoph, 1872) (16mm) (g), *Lobesia littoralis* (Humphreys & Westwood, 1845) (12mm) (h), *Eucosma catoptrana* (Rebel, 1903) (17mm) (i), *Eucosma tripoliana* (Barrett, 1880) (13mm) (j), *Eucosma lacteana* (Treitschke, 1835) (17mm) (k); wingspan in brackets.

Goniodoma limoniella could be verified as a new record for Germany in 2006 and seems to be spreading northwards. A first record for Denmark was found on Rømø in November 2008 (GREGERSEN & SZYSKA 2009). In Germany, the species was recorded in great abundances in salt marshes of St. Peter-Ording and Westerhever but could not be found further north (RICKERT 2009a) until autumn 2009, when first signs of infestation were recorded in the salt marshes at Morsum Cliff on Sylt and subsequently in other *Limonium*-rich salt marshes on Sylt. It is likely that *Goniodoma limoniella* is spreading in Schleswig-Holstein, gaining common distribution, but further proof remains necessary.

2686 *Coleophora adjunctella* Hodgkinson, 1882

Ovum: The eggs are placed on a floret of *Juncus gerardii* in June and July.

Larva: Larvae feed on the seeds of *Juncus gerardii* from late July, at first internally and then from the case (Plate 1g, k), attaching it to the side of another seed capsule (EMMET et al. 1996). The cases were hard to find and the best method was to look for holes in the seed-capsules where the larva has fed. The case of *C. adjunctella* consists of a hollowed-out complete seed-capsule, lined with silk (HECKFORD 1997). When fully grown in early September, the larvae leave the feeding place to hibernate close to the ground in the case. Pupation: In the case attached low down to a stem from May to June.

Imago: Wingspan: 8-11 mm (Plate 5e). The species is univoltine occurring in late June an July. It flies at sunrise, in the evening and at night and sometimes comes to light (EMMET et al. 1996). The few specimens caught in the salt marshes of Schleswig-Holstein corresponded to the descriptions by EMMET et al. (1996). The species rarely came to light and could only be caught by net sweeping or photoeclector traps infrequently. It therefore must be considered a less common species in Schleswig-Holstein.

2689 *Coleophora glaucicolella* Wood, 1892

Host plants: *Juncus gerardii* and other *Juncus* species

Ovum: The eggs are placed on a floret of various species of rush between July and August.

Larva: When fully grown in May, the case is about 5 to 6 mm long, pale buff with granular debris close to the mouth and resembles the case of *C. alticolella* (SMITH 2010). In April, the larvae were active on the plant (Plate 1j). Cases which had recently been expanded had a gusset of clean white silk along the underside and appeared somewhat laterally compressed (Plate 1i). Larval cases were found numerously on *Juncus gerardii* in salt marshes of St. Peter-Ording and Westerhever, less frequently on the Hamburger Hallig.

Pupation: In the case attached to a stem from June to July.

Imago: Wingspan: 10-12 mm (Plate 5f). The species is univoltine, occurring from June to August at sunrise, dusk and night. It is easily disturbed at daytime (EMMET et al. 1996). *C. glaucicolella* was rarely recorded coming to light, frequently caught by net sweeping and larval cases were regularly found where the food plant occurred. Thus, it can be considered a common species in most Schleswig-Holstein salt marshes.

2716 *Coleophora asteris* Mühlig, 1864

Host plant: *Aster tripolium*

Ovum: In August the eggs are deposited on the flower of the host plant.

Larva: In September and October the larvae feed on the seeds while the case is hidden in the pappus (Plate 2b). Young cases are whitish-grey whereas the fully formed case is made of brown silk, has a length of 6mm, is trivalved, cigar-shaped and with slight longitudinal ridges (Plate 2a). When fully grown, it leaves the feeding place to hibernate

close to the roots in the debris. In August, larval cases were recorded frequently in *Aster*-stands in the flowers, resembling the descriptions by EMMET et al. (1996).

Pupation: In May to June pupation takes place in the case.

Imago: Wingspan: 10-15 mm (Plate 5g). The species is univoltine, occurring from late June to early September. It is nocturnal, infrequently comes to light and can easily be disturbed by day. It is best obtained by collection of larval stages in September. The species is less common in the salt marshes of Schleswig-Holstein but occurs in smaller numbers in most habitats where its host plant is common.

2737 *Coleophora atriplicis* Meyrick, 1928

Host plant: *Atriplex portulacoides*, *Suaeda maritima*, *Salicornia* spp. and *Atriplex littoralis*

Ovum: The eggs are attached to the leaves of the host plant in July or August.

Larva: The larvae feed from late August, at first internally in the seeds and later, after making a case, again on the seeds or, less frequently, on the leaves (HECKFORD 1997). The fully formed case is 6.5 – 7.5 mm in length, sub-cylindrical, tapering slightly at each end and 2 mm in diameter at its broadest point. It is trivalved and made of greyish-brown silk with conspicuous darker longitudinal expansion stripes and heavily decorated with granular material except for the striped areas, giving the case a rather dirty appearance (Plate 2c, d). The larvae are fully grown in October and hibernate attached to a stem at ground level, often partly submerged in the mud. The descriptions by Emmet et al. (1996) on larval cases were confirmed by many (> 100) findings of larval cases in the salt marshes of Schleswig-Holstein.

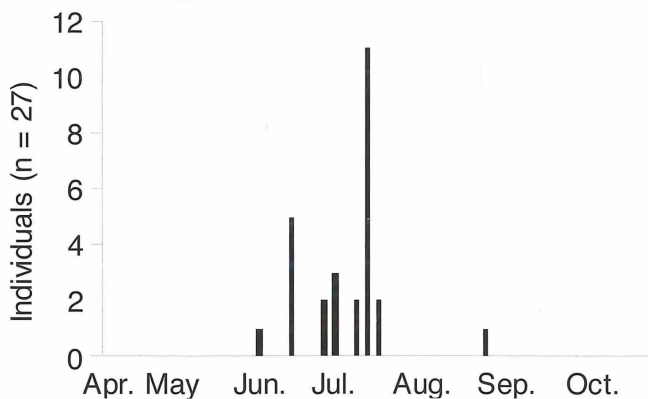


Fig. 8: Flight period of *C. atriplicis* in Schleswig-Holstein.

Pupation: Occurs in June in the case, attached to the vegetation at a higher level than that chosen for winter diapause (HECKFORD et al. 1997).

Imago: Wingspan: 12-14 mm (Plate 5h). The species is univoltine, in favourable years possibly with a short second generation and occurs in July and August (Fig. 8). It flies in the evening and at night and could be best obtained by sweeping or collection of larvae in September. *C. atriplicis* was only infrequently recorded coming to light but was caught in higher abundances by net sweeping and larval stages were commonly found on *Atriplex portulacoides* as well as on *Suaeda maritima*. It is a common species in the salt marshes of Schleswig-Holstein.

2751 *Coleophora deviella* Zeller, 1847

Host plant: *Suaeda maritima*

Ovum: In July, the eggs are attached to the leaves of the host plant.

Larva: The larvae feed on the seeds and leaves from August on (Plate 2e), probably until a late instar, as small cases have not been observed. After building the case, larvae feed on the leaves as well, the case usually being conspicuously placed near the top of the plant (EMMET et al. 1996). When fully grown in October, the larva attaches its case low down on a stem and sometimes just below the surface of the mud. Larval cases of *C. deviella* (Plate 2f) were recorded infrequently in the salt marshes of Schleswig-Holstein.

Pupation: From May to June in the case, attached to vegetation higher up than the site chosen for hibernation.

Imago: Wingspan: 9-10 mm (Plate 5i). The species is univoltine, occurring in late June and July. Bred specimens confirmed the descriptions by EMMET et al. (1996). *C. deviella* must be considered a rare species and could best be obtained by searching for larval cases. It could not be attracted by light.

2816 *Coleophora artemisiella* Scott, 1861

Host plant: *Artemisia maritima*.

Ovum: In late July and August the eggs were attached to the leaves of the host plant.

Larva: Larvae start feeding in August, first mining the leaves, later feeding on the flowers and seeds. The fully formed case is 6-7 mm long and made of greyish-brown silk with darker longitudinal stripes. The surface is granular except for the stripes (Plate 2g). Larval cases found in the salt marshes of Schleswig-Holstein were often covered by hairy white silk similar to the white cottony fibres covering the host plant, camouflaging the case. When fully grown in September (Plate 2h), larvae leave the host plant to hibernate close to the ground.

Pupation: In the case attached low down on a stem from June to July.

Imago: Wingspan: 10-13 mm (Plate 5j). The species is univoltine, occurring from mid June to early August (Fig. 9). All specimens caught in the higher salt marshes of Westerhever and the Hamburger Hallig showed only slight variation in colour and resembled the descriptions by EMMET et al. (1996). Larval cases of *C. artemisiella* were regularly found and adults were frequently caught by net sweeping, sometimes light-trapping on higher salt marshes of Schleswig-Holstein.

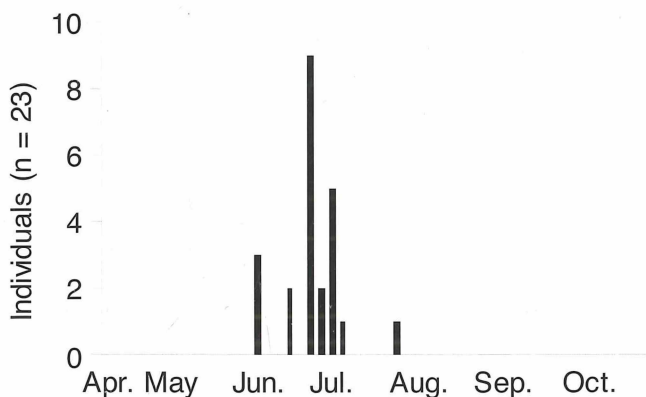


Fig. 9: Flight period of *C. artemisiella* in Schleswig-Holstein.



Plate 7: *Agdistis bennetii* (Curtis, 1833) (25mm) (a), *Agripha selasella* (Hübner, 1813) (24mm) (b), *Pediasia aridella* (Thunberg, 1788) (24mm) (c); wingspan in brackets.

2837 *Coleophora adpersella* Benander, 1939

Host plant: *Atriplex littoralis*, *Atriplex portulacoides*, *Suaeda maritima*

Ovum: In late June or August, the eggs are deposited on a floret.

Larva: The larvae feed from August at first internally and later from a case on the seeds. The case is made of pale ochreous silk only sparsely mixed with darker granular material, the expansion gussets forming pale brown, smooth longitudinal stripes (Plate 2i, k). When fully formed it is cylindrical, 7-8 mm long. Most are fully grown in September. During the last instar the larvae retreat rapidly into the case when disturbed and the case often drops to the ground (EMMET et al. 1996). The larvae leave the host plant for winter diapause.

Pupation: In the case from June to July.

Imago: Wingspan: 13-16 mm (Plate 5k). The species is univoltine, occurring from late June to August. It flies at night and comes to light. It could be recorded only infrequently in the salt marshes of Schleswig-Holstein and must be considered rare.

2858 *Coleophora salicorniae* Heinemann & Wocke, 1876

Host plant: *Salicornia* spp.

Ovum: In late July and August the eggs are attached to a spike of various species of *Salicornia*.

Larva: The larvae feed in September and October internally on the fleshy spikes and seeds, giving no evidence of their presence. In the last instar it makes a case of a cut-off tip of a spike and continues to feed by attaching this to another spike (Plate 3a). At this stage pale sawdust-like frass at the end of the spike betrays the presence of the larvae (EMMET et al. 1996). The larvae can only be found during the few days while feeding from the case (Plate 2j). Soon afterwards the cases drop to the surface of the mud and the larvae leave the case and burrow into the mud making a silk-lined tube and hibernating fully fed at the bottom in a parchment-like cocoon until June.

While signs of larval occurrences were frequently found on *Salicornia* sp. growing in the lower salt marsh next to *Aster tripolium* and *Suaeda maritima*, hardly any larvae were found on *Salicornia* sp. in the pioneer marsh adjacent to the mudflats. Descriptions by EMMET et al. (1996) were confirmed and larvae were found to readily accept provided fine-grained sand for pupation.

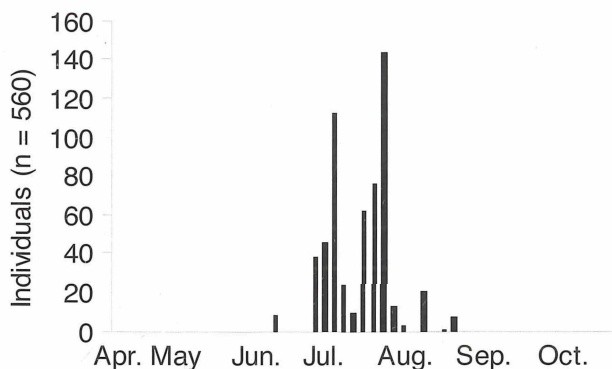


Fig. 10: Flight period of *C. salicorniae* in Schleswig-Holstein.

Pupation: In the cocoon, but in captivity occasionally within the case if mud has not been provided.

Imago: Wingspan: 12-14 mm (Plate 5l). The species is univoltine, occurring in the second half of July and August (Fig. 10). It flies at night and can disperse widely. The species was common throughout Schleswig-Holstein salt marshes and could most easily be obtained by collection of larvae in late August and September. It was mostly found in depressions and salt pans in lower salt marshes whereas *Salicornia*-plants in pioneer salt marshes were hardly infested.

3237 *Aristotelia brizella* (Treitschke, 1833)

Host plant: *Armeria maritima*, less frequently *Limonium vulgare*.

Ovum: In June the eggs are deposited on the flowers of the host plant.

Larva: The first generation larvae make a tubular silk tunnel in a seed head from which they feed on the unripe seeds in June and early July. Several larvae may occupy a single flower head (Plate 3b, c). The second generation larvae occur in a similar tunnel in a dead dry seed head in September and October and hibernate as a pupa. Descriptions by BLAND et al. (2002) could be verified on several larvae extracted from *Armeria maritima* collected at Schiermonnikoog (The Netherlands). However, flower heads were only infested infrequently without any sign of infestation and only one larva occupying one flower head. Second generation larvae were found to form a spinning of several florets, in which they hibernate. Larvae could not be found in Schleswig-Holstein.

Pupation: Both generations pupate in a slight cocoon spun in several florets of *Armeria* in the larval workings in the flower head (BLAND et al. 2002). Found from October-May and in July.

Imago: Wingspan: 9-10 mm (Plate 5m). The moths fly in early June in the earlier evening hours above *Armeria maritima* and were best obtained by net sweeping. The species is infrequently distributed along the coast of Schleswig-Holstein and must be considered to be very rare.

3320 *Monochroa tetragonella* (Stainton, 1885)

Host plant: *Glaux maritima*.

Ovum: The eggs are attached to the leaves of the host plant.

Larva: In April and May the larvae mine the stem and the root, causing brown discoloration and often killing the plant. Larvae burrow downward, ejecting frass through the entrance hole after reaching the base of the stem and penetrate the rootlets (BLAND et al. 2002). Presumably, young larvae hibernate in the roots. Larvae of *M. tetragonella* could not be found in the salt marshes of Schleswig-Holstein.

Pupation: Presumably pupation takes place in a cocoon in the roots of the food plant.

Imago: Wingspan: 9-11 mm (Plate 5n). The species is univoltine and occurs in June and July. It flew between eight and nine p.m. and was best caught by net sweeping and rarely came to light. Though the host plant was common in most salt marshes of Schleswig-Holstein, only few specimens could be obtained by net sweeping. Presumably, it is found more often on sandy soils (M. Jansen, pers. communication) but could be found in lower salt marshes on the Hamburger Hallig as well. *Monochroa tetragonella* is a rare species in all researched salt marshes.

3609 *Scrobipalpa instabilella* (Douglas, 1846)

Host plant: *Atriplex portulacoides*

Ovum: The eggs are deposited on the leaves of *Atriplex portulacoides* from early June to July.

Larva: Larvae feed in the leaves of the food plant causing an almost bladdered effect. The larvae make a small round hole in the skin of the leaf through which they eject their

frass, the mine itself being quite clean (BLAND et al. 2002). The larvae in the mines were seemingly unaffected by periodic submergence. Some larvae were found to spin leaves together in an untidy spinning during March to May (Plate 3d). Larvae resumed feeding in spring before pupation. During this study, descriptions by BLAND et al. (2002) could be confirmed and larvae were found abundantly feeding on leaves of *Atriplex portulacoides* in April (Plate 3e), sometimes causing severe damage.

Pupation: In a mud-covered cocoon on the ground, in which the larva remains for weeks before pupating (BLAND et al. 2002).

Imago: Wingspan: 12-14 mm (Plate 6a). The species occurs from June to early September and flies at dusk (Fig. 11), could easily be disturbed by day and came to light. The species is possibly univoltine with a prolonged flight period. *S. instabilella* was one of the commonest species in the salt marshes of Schleswig-Holstein and was regularly recorded in dominant stands of *A. portulacoides*. The study of more than 500 specimens could confirm the high variance in wing colouration and different variations were occurring in parallel.

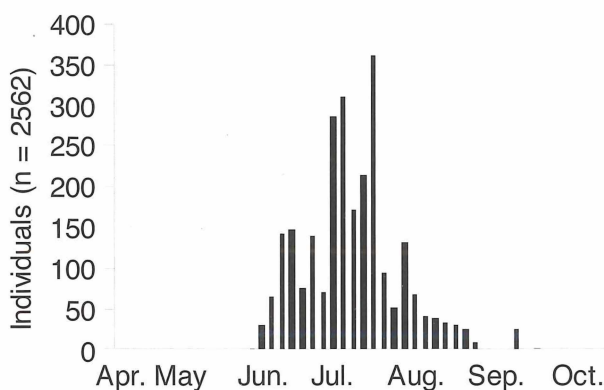


Fig. 11: Flight period of *S. instabilella* in Schleswig-Holstein.

3616 *Scrobipalpa nitentella* (Fuchs, 1902)

Host plant: *Atriplex prostrata*, *Atriplex littoralis*, *Atriplex portulacoides*.

Ovum: The eggs are attached to the leaves of the host plant in July and August.

Larva: The young larvae mine in the leaves. The first instar mines were typically U-shaped whilst later mines were irregular (Plate 3h). The penultimate instar larvae (Plate 3f) leave the mine and live until maturity in a silken tube amongst the seeds, feeding mostly on the unripe seeds (BLAND et al. 2002). They could be found from September to October. Larvae of *S. nitentella* were infrequently found on *Atriplex prostrata* and *A. littoralis*, the infrequency of occurrence induced by the scattered distribution of its host plants.

Pupation: Hibernates as larva in a cocoon made of detritus and sand grains spun together.

Imago: Wingspan: 12-15 mm (Plate 6b). The species is univoltine and occurs from July to August from dusk and can be disturbed by day. It flies at night and comes to light. Possibly due to a preference for *A. prostrata* and *A. littoralis* as host plant, *Scrobipalpa nitentella* is less common than *Scrobipalpa instabilella* in the salt marshes of Schleswig-Holstein.

3628 *Scrobipalpa salinella* (Zeller, 1847)

Host plant: *Suaeda maritima*, *Aster tripolium* and annual *Salicornia* species.

Ovum: The eggs are deposited on the leaves of the host plant.

Larva: The larvae can be found from April-June on spun leaves of *Suaeda maritima* (Plate 3g, j), and in mines and spinings on *Aster tripolium* and annual *Salicornia* spp.. The larvae can make a series of mines and spinings. It hibernates in a cocoon in dead stems of *Aster tripolium* or in the detritus (SMITH 2010). In the salt marshes of Schleswig-Holstein, larvae were frequently found on *Suaeda maritima*, less commonly on *Salicornia* spp..

Pupation: The pupa is found amongst the detritus between June and August. The cocoons have been found in the dead stems of sea aster, which must have been regularly submerged by high tide (SMITH 2010).

Imago: Wingspan: 11-15 mm (Plate 6c). The species is probably univoltine and flies between June and September (Fig. 12). It is regarded as a local and difficult-to-record species and could be most easily found by searching for larvae from late April to early June (BLAND et al. 2002). The larvae can live on the plants on the lowest parts of saltings, which are frequently immersed by the tide (SMITH 2010). Descriptions by BLAND et al. (2002) could be confirmed with more than 100 specimens. The species occurred in most researched salt marshes and therefore can be considered moderately common.

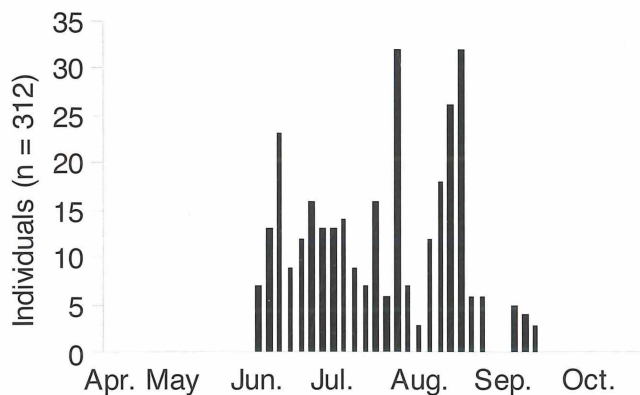


Fig. 12: Flight period of *S. salinella* in Schleswig-Holstein.

3629 *Scrobipalpa samadensis* (Pfaffen-zeller, 1870)

Host plant: *Plantago maritima*, *Plantago coronopus*

Ovum: Presumably, oviposition takes place on the leaves of the host plant close to the base of the leaf.

Larva: The larvae feed in the roots and in blotches in the leaves. Wilting and greying leaves can indicate the presence of larvae in the roots, as does frass in the centre of a plant (BLAND et al. 2002). Young larvae have been found on *Plantago maritima* lightly spinning two leaves together and eating parenchyma. Occasionally, early instars probably mine the leaves. They can be found from April to August. No larvae could be found during this study.

Pupation: It pupates in the root of the host plant from May to August.

Imago: Wingspan: 11-15 mm (Plate 6d). The species is probably univoltine, but emerging over a long period from June to September (Fig. 13). The adults came to light and flew at night. It is often confused with *Scrobipalpa stangei*, which was mentioned by STÜNING (1980) but could not be recorded in Schleswig-Holstein during this study. *S. samadensis*

could be caught infrequently by light trapping or net sweeping. It must be considered a rare species.

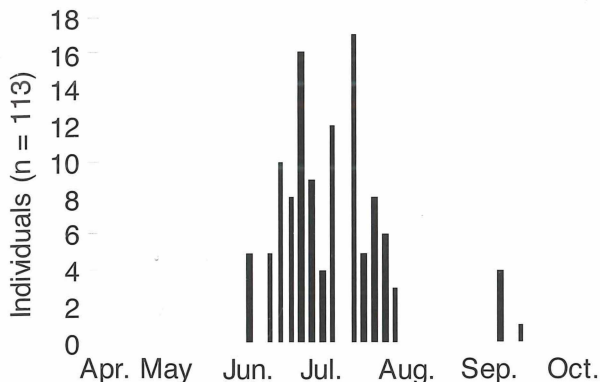


Fig. 13: Flight period of *S. samadensis* in Schleswig-Holstein

4256 *Phalonidia affinitana* (Douglas, 1846)

Host plant: *Aster tripolium*

Ovum: The eggs are placed on the flowers of the host plant in June and July.

Larva: The larvae hibernate fully grown until the following spring. They are feeding on *Aster tripolium*, at first on the pappus, later boring into the upper part of the flower stalk (Plate 4a). In early autumn, before the flower stalk breaks off, the larva bores down to the crown of the plant, and feeds in the rootstock until late autumn when it is full-grown (Plate 4b) (BRADLEY et al. 1979). Larvae were found in the roots in early autumn in all researched salt marshes.

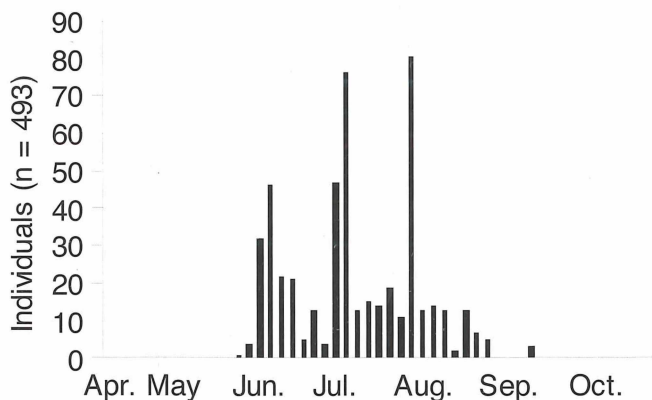


Fig. 14: Flight period of *P. affinitana* in Schleswig-Holstein.

Pupation: Pupation can be observed from late March to May in the larval habitation in the base of the stem or the rootstock, or in the immediate vicinity amongst tidal debris held by broken stems (BRADLEY et al. 1973).

Imago: Wingspan: 14-16 mm (Plate 6e). The species is apparently univoltine and flies from June to August (Fig. 14); however, some authors consider that specimens occurring in August belong to a small second brood (BRADLEY et al. 1979). Normal flight period

was in the late evening and at sunset. Descriptions by BRADLEY et al. (1979) could be confirmed examining more than 100 specimens. The species is widely distributed in the salt marshes of Schleswig-Holstein and was best obtained by net sweeping and was attracted by light frequently.

4263 *Phalonidia vectisana* (Humphreys & Westwood, 1845)

Host plant: *Triglochin maritima*

Ovum: The eggs of the first generation are placed on the flowers, whereas the eggs of the second generation are deposited on the stem close to the crown of the host plant.

Larva: Occurring in June, feeding on the flower heads of *Triglochin maritima*; a second generation occurs in September, burrowing first in the shoots just above the crown and eating the pith (Plate 3i), then working downwards into the crown and roots, where they hibernate until the following spring (BRADLEY et al. 1979). The presence of larvae is indicated by the yellow appearance of the affected shoot and traces of straw-coloured frass on the exterior. No larvae could be observed in the salt marshes of Schleswig-Holstein.

Pupation: The pupa is short and stout, dark orange-brown with the wings of the case and the appendages browner (BRADLEY et al. 1973). Found in April and May and again in June and July in a silken cocoon in a dead flower stem of the host plant, or amongst ground debris.

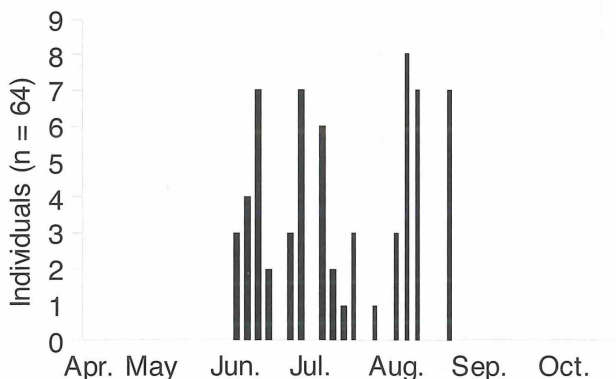


Fig. 15: Flight period of *P. vectisana* in Schleswig-Holstein.

Imago: Wingspan: 9-11 mm. It is an extremely variable species showing considerable variation in the fore-wing pattern (Plate 6f). The descriptions by BRADLEY et al. (1979) could be verified examining more than 20 specimens. Most specimens caught in the salt marshes of Schleswig-Holstein appeared almost uni-coloured olive-brown. The species is bivoltine occurring from mid May to the end of June (Fig. 15), and in a second generation from July to September. It becomes active in the evening as sunset approaches and during warm calm weather. *P. vectisana* was often seen flying until dusk above the host plant. The species was frequently caught by net sweeping and occasionally came to light. Its distribution however, was scattered and restricted to a few salt marsh spots. It can be considered a moderately common species.

4659 *Bactra robustana* (Christoph, 1872)

Host plant: *Bolboschoenus maritimus*

Ovum: In June and July the eggs are placed at the base of a leaf.

Larva: The larvae are found from August to June; feeding on *Bolboschoenus maritimus*, living in the stems and causing them to become discoloured and decay prematurely. Retarded growth and yellowish discolouration of the tips of sedge usually indicate the presence of larvae (BRADLEY et al. 1979). Larvae could be found only infrequently in stands of the host plant at Schobüll and St-Peter-Ording.

Pupation: It is brownish yellow and found in June. Pupation takes place in a strong, white silken cocoon in the larval habitation. A stem which contains a pupa shows signs of decay and is usually black in the region of the cocoon (BRADLEY et al. 1979).

Imago: Wingspan: 16-22 mm (Plate 6g). The species flies in June and July frequenting salt marshes with a freshwater supply, necessary for the occurrence of the host plant. The moths are generally lethargic, rest among the marsh vegetation and can easily be disturbed during daytime (BRADLEY et al. 1973). In the evening, it flies about its habitat and occasionally comes to light. It was only found in salt marshes of Schobüll and St. Peter-Ording, because of the restriction of its host plant, but occurred here frequently.

4806 *Lobesia littoralis* (Humphreys & Westwood, 1845)

Host plant: *Armeria maritima*

Ovum: The eggs are most likely attached to the florets of *Armeria maritima*.

Larva: Larvae are found from April to May, with a second generation in August. The larvae of the first generation live in the flower-heads, feeding on the unripe seeds, or in the heart of young shoots, spinning a silken tube among the leaves. The larvae of the second generation live in the dead flower-heads, feeding on the seeds. Larvae bore into young shoots and flowers, sometimes leaving infested flower-heads slightly distorted. The species hibernates as a larva in the shoots of *Armeria maritima* (BRADLEY et al. 1979). No larvae of *L. littoralis* could be found in the salt marshes of Schleswig-Holstein.

Pupation: It is light olive-brown and found from May to June and August to September. Pupation takes place in a strong, white silken cocoon concealed in a flower-head or amongst the leaves of the host plant (BRADLEY et al. 1979).

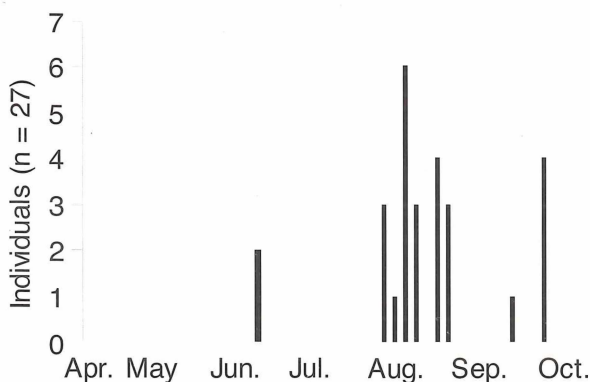


Fig. 16: Flight period of *L. littoralis* in Schleswig-Holstein.

Imago: Wingspan: 11-16 mm. It is an extremely variable species and shows a wide range of individual variation in the fore-wing markings and colouration (Plate 6h). Descriptions by BRADLEY et al. (1979) could be verified by examination of more than 20 specimens, though variations were less distinct. The species is bivoltine flying in June and July (Fig. 16), and with a second generation in September and October (BRADLEY et al. 1979). Frequenting coastal cliffs and places along estuaries and saltings where *Armeria*

maritima flourishes. The moths were flying in the afternoon sunshine and later were sometimes attracted to light. It is one of the rarer species in the salt marshes of Schleswig-Holstein, though in the Netherlands an increase was reported which was connected to the cultivation of *Armeria maritima* as a garden plant with *L. littoralis* following its host plant and extending its range of distribution (KUCHLEIN 1993).

4947 *Eucosma catoptrana* (Rebel, 1903) syn. *rubescana* (Constant, 1895)

Host plant: *Aster tripolium*

Ovum: In June and from late July to August the eggs are deposited on a flower of *Aster tripolium*.

Larva: Descriptions by BRADLEY et al. (1979) could be confirmed examining more than 20 larvae, though the distinction between *E. catoptrana* and *E. tripoliana* is difficult and can only be made for certain by breeding. The larvae can be found in August, feeding amongst spun flowers of *Aster tripolium* (Plate 4c, d) in a manner similar to that of the seemingly more common *E. tripoliana*, but occurring somewhat earlier in the season and usually fully grown by the end of August. It then leaves the spinning and constructs a cocoon beneath tidal debris close to the host plant in which it overwinters until the following spring.

Pupation: Pupation takes place in a cocoon spun up in tidal debris amongst the stems of the host plant.

Imago: Wingspan: 16-20 mm (Plate 6i). The species is possibly bivoltine occurring with a peak in June and again in late July and August (Fig. 17). The moths were most active at dusk and were frequently coming to light. Specimens caught in the salt marshes of Schleswig-Holstein corresponded to the descriptions by BRADLEY et al. (1979), and most specimens were ochreous-white with distinct markings to dark brownish, almost seeming uni-coloured. Bright reddish specimens were not encountered. The species occurred abundantly in Schleswig-Holstein salt marshes and is one of the commonest species, although it is known to be rare in The Netherlands and Great Britain.

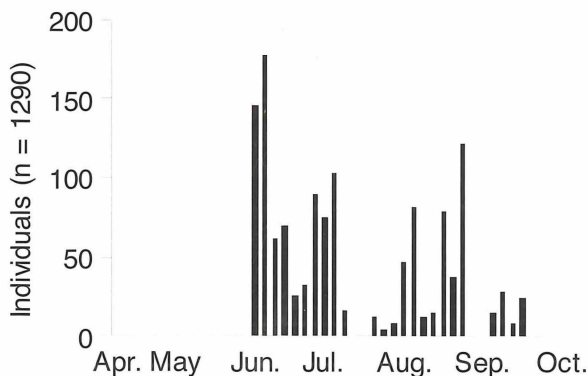


Fig. 17: Flight period of *E. catoptrana* in Schleswig-Holstein.

4948 *Eucosma tripoliana* (Barrett, 1880)

Host plant: *Aster tripolium*

Ovum: Eggs are placed in the flower of *Aster tripolium* in August and September.

Larva: The larvae can be found from late August to October in a loose spinning among the pappus hairs of a flower of *Aster tripolium* (Plate 4a) similar to those of *E. catoptrana*,

feeding on the unripe seeds. Larvae were found frequently like those of *E. catoptrana* and were concordant to the descriptions of BRADLEY et al. (1979). They hibernate from November to May in a silk cocoon covered in detritus fragments and on the ground among debris.

Pupation: It takes place in June and July in a compact cocoon amongst the surface of the debris or the ground, the pupa is chestnut-brown (BRADLEY et al. 1979).

Imago: Wingspan: 13-17 mm. The moths are univoltine and on the wing in late July and August (Fig. 18), frequenting coastal and estuarine salt marshes. Moths caught in the salt marshes of Schleswig-Holstein were mostly of darker complexion, often with less distinct markings (Plate 6j). They fly during the late afternoon and evening and later come to light. Like *E. catoptrana* it is a common species and occurred in all studied salt marshes.

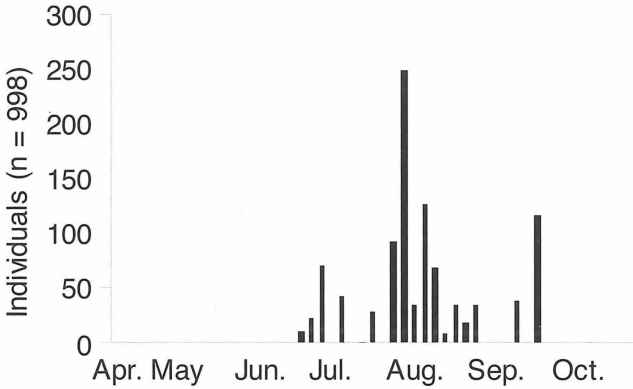


Fig. 18: Flight period of *E. tripoliana* in Schleswig-Holstein.

4949 *Eucosma lacteana* (Treitschke, 1835) syn. *maritima*

Host plant: *Artemisia maritima*.

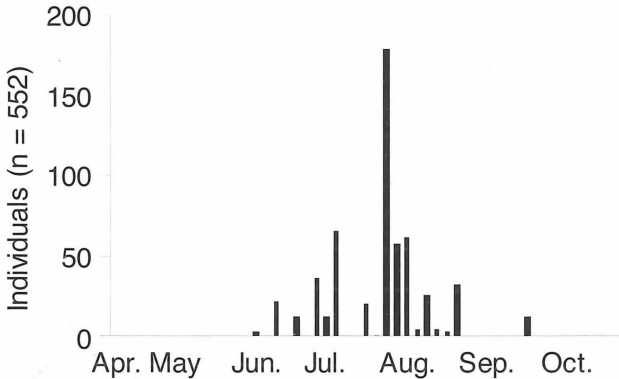


Fig. 19: Flight period of *E. lacteana* in Schleswig-Holstein.

Ovum: The eggs are placed on the floret of *Artemisia maritima* in August.

Larva: Larvae can be found in September and October feeding on the florets and unripe seeds of *Artemisia maritima*, living in the flower spike and spinning the florets and

leaves together to form a silken tube (Plate 4g). Larvae were frequently observed in the studied high marshes and agreed to the descriptions by BRADLEY et al. (1973, 1979) (Plate 4g). When fully grown, the larva leaves the spinning and constructs a cocoon in the ground in which it hibernates before pupating. Larvae readily accepted the provided sandy material and built a cocoon when in captivity (Plate 4h).

Pupation: In June in a silken cocoon amongst debris or in the earth.

Imago: Wingspan: 13-17 mm (Plate 6k). The species is univoltine and moths can be found flying above their host plant in July and August (Fig. 19). The species was rarely found until twilight, when the flight period commences. Most specimens caught in the studied area were conspicuously white with more or less distinct markings on the forewing, agreeing with the descriptions by BRADLEY et al. (1979). It is a common species in the higher salt marshes of Schleswig-Holstein.

5348 *Agdistis bennettii* (Curtis, 1833)

Host plant: *Limonium vulgare*

Ovum: The eggs are attached to the underside of a leaf close to the midrib. For oviposition, the species preferred plants growing on the margin of a group of plants, using those leaves, which are shaded by others.

Larva: Descriptions on the larval appearance by ARENBERGER (1997) were confirmed examining 20 larvae. Larvae were observed to live free, feeding on the underside of a leaf of *Limonium vulgare* being perfectly camouflaged by the colour of the leaves (Plate 4i, j). Larvae turned dirty reddish brown when held in captivity without supply of fresh *Limonium*-leaves. The species hibernates as larvae close to the base of the plant and restart feeding in spring. Young larvae could be found from late April to May, mature larvae mostly in July.

Pupation: Observed on the base of a leaf in June and July, sometimes falling to the ground. Young pupae were as green as the leaf and about 20 mm long, later turning brown (Plate 4k).

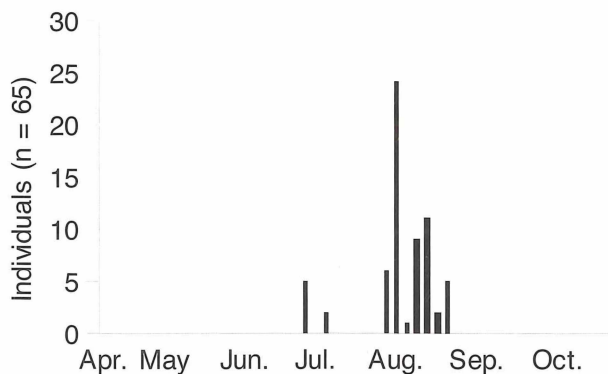


Fig. 20: Flight period of *A. bennettii* in Schleswig-Holstein.

Imago: Wingspan: 24-30 mm (Plate 7a). The species is likely univoltine with a prolonged flight period from late May to late August with peak occurrences in July (Fig. 20). During daytime, the moths rest in stands of their food plant, becoming active at night and occasionally coming to light (GIELIS 1996). The species belongs to the rarer species of the Schleswig-Holstein salt marshes with fluctuating numbers, seemingly affected by strong and long winters.

6266 *Agriphila selasella* (Hübner, 1813)

Host plant: *Puccinellia maritima*, *Festuca ovina* and other *Poaceae*.

Ovum: Eggs are attached to a grass blade and have 23 ridges.

Larva: The larvae live from May to June in a silken gallery covered with plant material and feed on grasses at the base of the shoots (GOATER et al. 2005). No larval stages could be found during this study.

Pupation: Presumably, pupation takes place in June in the silken tube at the roots of the host plant.

Imago: Wingspan: 23-26 mm (Plate 7b). The species is univoltine and adults can be observed from July to September flying at night (Fig. 21). The species occurred infrequently in the salt marshes of Schleswig-Holstein but at times appeared in greater numbers and could be attracted by light.

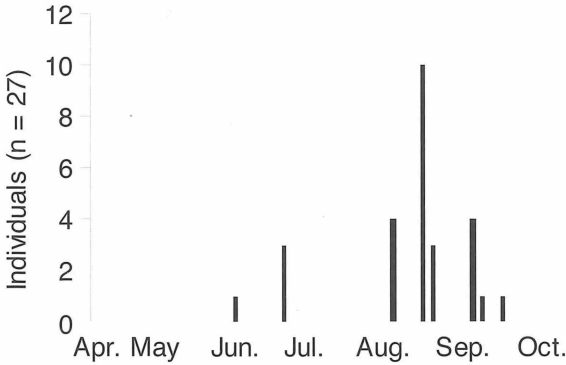


Fig. 21: Flight period of *A. selasella* in Schleswig-Holstein.

6367 *Pediasia aridella* (Thunberg, 1788)

Host plant: *Puccinellia maritima* and *Festuca rubra littoralis*.

Ovum: Eggs are attached to grasses close to the base of the shoots.

Larva: Larva feed on the stem basis of the host plant, living in a tubular silken frass covered gallery on the ground, being found from September to May (GOATER et al 2005). They hibernate on the stem basis or in the root stock in the silken gallery. Larvae were not observed during this study.

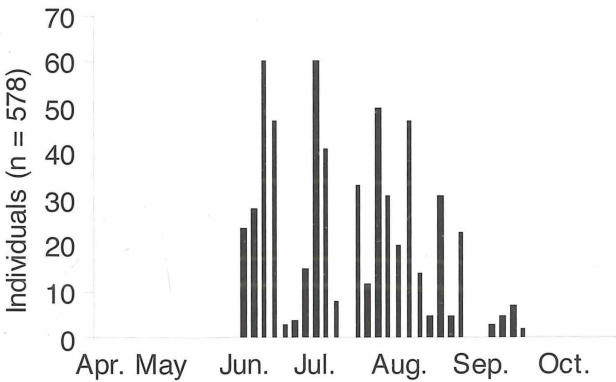


Fig. 22: Flight period of *P. aridella* in Schleswig-Holstein.

Pupation: In an oval cocoon covered with particles of soil in June and July (GOATER et al. 2005).

Imago: Wingspan: 23-26 mm (Plate 7c). The species is probably bivoltine with a prolonged flight period, frequents salt marshes and flies between June and September (Fig. 22), readily coming to light. It hides by day and is rarely encountered until after dark when it flies close to the ground; it rests upon the stems of salt marsh grasses (HASENFUSS 1960, BLESZYNSKI 1965). The species is one of the more common pyralid species in the salt marshes of Schleswig-Holstein though rarely recorded in great abundances.

4.2 Microlepidoptera in salt marshes of Schleswig-Holstein

4.2.1 Current species richness and abundance

In the course of this study a total of 13,018 individuals of moths were caught in the years 2006 to 2009 on the salt marshes of Westerhever, the Hamburger Hallig and St. Peter-Ording. In total 87 species of Microlepidoptera were determined, belonging to 15 different families (Tab. 3, Tab. A1).

Tab. 1: Number of species and individuals caught in the different research localities along the coast of Schleswig-Holstein.

Location	Number of species	Number of halobiontic species	Number of individuals
St. Peter-Ording	21	21	657
Westerhever	65	27	4,443
Hamburger Hallig	50	26	7,918
Schobüll	10	10	not counted
Sylt Hörnum	15	15	not counted
Sylt Morsum	7	7	not counted
Total	87	27	13,018

Of these moths, 27 are described as halobiontic, occurring predominantly in salt marshes, feeding monophagously or oligophagously on halophilic plants. In 2006 *Goniódoma limoniella* (Stainton, 1852) was first proved to be a new record for Germany, and in 2007 *Whittleia retiella* (Newman, 1847), which had not been found since 1959, was recorded in great abundances (RICKERT et al. 2009).

In the salt marshes of the Hamburger Hallig less species (50) were caught overall than in Westerhever (65). This must be explained by the remote location of the salt marshes of the Hamburger Hallig. Additionally, the garden at the light house of Westerhever lead to more tourist species caught by light traps, and thus to a higher species richness. The only halobiontic moth species not caught on the Hamburger Hallig was *Aristotelia brizella*, which feeds on *Armeria maritima*. Figure 23 shows the abundance of moths caught with photoeclector and light traps in all sampled salt marshes. The overall most abundant species were the Gelechidae *Scrobipalpa instabilella*, feeding on *Atriplex portulacoides*, followed by *Bucculatrix maritima* and the two Tortricidae *Eucosma tripoliana* and *E. catoptrana*, which feed on *Aster tripolium*. All four species are halobiontic, occurring mainly on salt marshes.

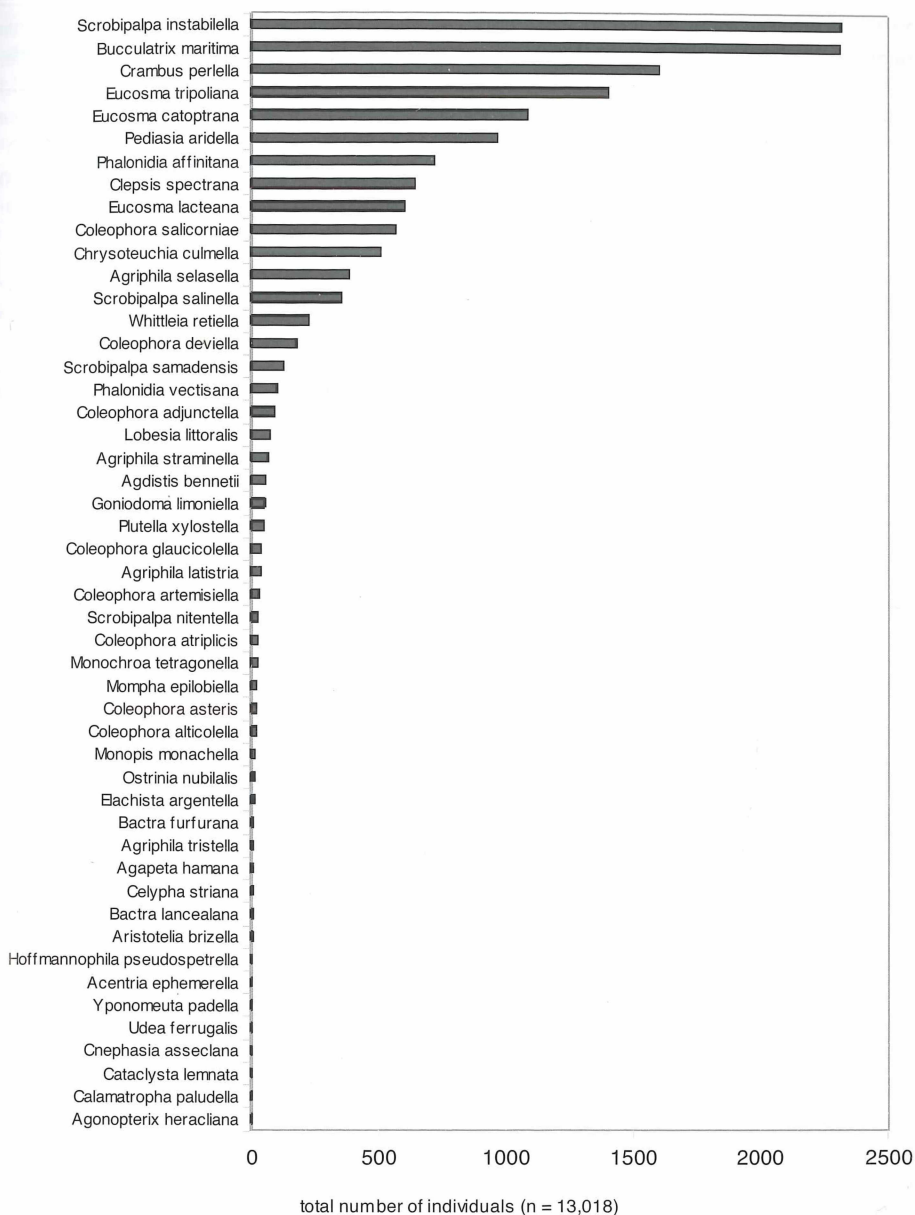


Fig. 23: Allocation of moth species caught in the salt marshes of Westerhever and the Hamburger Hallig by light trapping according to the number of individuals. Singletons and doubletons were excluded.

The third most abundant but eurytopic species found was *Crambus perlella*, which feeds on grasses and is able to develop even in salt marshes. The least frequently found halo-

biontic species by means of trapping methods were *Aristotelia brizella* and *Monochroa tetragonella* as well as the Coleophoridae *Coleophora asteris*, *C. atriplicis* and *C. artemisiella*. *A. brizella* and *M. tetragonella* must be considered rare in salt marshes, since they could not be found abundantly with any method though their food plants *Armeria maritima* and *Glaux maritima* were frequently distributed. Larvae and pupae of the three mentioned Coleophoridae, however, were found regularly. Their under-representation in trapping data must be attributed to a low attraction by light traps and they can be considered moderately common in the salt marshes of Schleswig-Holstein.

Tab. 2: Halobiontic Microlepidoptera caught in the salt marshes of Westerhever, St. Peter-Ording, Hamburger Hallig, Schobüll, Sylt using different methods. The IDKR gives the systematical identification after KARSHOLT & RAZOWSKI (1996).

IDKR	Species	Net sweeping	Light trap	Mercury-Vapour-Lamp	Larvae/Pupa	Photoelectric trap
937	<i>Whittleia retiella</i>	x	-	-	x	x
1081	<i>Bucculatrix maritima</i>	x	x	-	x	x
2442	<i>Goniodoma limoniella</i>	x	x	-	x	-
2686	<i>Coleophora adjunctella</i>	x	x	-	x	x
2689	<i>Coleophora glaucicolella</i>	x	x	x	x	x
2716	<i>Coleophora asteris</i>	-	x	-	x	x
2737	<i>Coleophora atriplicis</i>	x	x	-	x	x
2751	<i>Coleophora deviella</i>	-	x	-	x	-
2816	<i>Coleophora artemisiella</i>	x	-	-	x	x
2837	<i>Coleophora adpersella</i>	x	x	-	-	x
2858	<i>Coleophora salicorniae</i>	x	x	x	x	x
3237	<i>Aristotelia brizella</i>	x	-	-	x	-
3320	<i>Monochroa tetragonella</i>	x	x	-	-	x
3609	<i>Scrobipalpa instabilella</i>	x	x	x	x	x
3616	<i>Scrobipalpa nitentella</i>	x	x	x	x	x
3628	<i>Scrobipalpa salinella</i>	x	x	-	x	x
3629	<i>Scrobipalpa samadensis</i>	x	x	x	-	-
4256	<i>Phalonidia affinitana</i>	x	x	-	x	x
4263	<i>Phalonidia vectisana</i>	x	x	x	-	x
4659	<i>Bactra robustana</i>	x	-	-	x	-
4806	<i>Lobesia littoralis</i>	x	x	x	-	x
4947	<i>Eucosma catoptrana</i>	x	x	-	x	x
4948	<i>Eucosma tripoliana</i>	x	x	x	x	x
4949	<i>Eucosma lacteana</i>	x	x	x	x	x
5348	<i>Agdistis bennetii</i>	-	x	x	x	x
6266	<i>Agriphila selasella</i>	x	x	-	-	-
6367	<i>Pediasia aridella</i>	-	x	-	-	x
Number of species caught by method		23	23	10	20	21

When comparing the different methods, the highest number of species was obtained by light-trapping using a UV-light trap. Especially the rarely caught eurytopic species were exclusively caught with this method. All other methods yielded less 'tourist species' and therefore fewer species in total.

Tab. 3: Halobiontic moth species occurring in the research areas along the Western coast of Schleswig- Holstein.

Species	WeHe	HH	SPO	Schobüll	Sylt Hörnum	Sylt Morsum
<i>Whittleia retiella</i>	+	+	-	-	-	-
<i>Bucculatrix maritima</i>	+	+	+	+	+	+
<i>Goniodoma limoniella</i>	+	+	+	-	-	-
<i>Coleophora adjunctella</i>	+	+	-	-	+	-
<i>Coleophora glaucicolella</i>	+	+	-	-	+	-
<i>Coleophora asteris</i>	+	+	+	+	+	+
<i>Coleophora atriplicis</i>	+	+	+	+	+	-
<i>Coleophora deviella</i>	+	+	+	-	+	-
<i>Coleophora artemisiella</i>	+	+	-	-	-	-
<i>Coleophora salicorniae</i>	+	+	+	+	+	+
<i>Aristotelia brizella</i>	+	-	+	-	-	-
<i>Monochroa tetragonella</i>	+	+	-	-	-	-
<i>Scrobipalpa instabilella</i>	+	+	+	-	+	-
<i>Scrobipalpa nitentella</i>	+	+	-	-	-	-
<i>Scrobipalpa salinella</i>	+	+	+	+	+	-
<i>Scrobipalpa samadensis</i>	+	+	-	-	-	-
<i>Phalonidia affinitana</i>	+	+	+	+	+	+
<i>Phalonidia vectisana</i>	+	+	+	+	+	+
<i>Clepsia spectrana</i>	+	+	+	-	+	+
<i>Bactra robustana</i>	-	-	+	+	-	-
<i>Lobesia littoralis</i>	+	+	-	-	+	-
<i>Eucosma catoptrana</i>	+	+	+	+	+	-
<i>Eucosma tripoliana</i>	+	+	+	+	+	+
<i>Eucosma lacteana</i>	+	+	+	-	-	-
<i>Agdistis bennetii</i>	+	+	-	-	-	-
<i>Agriphila selasella</i>	+	-	-	-	-	-
<i>Pediasia aridella</i>	+	+	+	-	-	-

Table 2 shows the caught halobiontic moth species and the effectiveness of the trapping method in respect to caught species numbers. Net-sweeping and light-trapping with a UV-lamp yielded the most halobiontic species, whereas light-trapping with a Mercury-Vapour-lamp was the least successful method. During the four years of research, larvae and pupa of 20 different species could be obtained, which were bred for proof of identification (pictures of larvae displayed on plates 5 to 10 in chapter 4 on the life history of halobiontic moth). Sampling with photoeclector traps on the Hamburger Hallig resulted in 21 moth species. *Goniodoma limoniella* could only be recorded with single occurrences of larvae in the stems of *Limonium vulgare* but was very rare in the salt marshes of the Hamburger Hallig, while it occurred abundantly in Westerhever and St. Peter-Ording. *Aristotelia brizella* could not be found on the Hamburger Hallig though the host plant *Armeria maritima* was abundant in the moderately grazed salt marshes.

Additional salt marshes in St. Peter-Ording, Schobüll and on Sylt were infrequently visited. Larvae were searched and sweep net samples taken to gain further insight into the distribution of halobiontic Microlepidoptera along the coast of Schleswig-Holstein (Tab. 3).

Tab. 4: Halobiontic Microlepidoptera caught in the salt marshes of Schleswig-Holstein in the years of 1968-1975 by STÜNING (1980) and 2006-2009 by Rickert. Underlined species are additions to the species list of 1968-1975. Symbols: O = found for the first time since 1958; N = new record for Germany; SH = new record for Schleswig-Holstein.

Species	1968-1975	2006-2009
<i>Whittleia retiella</i>	.	O
<i>Bucculatrix maritima</i>	+	+
<u><i>Goniodoma limoniella</i></u>	.	N
<i>Coleophora adjunctella</i>	+	+
<i>Coleophora glaucicolella</i>	+	+
<i>Coleophora alticolella</i>	+	+
<i>Coleophora asteris</i>	+	+
<i>Coleophora atriplicis</i>	+	+
<i>Coleophora deviella</i>	+	+
<i>Coleophora artemisiella</i>	+	+
<i>Coleophora salicorniae</i>	+	+
<u><i>Aristotelia brizella</i></u>	.	+
<i>Monochroa tetragonella</i>	+	+
<u><i>Scrobipalpa instabilella</i></u>	.	+
<i>Scrobipalpa nitentella</i>	+	+
<i>Scrobipalpa obsoletella</i>	+	.
<i>Scrobipalpa salinella</i>	+	+
<i>Scrobipalpa samadensis</i>	+	+
<i>Phalonidia affinitana</i>	+	+
<i>Phalonidia vectisana</i>	+	+
<i>Clepsis spectrana</i>	+	+
<i>Bactra robustana</i>	+	+
<i>Lobesia littoralis</i>	+	+
<u><i>Eucosma catoptrana</i></u>	.	+
<i>Eucosma tripoliana</i>	+	+
<i>Eucosma lacteana</i>	+	+
<u><i>Agdistis bennetii</i></u>	.	SH
<i>Agriphila latistria</i>	.	+
<i>Agriphila selasella</i>	+	+
<i>Pediasia aridella</i>	+	+

Bactra robustana was only caught in St. Peter-Ording and Schobüll since its single host plant *Bolboschoenus maritimus* only occurs in coastal habitats with fresh water seepage. Only few places along the coast of Schleswig-Holstein show these characteristics. As a result, *Bactra robustana* is restricted to these few habitats, where it occurred abundantly. On the isle of Sylt, two different salt marshes located close to Hörnum, sheltered by dunes, and near the Morsum cliff were sampled. Since the salt marsh at the Morsum cliff must be considered a pioneer to low salt marsh mostly without grassy vegetation, only

seven halobiontic species feeding on *Aster tripolium*, *Suaeda maritima* and *Triglochin maritimum* were caught. The salt marshes close to Hörnum are on a higher elevation level, harbouring a greater number of plant species, as well as 15 halobiontic species.

4.2.2 Recorded species richness in the context of known distributions and older studies

The Microlepidoptera of Schleswig-Holstein have been studied infrequently and in varying intensities (ROWECK & SAVENKOV 2002). The halobiontic moths have been more or less neglected, except for a few more conspicuous species which have been recorded by collectors, but no monitoring or research has been conducted since the research of Stün- ing (1980) from 1968 to 1975. To classify the species richness of halobiontic moths re- corded during these studies with the so far known species in Schleswig-Holstein and Germany (GÄDIKE & HEINICKE 1999), comparisons to the species found by STÜNING (1980) were made, as well as to the distributions according to the literature (KARSHOLT & RA- ZOWSKI 1996, GÄDIKE & HEINICKE 1999). Compared to the intensive work in salt marshes by STÜNING (1980), in total eight more species, of which five are halobiontic, have been recorded. Only one halobiontic species (*Scrobipalpa obsoletella*) found by Stün- ing, was not detected during the recent research (Tab. 4).

4.3 The effect of grazing in salt marshes of Schleswig-Holstein

4.3.1 Effects of grazing on the vegetation of salt marshes on the Hamburger Hallig

The environmental variables 'plant height', 'plant cover', 'number of plant species' and 'percentage of bare soil' showed a significant impact of grazing, with significant differ- ences between different grazing intensities. Only 'plant cover' differed non-significantly between ungrazed and extensively grazed, and 'plant height' did not differ between moderately and extensively grazed plots. The litter layer was hardly influenced by graz- ing (Tab. 5).

Tab. 5: Means of the environmental variables plant height, plant cover, plant species, plant litter and bare soil of the four different grazing intensities. Different letters indicate significant differences (n = 132, p < 0.05, Bonferroni corrected) according to ANOVA followed by Wilcoxon-Mann-Whitney U-test.

	Ungrazed	Extensive	Moderate	Intensive
Plant species number	10.10 ^a	12.20 ^b	9.90 ^c	6.70 ^d
Plant height in cm	20.35 ^a	14.03 ^b	13.67 ^b	6.31 ^c
Plant cover in %	87.19 ^a	85.94 ^a	88.96 ^b	82.22 ^c
Litter in %	7.07 ^{ab}	7.77 ^a	6.80 ^b	7.59 ^{ab}
Litter thickness in cm	2.00 ^a	2.00 ^a	2.00 ^a	1.00 ^b
Bare soil in %	5.46 ^{ab}	5.98 ^a	4.09 ^b	10.11 ^c

The vegetation data of 1 m² plots were summarised for each year and the non- parametric multidimensional scaling (NMDS) based on a Bray-Curtis dissimilarity ma- trix shows a clear separation between the intensively and moderately grazed plots and the ungrazed and extensively grazed plots. The ungrazed and extensively grazed plots show high similarities and are positioned on the left bottom of the ordination plot, sepa- rated from the intensively grazed plots on the first and second axis, and from the mod- erately grazed plots on the first axis (Fig. 24). The moderately and intensively grazed plots are separated by the second axis.

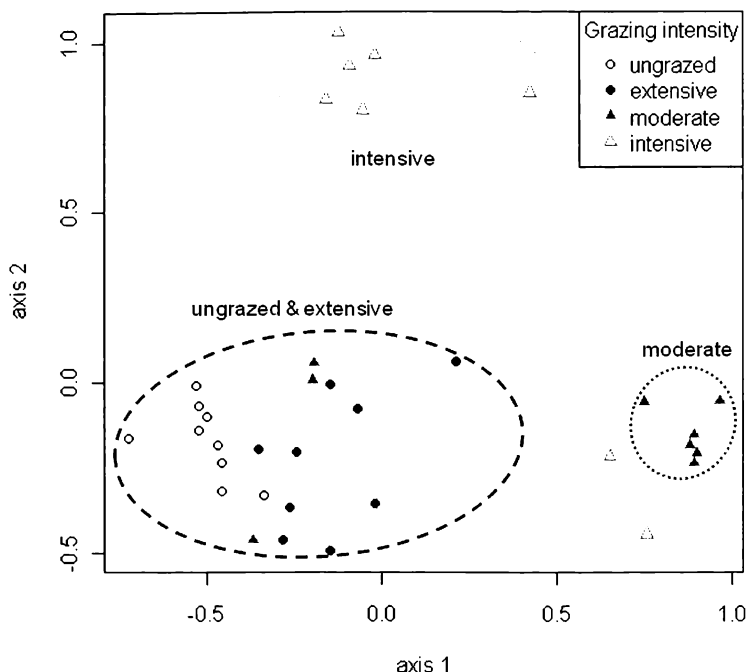


Fig. 24: NMDS of the vegetation data from photoeclector traps of the Hamburger Hallig for the years 2007 to 2009 (Bray-Curtis dissimilarity, stress = 9.26, ADONIS $p < 0.001$).

4.3.2 Effects of grazing on moth assemblages in salt marshes of Westerhever and the Hamburger Hallig

The number of caught species and individuals varied between the years due to climatic factors and trapping intensity. Nevertheless, a clear response of moths to grazing is recognisable in all sampling locations.

Light-trapping in the salt marshes of Westerhever resulted in almost twice as many species in the ungrazed than in the moderately grazed plots with more than four times as many individuals in 2007 (Fig. 25). The least number of species and individuals were caught in the intensively grazed salt marsh.

Results of light and photoeclector traps on the Hamburger Hallig show a similar response to grazing as samples from Westerhever, with an additional differentiation between extensively, moderately and intensively grazed plots.

In total, 33 species of Microlepidoptera could be caught light trapping in the ungrazed salt marsh of the Hamburger Hallig, whereas 37 species were found in the extensively, 23 species in the moderately, and 13 species in the intensively grazed salt marsh (Table A2). The highest number of individuals was recorded in the ungrazed salt marsh, with 3,217 individuals. 2,014 individuals were trapped in the extensively, 1,041 in the moderately, and 280 in the intensively grazed salt marsh.

In comparison to light traps, photoeclector traps yielded less species and individuals, since only those species are trapped which have their life-cycle in the 1 m² underneath the trap and can thus be considered to be resident species.

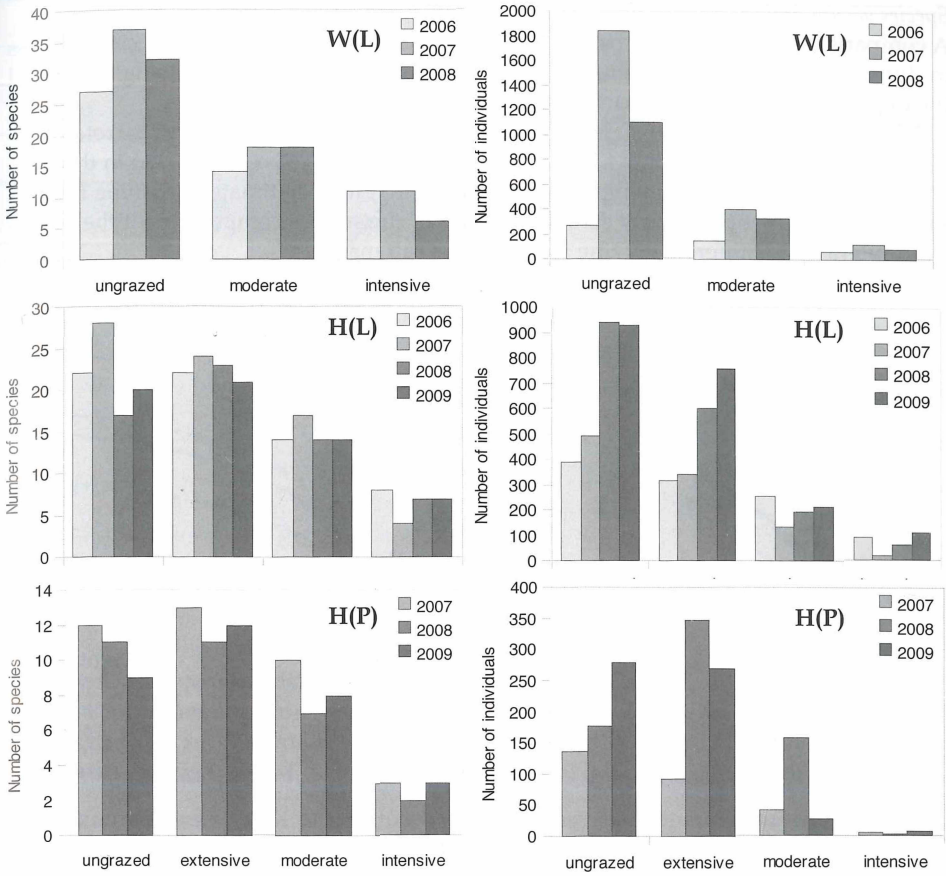


Fig. 25: Number of species and individuals of moths caught in the salt marshes of Westerhever (W) and Hamburger Hallig (H) in the years 2006 to 2009 according to the different grazing intensities and methods (L: light trap, P: Photoeclector).

Figure 25 also shows the number of species and individuals caught with photoeclector traps on the Hamburger Hallig in the years 2007 to 2009 according to the four different grazing intensities. As with light traps, most species were caught in the extensively grazed salt marsh (22 species), whereas only a slight difference in species numbers in the ungrazed (18 species) and the moderately grazed (16 species) was found. With only five species developing, the lowest species richness was recorded in the intensively grazed plots.

A similar pattern was observed if individuals are regarded developing in the salt marshes of the Hamburger Hallig, with 503 specimens caught in the ungrazed, 709 in the extensively, 228 in the moderately, and 16 in the intensively grazed salt marsh (for further details on the numbers of species and individuals see Table A3). Only in 2007 with 93 individuals, less specimens were caught in the extensively than in the ungrazed salt marsh (136 individuals).

Species accumulation curves (SAC)

A comparison of the species accumulation curves, and thus the expected species richness in differently grazed salt marshes in Westerhever and the Hamburger Hallig confirmed the impression of a strong impact of grazing on species richness of moths.

All computed SACs show a clear approximation towards a plateau and therefore justify the presumption, that only a few more species could have been expected in the sampled habitats by higher trapping effort. Consequently, it is legitimate to assume that the sampled data describe a nearly complete extract of the species composition of the Microlepidoptera in the different grazing treatments in salt marshes.

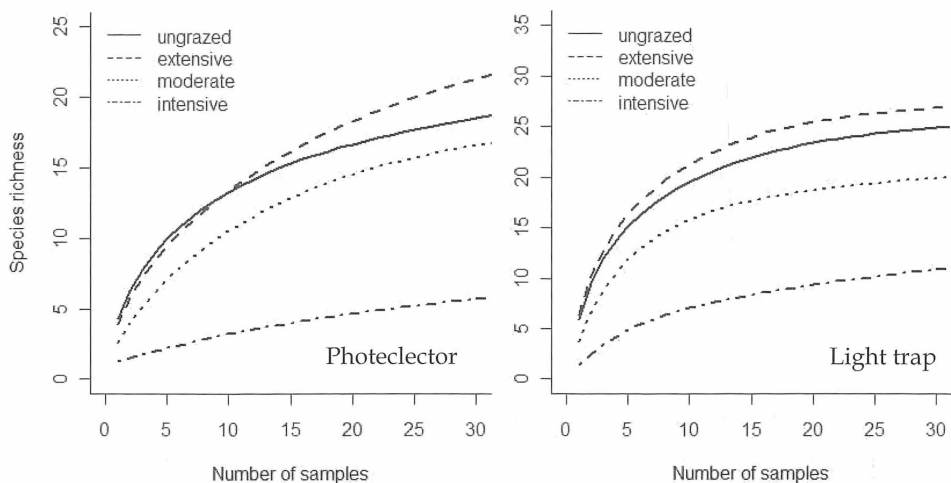


Fig. 26: Species accumulation curves computed according to Kindt's exact accumulator for light trap and photoeclector data of the Hamburger Hallig in different grazing intensities .

In the salt marshes of Westerhever more than twice as many species were caught in the ungrazed than in the moderately grazed salt marsh with the lowest number of species found in the intensively grazed sites (Fig. 26)

A comparison to the species accumulation curves based on the number of light trap samples taken in each paddock of the Hamburger Hallig, however, suggests a higher expected mean number of species for the extensively than the ungrazed sites. The moderately and intensively grazed salt marshes again harboured less species than both the extensively and ungrazed plots (Fig. 26). A similar pattern could be observed when comparing the species accumulation curves of Lepidoptera that developed in different grazing regimes, based on photoeclector samples (Fig. 27).

The expected number of species for the ungrazed and moderately grazed salt marsh differed only slightly, whereas the expected mean number of species was highest in the extensively grazed salt marsh and lowest in the intensively grazed plots.

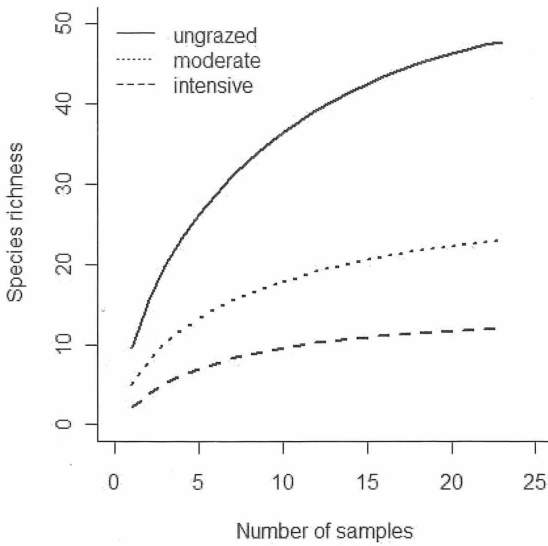


Fig. 27: Species accumulation curves for the ungrazed and grazed salt marshes of Westerhever.

The impact of mid-term grazing duration on species richness of Microlepidoptera

The effect of different grazing intensities on species richness of Microlepidoptera caught with light traps in Westerhever and light and photoeclector traps on the Hamburger Hallig was analysed with a Generalised Estimation Equation (GEE) model (Fig. 28, 29, 30).

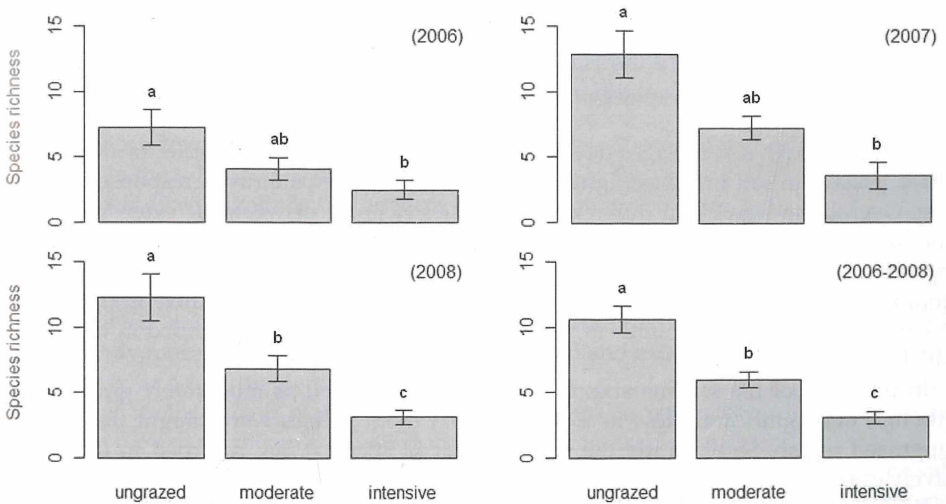


Fig. 28: Mean species richness per m² (± SE) of Microlepidoptera obtained by light trapping in the salt marshes of Westerhever in the years 2006 to 2008. Different characters indicate significant differences ($P < 0.05$, Bonferroni corrected).

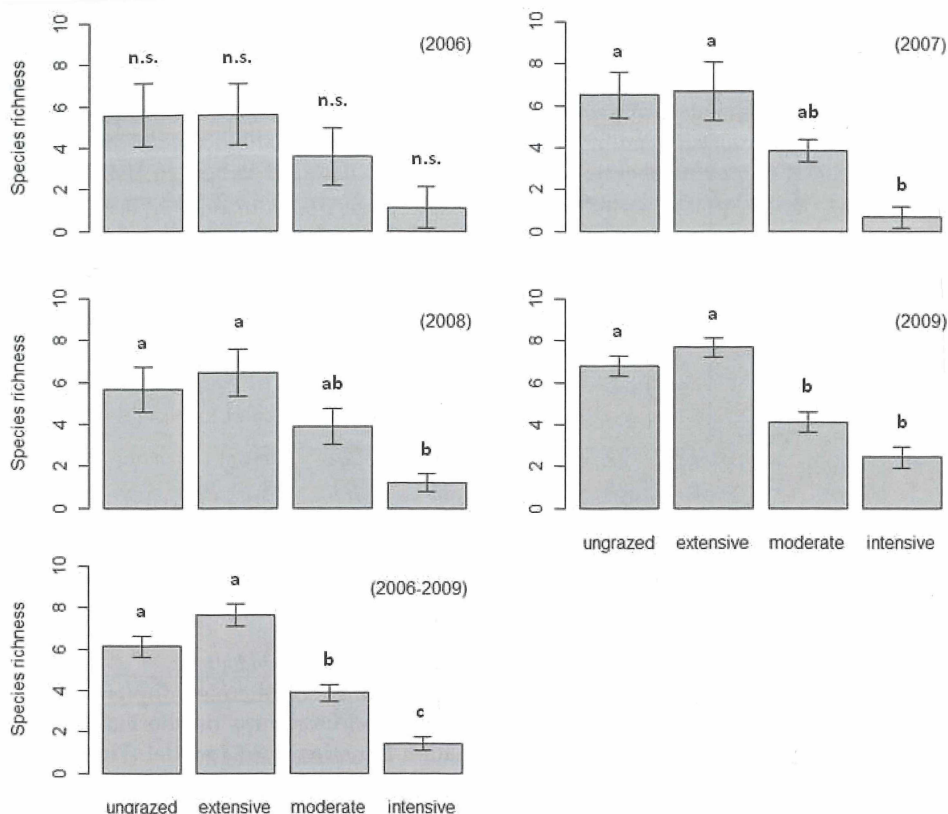


Fig. 29: Mean species richness per m²(± SE) of Microlepidoptera obtained by light trapping in the salt marshes of the Hamburger Hallig in the years 2006 to 2009. Different characters indicate significant differences (P < 0.05, Bonferroni corrected).

Results of moth assemblages developing in the salt marshes (photoeclector traps) and those present in salt marshes (light traps) revealed similar patterns in response to grazing. Overall, no significant differences in species richness between the extensively and the ungrazed control were found, though light trap samples on the Hamburger Hallig revealed a tendency towards higher species numbers in extensively grazed plots. In comparison to the extensively and ungrazed salt marshes, the moderately grazed treatments had lower species numbers whereas the least species were recorded in the intensively grazed plots.

In the plots of the salt marshes of Westerhever classified as moderately grazed, less (though not significantly less in 2006 and 2007) moth species were caught than in the ungrazed marsh. Significantly the least number of species were recorded in the intensively grazed areas.

With light-trapping on the Hamburger Hallig, no significant impact of grazing management on the occurrence of moths species could be detected in 2006, while in the years 2007 to 2009 significant differences in species richness could be observed between the extensively and ungrazed plots and the intensively grazed plots. In 2007 and 2008 differ-

ences in species richness and abundance of the moderately grazed to ungrazed salt marshes were not significant, though a tendency towards lower species numbers compared to the ungrazed control was found. In 2009 significantly less species were found in the moderately grazed than in the ungrazed and extensively grazed plots. In the intensively grazed treatments the least species numbers were detected in each year.

The pattern derived from the photoeclector traps resembles that of the light traps. A similar number of species developed in the extensively and moderately grazed parts of the salt marsh, and for both a significant difference to the intensively grazed plots could be observed in 2007, while no difference in species richness between the extensively and ungrazed plots was found. In 2008, differences between the ungrazed, extensively and moderately grazed areas were less pronounced, but all showed a significant difference in developing species to the intensively grazed plots. The pattern in 2009 was similar, but a significant difference was only found between the two lowest and the two highest grazing intensities.

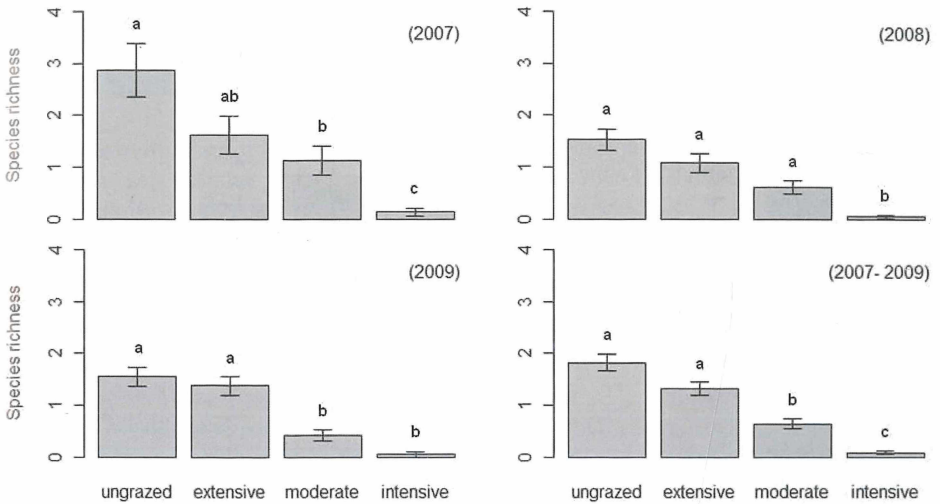


Fig. 30: Mean species richness per m^2 ($\pm$ SE) of Microlepidoptera obtained by photoeclector traps in the salt marshes of the Hamburger Hallig in the years 2007 to 2009. Different characters indicate significant differences ($P < 0.05$, Bonferroni corrected).

The effect of grazing on the abundance of Microlepidoptera

The number of individual moths caught in the salt marshes by light and photoeclector traps showed a similar distribution pattern as was observed for species numbers, with significantly more individuals caught in the ungrazed and extensively grazed than in the moderately and intensively grazed salt marshes (Fig. 31, 32, 33). Concerning the development of moths in salt marshes (photoeclector traps) a trend towards higher abundances in the extensively grazed salt marshes was recognisable.

No significant differences in abundances of moths were recognised in 2006. In the salt marshes of Westerhever, significantly the most moths were trapped in the ungrazed and the least in the intensively grazed plots in the following years. Only in 2008 moderately grazed plots did not differ from the ungrazed plots and significant differences to the intensively grazed plots could only be found when considering the entire sampling period.

For light trap samples of the Hamburger Hallig, in 2007 significantly more individuals were found in the ungrazed and extensively grazed plots than in the moderately and intensively grazed areas, and a significantly higher abundance of moths in the moderately grazed compared to the intensively grazed paddock was observed. In 2008 no significant difference between the extensively and moderately grazed or the moderately and intensively grazed plots could be derived from the data. This pattern again was repeated in 2009, with the difference of a clear distinction between the parts of the salt marsh with no or low grazing intensity compared to those with a higher grazing intensity.

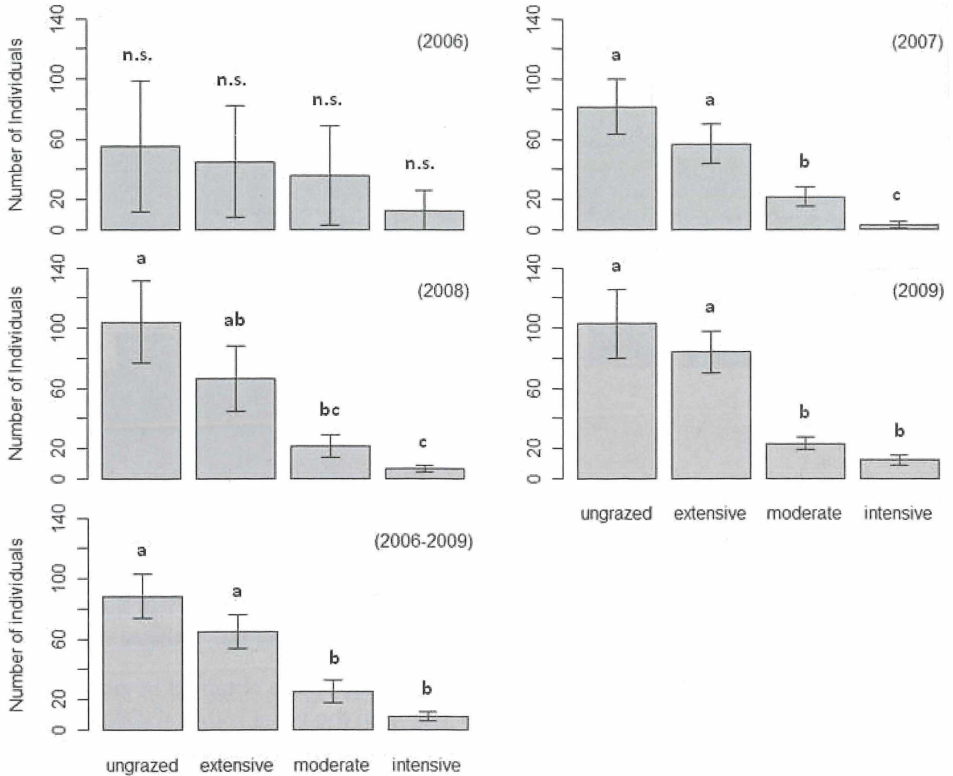


Fig. 31: Mean number of individuals per m² ($\pm$ SE) of Microlepidoptera in the salt marshes of the Hamburger Hallig in the years 2006 to 2009, trapped with light traps. Different characters indicate significant differences ($P < 0.05$, Bonferroni corrected).

Concerning the number of individuals developing in the salt marsh, in 2007 the abundance of moths followed the same pattern as the number of species. In 2008, though not significant, more individuals were caught in the extensively grazed salt marsh than in the ungrazed and the moderately grazed plots. All three of them differed significantly from the number of individuals caught in the intensively grazed salt marsh. In 2009, again significantly more individuals developed in the ungrazed and extensively grazed than in the moderately and intensively grazed paddocks.

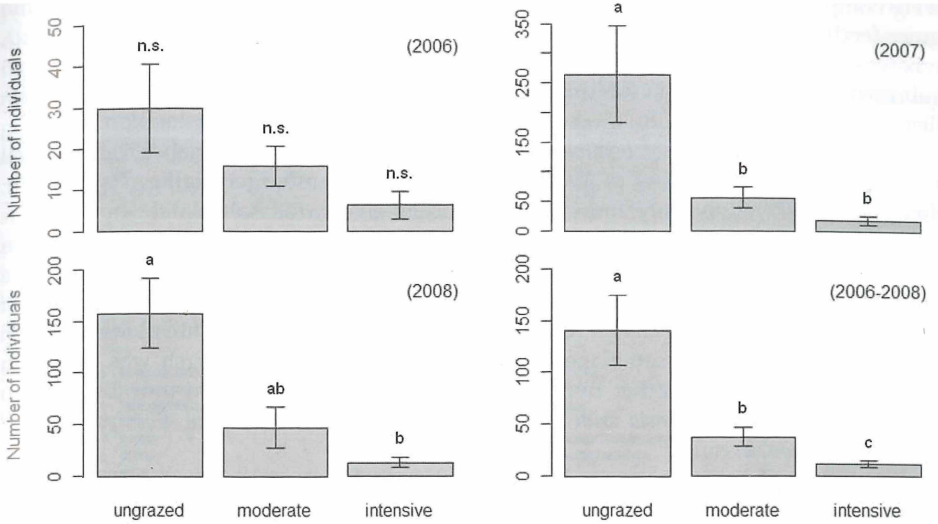


Fig. 32: Mean number of individuals per m² ($\pm$ SE) of Microlepidoptera caught with light traps in the salt marshes of Westerhever in the years 2006 to 2008. Different characters indicate significant differences ($P < 0.05$, Bonferroni corrected).

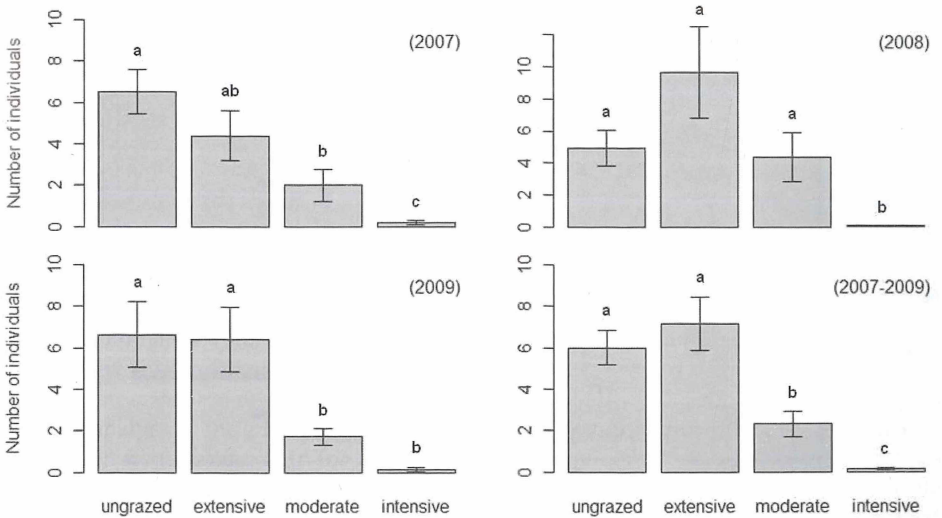


Fig. 33: Mean number of individuals per m² ($\pm$ SE) of Microlepidoptera obtained by pho-toeclector traps in the salt marshes of the Hamburger Hallig in the years 2007 to 2009. Different characters indicate significant differences ($p < 0.05$, Bonferroni corrected).

Dominance

A change in dominant species from the ungrazed to the intensively grazed salt marshes could be recognised. Moth communities in ungrazed salt marshes were dominated by species feeding on herbaceous plants like *Aster tripolium* and *Atriplex portulacoides* and

were composed of a high number of different species. With increasing grazing intensity, grass-feeding species reached higher levels of dominance (subdominant to dominant), whereas *Aster*-feeding moths like *Eucosma catoptrana* and *E. tripoliana* were recedent to subrecedent and missing in intensively grazed plots. In comparison to moth communities of ungrazed salt marshes, those of intensively grazed plots were species poor.

In light trap samples, *Scrobipalpa instabilella* reached highest dominance values in all researched salt marsh areas of Westerhever and the Hamburger Hallig (Fig. 34, 35), though highest values were found in the moderately grazed salt marshes of Westerhever. Additionally, the ungrazed salt marsh of Westerhever was dominated by the *Aster tripolium*-feeding species *Eucosma catoptrana* and *Eucosma tripoliana*, together with the grass-feeding *Crambus perlella*. In contrast, in the moderately grazed salt marsh, *Pediasia aridella* and *Coleophora salinella* were the only species reaching dominant values next to *S. instabilella*. The species assemblage of the intensively grazed salt marsh was poorer in species compared to the other two sites, and additionally dominated only by the two grass-feeding species *Pediasia aridella* and *Crambus perlella*. *E. catoptrana*, *E. tripoliana* and *B. maritima* were missing.

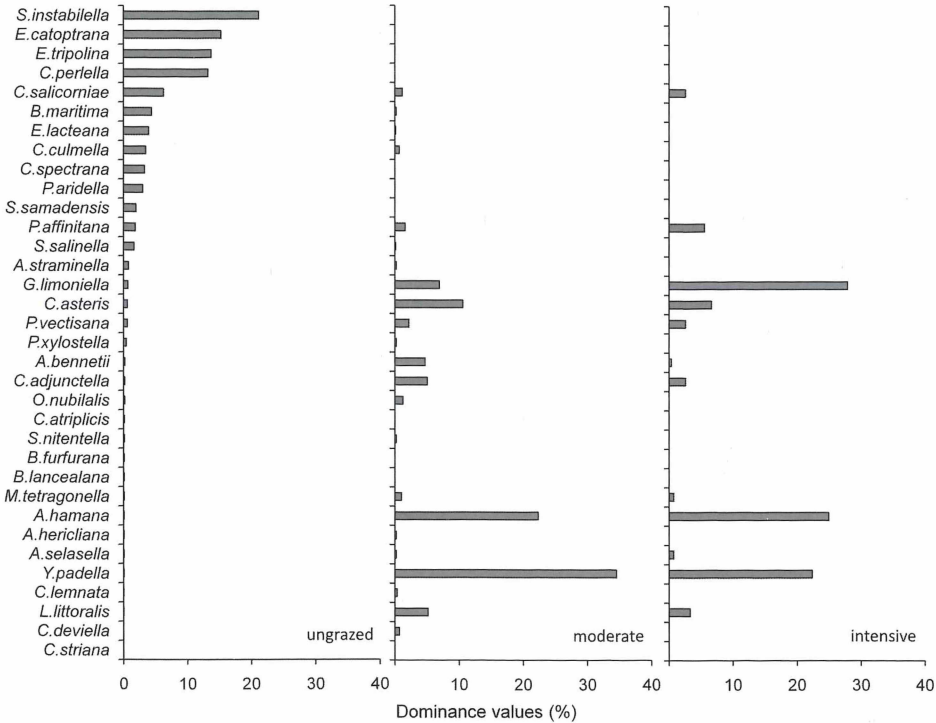


Fig. 34: Dominance values of moths species in the ungrazed, moderately, and intensively grazed salt marsh of Westerhever in the years 2006 to 2008.

In the ungrazed salt marsh of the Hamburger Hallig again, *Eucosma catoptrana* (20%) and *Eucosma tripoliana* (19%) were dominant (Fig. 36). Here, *Crambus perlella* was replaced by a third *Aster*-feeding species *Bucculatrix maritima* (13%). In the extensively grazed salt marsh, only *B. maritima* (17%) and *Phalonidia affinitana* (10.5%), also feeding on *A. tripolium*, reached dominance, while both *Eucosma* species were subdominant. The

moderately grazed salt marsh was dominated by *Eucosma lacteana* (37.8%), feeding on *Artemisia maritima* and reaching eudominant status. Additionally, only the two grass-feeding species *Crambus perlella* (25.4%) and *Chrysoteuchia culmella* (11.5%) were dominant. *Scrobipalpa instabilella* (25%) was the most dominant species in the intensively grazed marsh, followed by *Crambus perlella* (23%), *Chrysoteuchia culmella* (13%) and *Pediasia aridella* (13%), all of them feeding on grasses.

From the light-trap samples on the Hamburger Hallig, a clear change in dominance of species from the Aster-feeding to grass-feeding species was evident. Additionally, the moderately to intensively grazed salt marshes were lacking rarely occurring species, indicating a disturbed habitat, whereas the ungrazed and extensively grazed salt marsh harboured a heterogeneous microlepidopteran community with a few dominant, some rather common and a number of rare species.

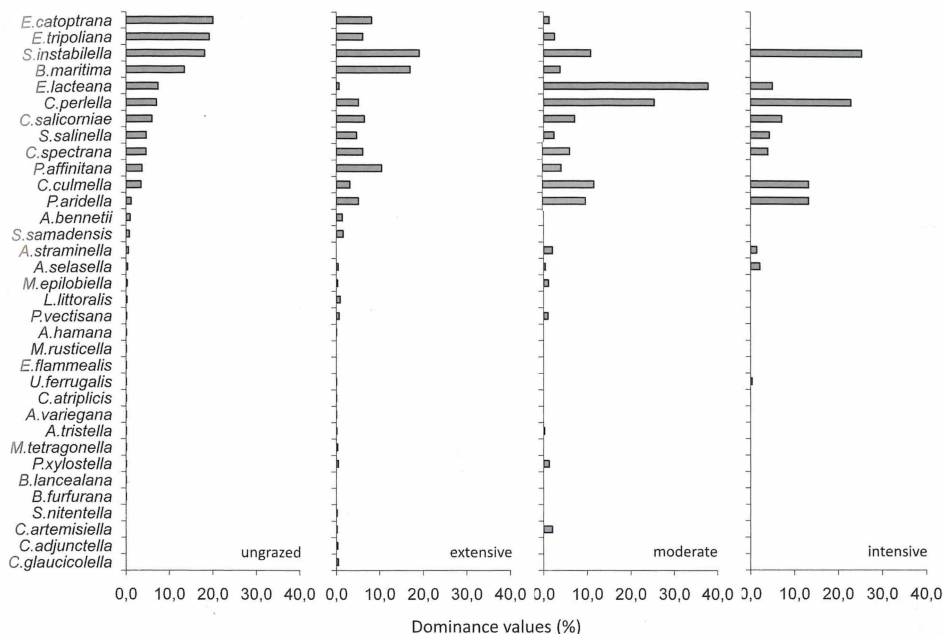


Fig. 35: Dominance values of moths species caught with light traps in 2006 - 2009 in the different grazing treatments of the Hamburger Hallig.

When analysing the photoelector data according to dominance levels of species, a slightly different pattern than for the light trap data was found. *Bucculatrix maritima* was eudominant from the ungrazed (53%) to the moderately grazed (47%) salt marsh, while *Scrobipalpa instabilella* reached dominant values (21% to 30%) (Fig. 36). In the ungrazed salt marsh, *Eucosma catoptrana* (6%), *Eucosma tripoliana* (4%) and *Phalonidia affinitana* (4%) were subdominant, whereas *Phalonidia affinitana* (6%) reached only subdominant values in the extensively grazed marsh. The moderately grazed salt marsh was dominated by *B. maritima* and *S. instabilella*, while *Phalonidia affinitana* (4%) and *Eucosma lacteana* (3.5%) reached subdominant status. Next to *S. instabilella*, the grass-feeding species *Crambus perlella* (15.4%) was dominant in the intensively grazed salt marsh, and *Chrysoteuchia culmella* (7.7%) and *Phalonidia vectisana* (7.7%) had only subdominant status. Recedent or sporadic species were found more often in the ungrazed and the extensively grazed salt

marsh compared to the moderately and intensively grazed plots. From the photoeclector samples on the Hamburger Hallig again a change in dominance from the *Aster*-feeding species *Bucculatrix maritima* to grass-feeding species was evident from the ungrazed to the intensively grazed salt marsh. Additionally, *Scrobipalpa instabilella* gained eudominance in the intensively grazed marsh, but was only dominant in lower grazing intensities. Again, the intensively grazed salt marsh showed a lack of rarely occurring species, indicating a disturbed habitat, whereas the ungrazed and extensively grazed salt marsh harboured a more heterogeneous microlepidopteran community.

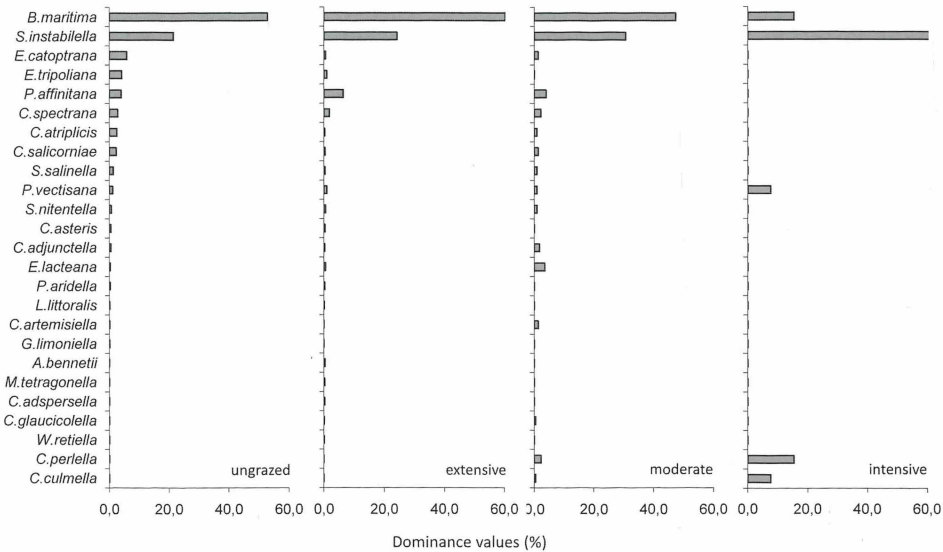


Fig. 36: Dominance values of moths species caught with photoeclector traps in 2007 - 2009 in the different grazing treatments of the Hamburger Hallig.

4.3.3 The Ecosystem Research Wadden Sea Project

Effects of short-term grazing experiments on invertebrates

In total, 2,080 moths were determined and analysed during this study, belonging to 25 species and nine families. To compare the impact of grazing on species richness and the composition of moth communities to those of spiders, beetles and flies, the data of Araneae, Coleoptera and Diptera (DIERBEN et al. 1994b, REINKE & MEYER 1999, MEYER et al. 1997) were re-evaluated and advanced statistical methods were applied. A short summary of the numbers of species and individuals is shown in Table 6. For more detailed information on the results on Araneae, Coleoptera and Diptera of the Ecosystem Research Wadden Sea Project see DIERBEN et al. (1994a), DIERBEN et al. (1994b), MEYER et al. 1997, REINKE & MEYER (1999) and REINKE et al. (2000).

In the *Festuca rubra*-dominated salt marshes of Friedrichskoog, 16 species of Lepidoptera with 447 individuals were caught (Tab. A4). The highest number of species was trapped in the ungrazed salt marsh (twelve species), followed by the extensively and moderately grazed plots (each seven species), and the lowest species richness in the low intensity and high intensity grazing with only five species. The highest number of individuals was caught in the ungrazed plots, the lowest number of individuals in the intensively grazed paddocks, and intermediate numbers of individuals in the low, extensively and moderately grazed salt marsh plots (Fig. 37).

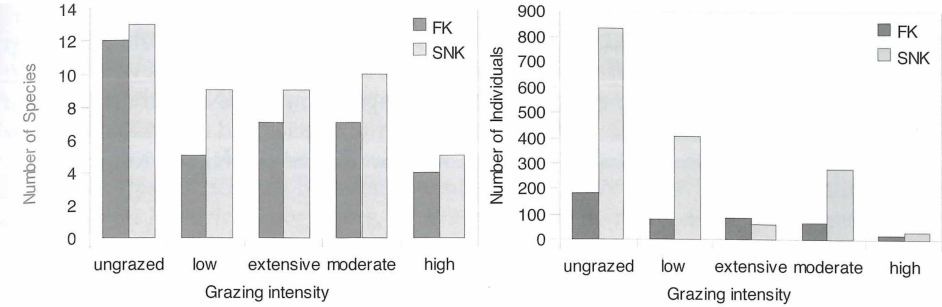


Fig. 37: Total number of moths species and individuals caught with photoelector traps on the salt marshes of Friedrichskoog (FK) and the Sönke-Nissen-Koog (SNK) under different grazing intensities (ungrazed to high) in the years 1990 to 1993.

From the *Puccinellia maritima*-dominated salt marshes of the Sönke-Nissen-Koog, 16 moth species with a total of 1,615 individuals were determined, with an increase in species richness from 1990 to 1993 (Tab. A5). When comparing species richness and abundance of Lepidoptera in the five different grazing intensities, the highest species richness was recorded in the ungrazed salt marsh with thirteen species. Ten species were found in the moderately grazed plots and nine species in plots with low and extensive grazing management. The lowest number of species (five) was recorded in plots with high grazing intensity. Most individuals were caught in the ungrazed salt marsh, followed by the plots with either low or moderate grazing intensity. The paddocks with the highest grazing intensity showed the lowest number of individuals (Fig. 37).

Tab. 6: Species richness and abundance of Araneae, Coleoptera and Diptera caught with photoelector traps in the salt marshes of Friedrichskoog (FK) and the Sönke-Nissen-Koog (SNK) from 1990 to 1993 under different grazing intensities (DIERBEN et al. 1994a & b).

Orga- nisms/site	ungrazed		low intensity		extensive		moderate		intensive	
	rich- ness	abun- dance	rich- ness	abun- dance	rich- ness	abun- dance	rich- ness	abun- dance	rich- ness	abun- dance
Friedrichskoog										
Araneae	33	3775	35	4771	32	5023	33	4098	36	4837
Coleoptera	40	1704	43	2407	49	2814	44	2630	43	2437
Diptera	39	6339	40	4246	43	7618	28	6768	35	7025
Sönke-Nissen-Koog										
Araneae	32	2129	30	1364	25	1446	33	1640	37	2465
Coleoptera	40	1806	42	3566	39	1960	39	2965	36	3482
Diptera	31	6195	26	6344	25	7585	28	5941	23	7461

In the salt marshes of Friedrichskoog (FK) and the Sönke-Nissen-Koog (SNK), 55 and 58 spider species with individual totals of 22,504 and 9,044 respectively were recorded, of which most species were caught in the intensively grazed salt marsh. In the FK, most beetle species were caught in the extensively grazed salt marsh, whereas in SNK most species were found in plots with low grazing intensity. In total, 70 and 62 beetle species

with individual totals of 11,992 and 13,779 respectively were trapped in photoelector traps. Flies were the most abundant group with 31,996 and 33,536 individuals belonging to 56 and 41 species, respectively. Most fly species and individuals in the FK were caught in the extensively grazed treatments, while most fly species in the SNK were trapped in the ungrazed control plots. Table 6 shows the number of species and individuals caught in the different grazing treatments of Friedrichskoog and the Sönke-Nissen-Koog.

Species accumulation curves

A comparison of the species accumulation curves, computed for the communities of Lepidoptera occurring under different grazing regimes of Friedrichskoog (Fig. 38) and the Sönke-Nissen-Koog (Fig. 38) suggested a lower expected mean number of species for the grazed plots compared to the ungrazed. The lowest species richness was always found in the intensively grazed marsh. At both sites, the Friedrichskoog and the Sönke-Nissen-Koog, more species were caught in the moderate than the low intensity grazing. An additional factor next to grazing intensity determining moths species richness in these salt marshes thus seems likely, which could not be determined due to the age of the dataset. While in Friedrichskoog species numbers of the sites grazed with low intensity were lower than in the extensively grazed sites as well, in the Sönke-Nissen-Koog extensively grazed sites showed a slightly lower species richness than the low intensity grazed sites.

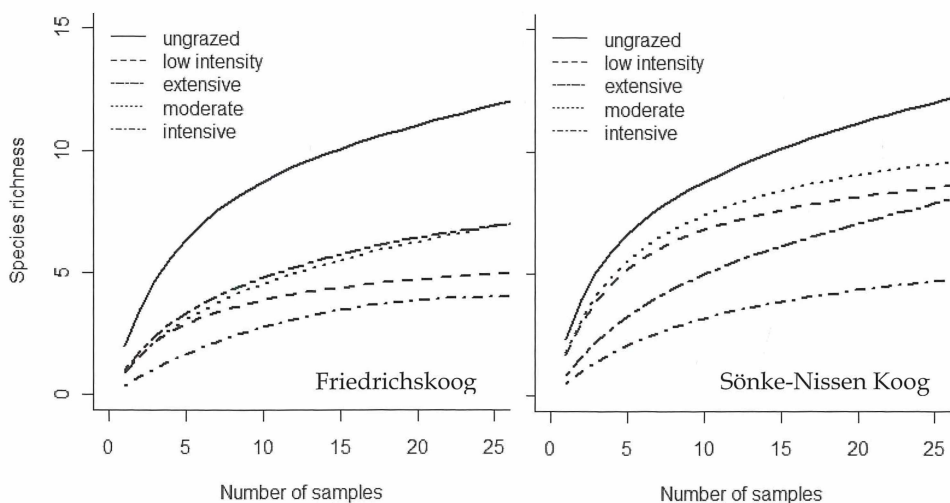


Fig. 38: Expected mean species richness for the grazing intensities according to species accumulation curves following Kindt's exact accumulator for the lepidopteran assemblages of Friedrichskoog and Sönke-Nissen Koog.

Species richness of moths in response to short-term grazing management

The Generalised Estimation Equation model (GEE) measures the effect of different grazing regimes, while considering the time-dependent replication of measurements (LIANG & ZEGER 1986, ZUUR et al. 2009). The results allow an interpretation of the responses of insect and spider communities in their species richness and abundance, and therefore enable us to draw conclusions about the species distribution under different management regimes.

The results of the GEE showed a significant effect of grazing intensity on the species richness of lepidopteran assemblages of the salt marshes of Friedrichskoog (Fig. 39) and the Sönke-Nissen-Koog (Fig. 40). Moth assemblages in the ungrazed salt marshes were the species richest and the lowest number of species were caught in the intensively grazed treatments.

In the first year (1990) after the set-up of the grazing experiment, only a significant difference in species richness between the intensively grazed and all other paddocks was detectable in Friedrichskoog. Here, in 1991, only the moderately grazed plots differed significantly from all other plots, while in 1992, a general distribution pattern was recognisable, but no significant differences between the plots existed. The same distribution pattern was obvious in 1993, showing significant differences in species richness between the ungrazed and the moderately and intensively grazed salt marsh, but not with respect to the low and extensive grazing management. No significant differences between the other grazing intensities could be recognised.

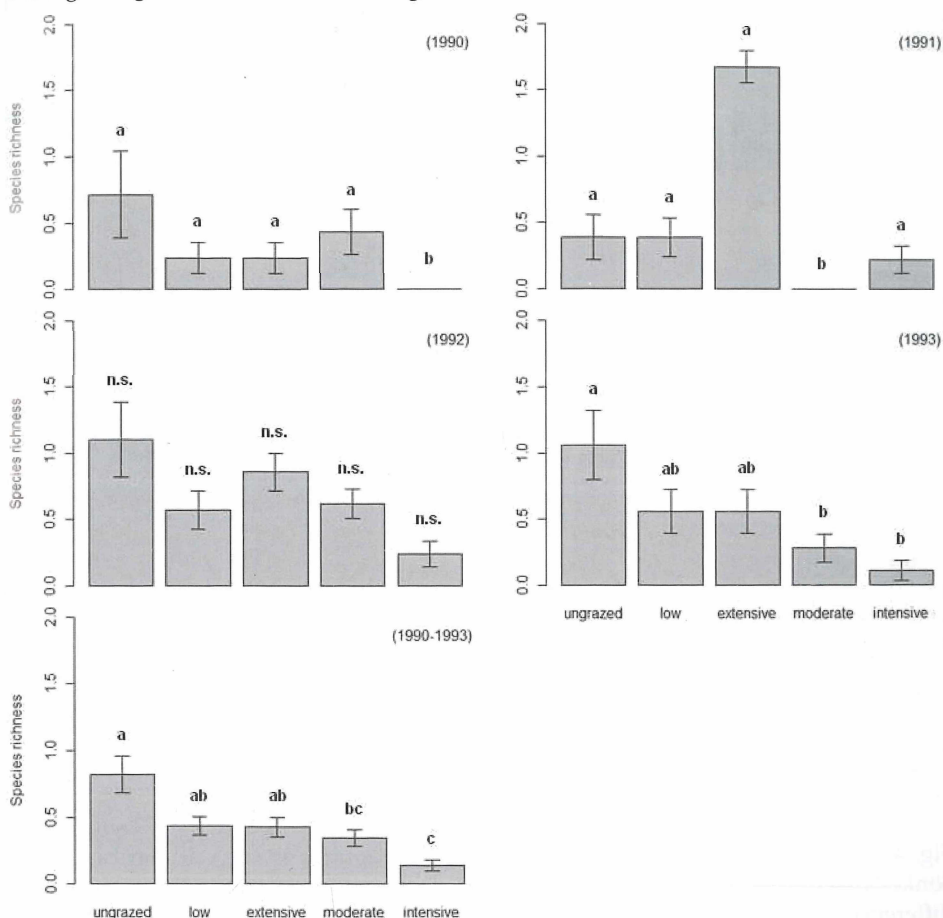


Fig. 39: Mean species richness per m² ($\pm$ SE) of Lepidoptera in the salt marshes of Friedrichskoog in the years 1990 to 1993. Different characters indicate significant differences ($P < 0.05$, Bonferroni corrected).

In the lower salt marshes of the Sönke-Nissen-Koog, no distinct response of the Lepidoptera assemblage to grazing management was identified in 1990, while in 1991 significantly lower species numbers in the extensively and intensively grazed paddocks compared to the ungrazed plots was recognisable (Fig. 40). With increasing duration of the grazing experiment, the differences in species richness of the lepidopteran assemblages in the different grazing regimes became more pronounced. In 1992, the same differences were apparent as in 1991 with significantly more species in plots with low intensively than in intensively grazed plots. For 1993, additionally significant differences between the extensively and moderately grazed paddocks were evident, with more species per trap being found in the moderately grazed salt marsh.

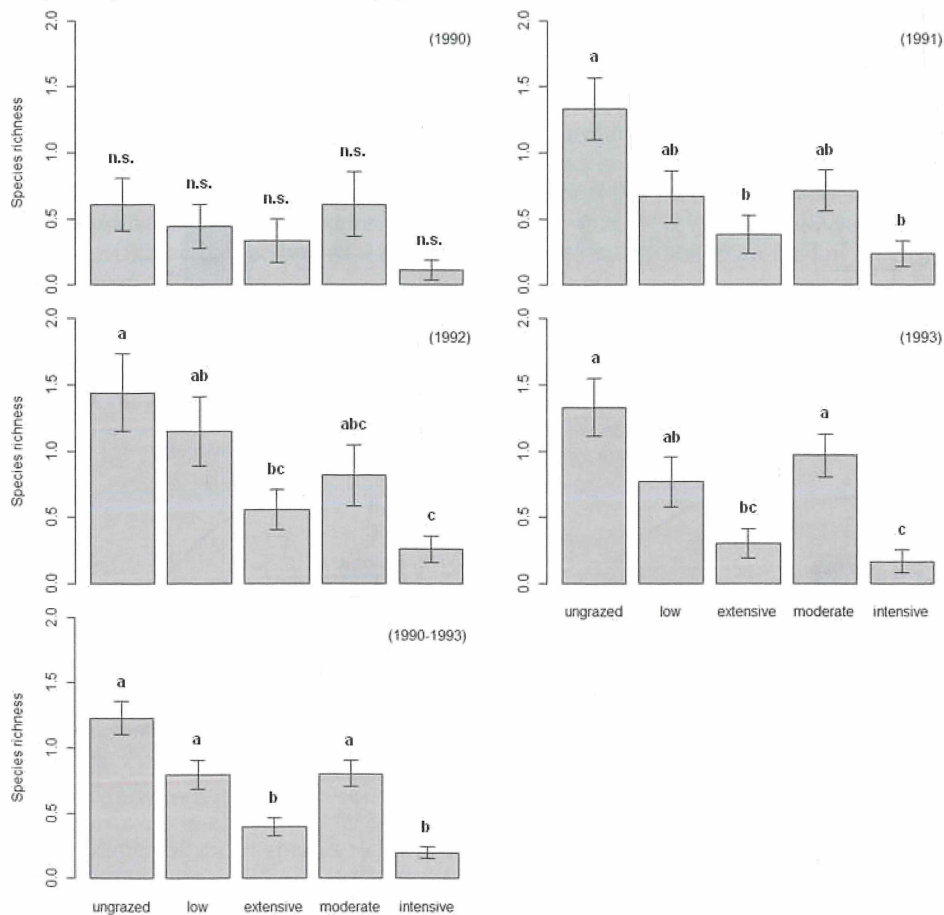


Fig. 40: Mean species richness per m² ($\pm$ SE) of Lepidoptera in the salt marshes of the Sönke-Nissen-Koog in the years 1990 to 1993. Different characters indicate significant differences ($P < 0.05$, Bonferroni corrected).

Abundance of moths in response to short-term grazing management

With respect to the abundance of Lepidoptera in the salt marshes of Friedrichskoog and the Sönke-Nissen-Koog, similar patterns as for the species richness were recognised,

with significantly more moths caught in the ungrazed than in the intensively grazed marsh (Fig. 41, 42).

In the higher salt marshes of Friedrichskoog, significant responses to grazing management were variable, with the least number of individuals in the moderately grazed marsh in 1991, in the intensively grazed in 1992 and no differences between any of the treatments in 1993. Only the consideration of the four year research period showed significantly less individuals in the intensively and moderately grazed plots than in the other three that, in turn, did not significantly differ from each other.

In the lower salt marshes of the Sönke-Nissen-Koog, no significant variation was found in the first year of research, but significantly more individuals occurred in the ungrazed plot than in any other grazing regime, and significantly more individuals in the low intensity grazing compared to a high grazing intensity in 1991. By tendency, more moths were recorded in the ungrazed, low and moderately grazed than in the extensively and intensively grazed salt marshes.

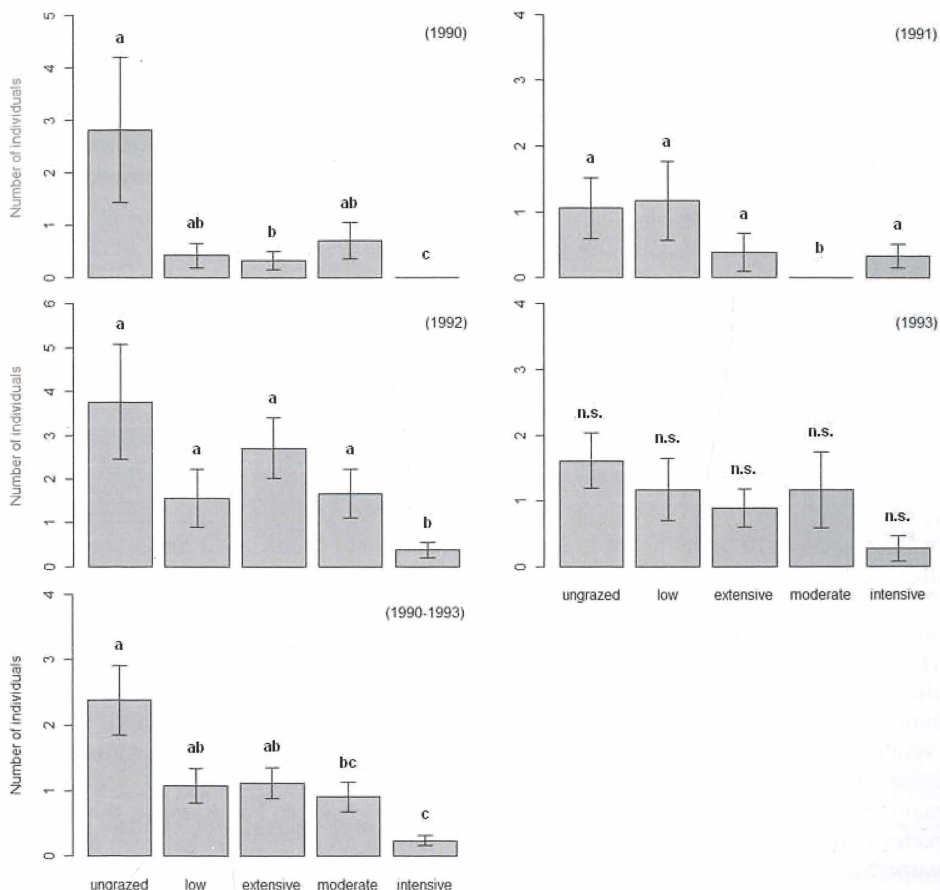


Fig. 41: Mean number of individuals per m^2 ($\pm$ SE) of Lepidoptera in the salt marshes of Friedrichskoog in the years 1990 to 1993. Different characters indicate significant differences ($P < 0.05$, Bonferroni corrected).

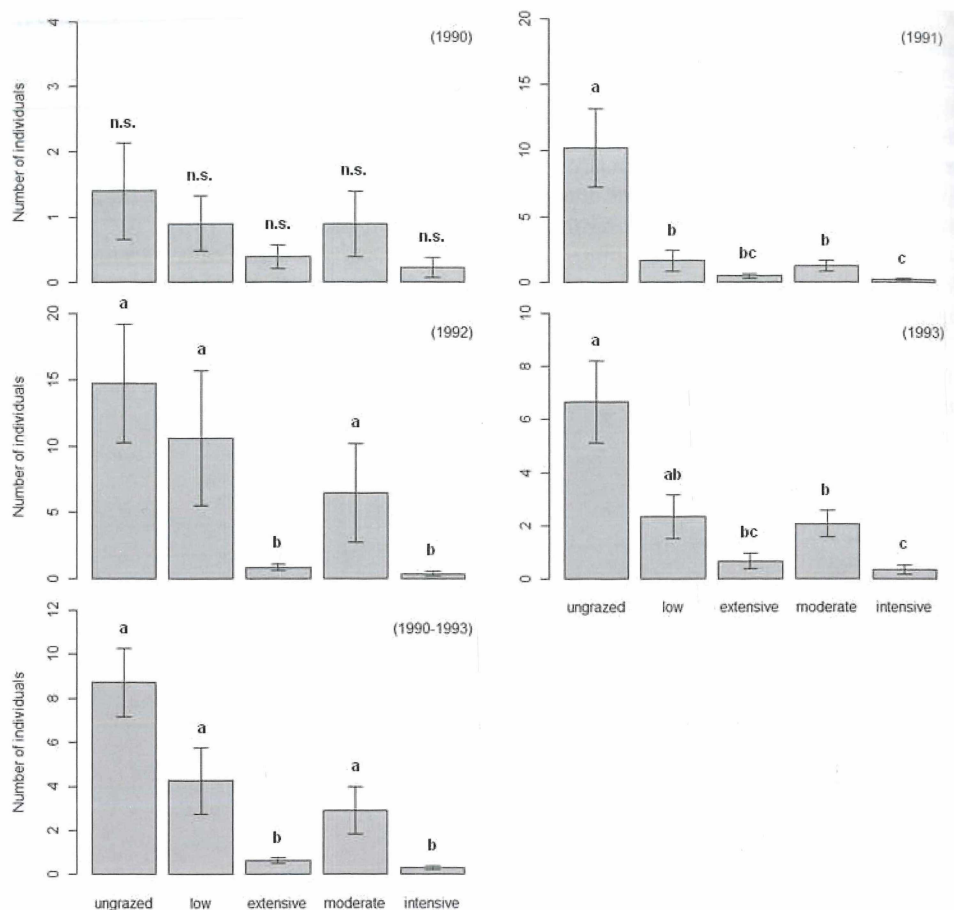


Fig. 42: Mean number of individuals per m² ($\pm$ SE) of Lepidoptera in the salt marshes of the Sönke-Nissen-Koog in the years 1990 to 1993. Different characters indicate significant differences ($p < 0.05$, Bonferroni corrected).

Species richness of invertebrates in response to short-term grazing management in comparison to moths

Additionally, a GEE model was fitted to the data on Araneae, Coleoptera and Diptera obtained and determined during the study by DIERBEN et al (1994a, b).

When comparing the results of the GEE for Araneae, Coleoptera, Diptera and Lepidoptera, only Araneae and Lepidoptera showed significant differences between the five grazing intensities regarding species richness in Friedrichskoog. For Araneae, the lowest species number was found in the ungrazed plots, with no differences between all other treatments, whereas for Lepidoptera the highest number of species was found in the ungrazed, the lowest in the intensively grazed salt marsh (Fig. 43).

In the salt marshes of the Sönke-Nissen-Koog, only Lepidoptera showed significant effects of the varied grazing intensities regarding species richness per trap when considering the complete research period from 1990 to 1993 (Fig. 44). Coleoptera species showed

a response to different grazing intensities only in 1993, when a significant difference in species richness could be detected between the ungrazed and extensively grazed plots.

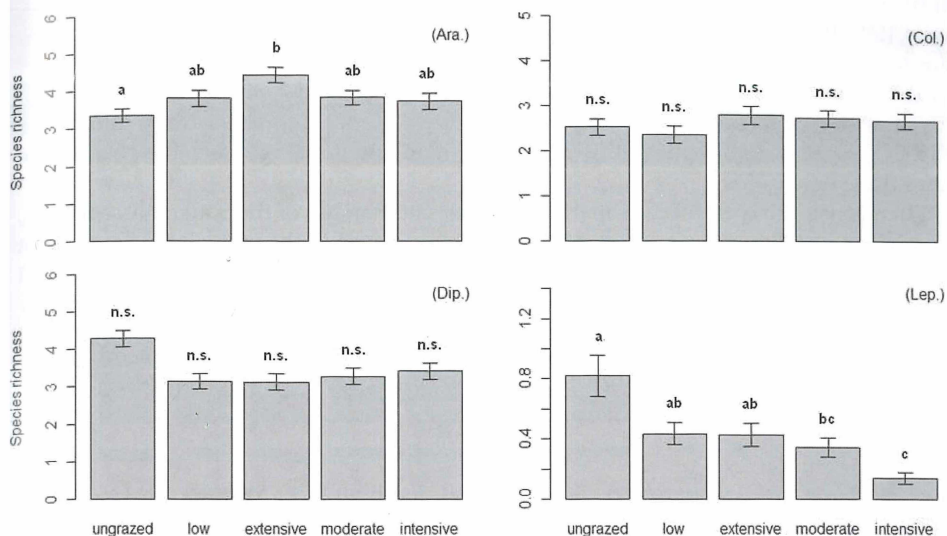


Fig. 43: Mean species richness per m² (± SE) of Araneae, Coleoptera, Diptera (DIERBEN et al 1994a, b) and Lepidoptera in the salt marshes of Friedrichskoog in the years 1990 to 1993. Different characters indicate significant differences (P < 0.05, Bonferroni corrected).

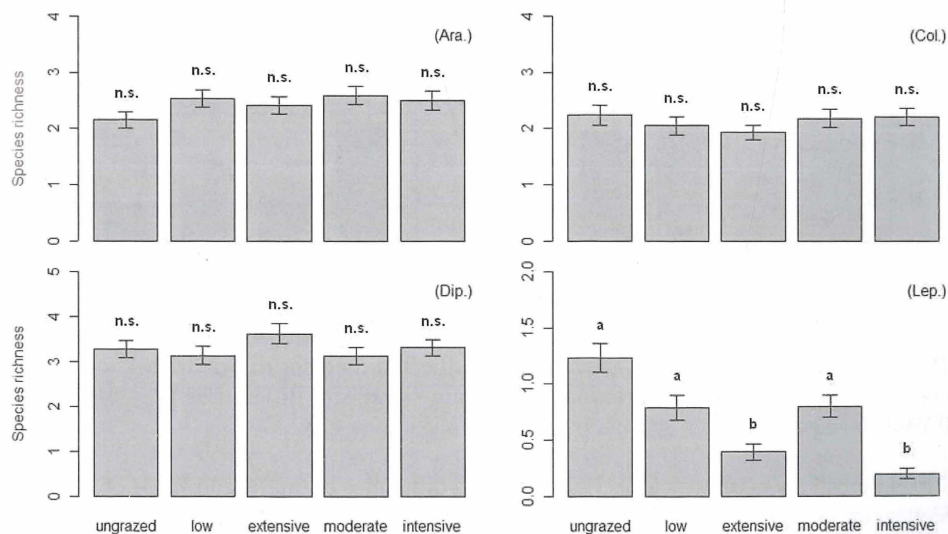


Fig. 44: Mean species richness per m² (mean ± SE) of Araneae, Coleoptera, Diptera (DIERBEN et al. 1994a, b) and Lepidoptera in the salt marshes of the Sönke-Nissen-Koog in the years 1990 to 1993. Different characters indicate significant differences (P < 0.05, Bonferroni corrected).

Abundance of invertebrates in response to short-term grazing management in comparison to moths

Similar to the results for the species richness, when considering the whole sampling period (1990-1993), only Lepidoptera showed significant differences between grazing intensities considering individuals caught per trap (Fig. 45, 46).

In the salt marshes of Friedrichskoog, Coleoptera showed a significant variation in their number of individuals in the year 1991, with higher numbers of individuals per trap in the salt marsh managed with low and moderate grazing intensities than in the other three treatments.

When considering each year separately, in the salt marshes of the Sönke-Nissen-Koog, the highest number of individuals of Araneae were found in the intensively grazed plot only in 1990. Here, Coleoptera however, showed a more distinct response to different grazing intensities, with significantly higher numbers of individuals in the moderately grazed paddocks than in the low intensity and extensive grazing in 1991, and significant differences in abundance between moderately and extensively grazed salt marshes in 1993.

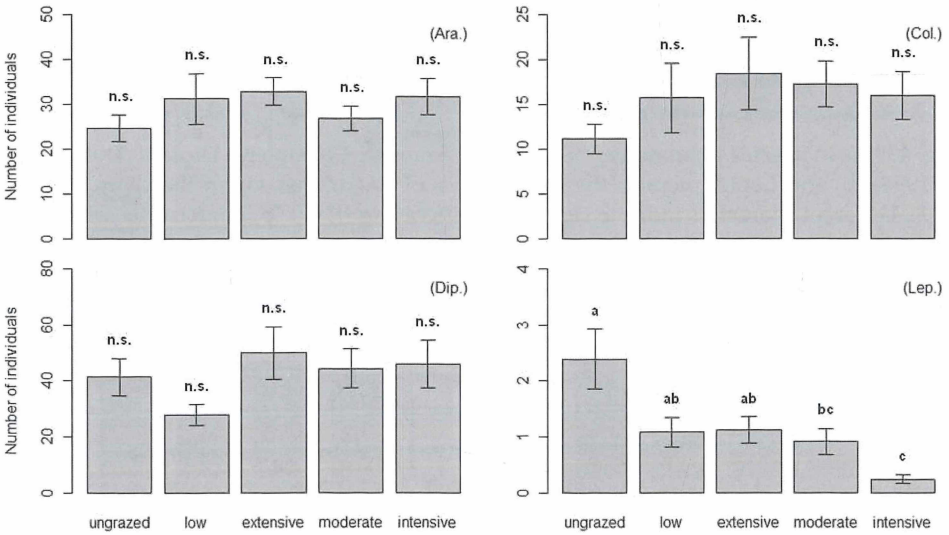


Fig. 45: Mean number of individuals per m² (± SE) of Araneae, Coleoptera, Diptera (DIERBEN et al. 1994a & b) and Lepidoptera in the salt marshes of Friedrichskoog in the years 1990 to 1993. Different characters indicate significant differences ($P < 0.05$, Bonferroni corrected).

Correlations between the species richness and abundance of moths and those of spiders, beetles and flies, determined during the Ecosystem Research Wadden Sea Project (DIERBEN et al. 1994a & b) was, if significant, weak in both researched locations. As were correlations between the other groups and no conclusions could be drawn from the species richness or abundance of one group in relation to any other (Tab. 7, 8)

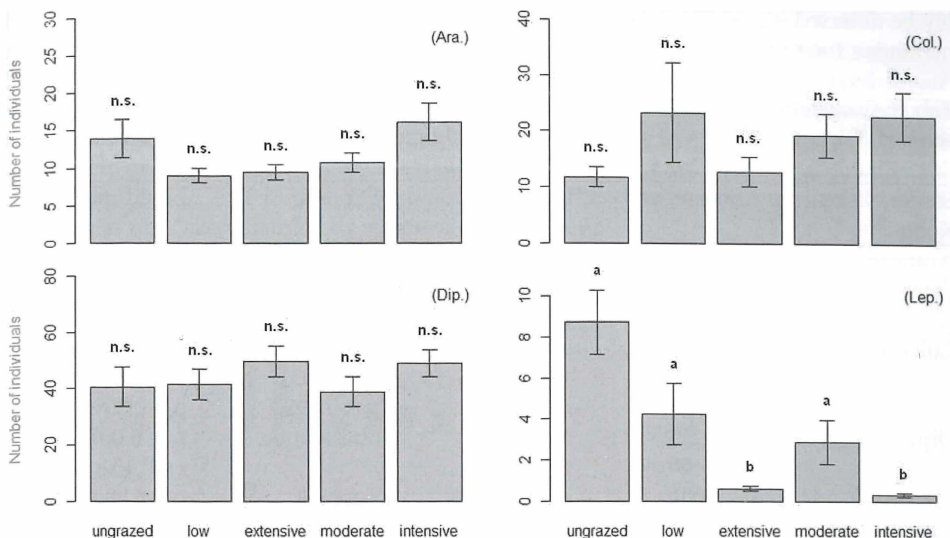


Fig. 46: Mean number of individuals per m² (± SE) of Araneae, Coleoptera, Diptera (DIERBEN et al. 1994a, b) and Lepidoptera in the salt marshes of the Sönke-Nissen-Koog in the years 1990 to 1993. Different characters indicate significant differences ($P < 0.05$, Bonferroni corrected).

Tab. 7: Correlation coefficients between species richness and abundance of Araneae, Coleoptera, Diptera (DIERBEN et al. 1994a & b) and Lepidoptera caught in the salt marshes of Friedrichskoog from 1990-1993. $n = 388$.

Friedrichskoog	Araneae	Coleoptera	Diptera	Lepidoptera
Araneae	abundance	$r_p = 0.151$ $t = 3.022$ $p = 0.003$	$r_p = 0.001$ $t = 0.021$ $p = 0.983$	$r_p = 0.012$ $t = 0.247$ $p = 0.805$
	richness	$r_p = 0.359$ $t = 7.583$ $p < 0.001$	$r_p = 0.041$ $t = 0.813$ $p = 0.417$	$r_p = 0.140$ $t = 2.793$ $p = 0.005$
		richness	abundance	richness
Diptera	$r_p = 0.122$ $t = 2.415$ $p = 0.016$	$r_p = -0.077$ $t = -1.514$ $p = 0.131$	$r_p = 0.060$ $t = 1.185$ $p = 0.237$	$r_p = 0.108$ $t = 2.149$ $p = 0.032$
	abundance	abundance	abundance	abundance
	richness	richness	richness	richness
Lepidoptera	$r_p = 0.172$ $t = 3.437$ $p < 0.001$	$r_p = 0.195$ $t = 3.919$ $p < 0.001$	$r_p = 0.060$ $t = 1.185$ $p = 0.237$	$r_p = 0.108$ $t = 2.149$ $p = 0.032$
	abundance	abundance	abundance	abundance
	richness	richness	richness	richness

Dominance

Dominance patterns in assemblages can reveal influences of grazing on species composition not displayed by species richness or abundances (MAGURRAN 2004).

By comparison of the dominance structure in the newly determined moth communities and the spider, beetle and fly assemblages determined during the Ecosystem Research Wadden Sea Project (DIERBEN et al. 1994a, b), sensitive responses to grazing could possi-

bly be detected in a shift in species occurrences from ungrazed to intensively grazed salt marshes.

Tab. 8: Correlation coefficients between species richness and abundance of Araneae, Coleoptera, Diptera (DIERBEN et al. 1994a & b) and Lepidoptera caught in the salt marshes of the Sönke-Nissen-Koog from 1990-1993. n = 480.

Sönke-Nissen-Koog	Araneae	Coleoptera	Diptera	Lepidoptera
Araneae	abundance	$r_p = 0.187$ $t = 4.170$	$r_p = 0.056$ $t = 1.244$	$r_p = 0.069$ $t = 1.507$
	richness	$p < 0.001$	$p = 0.214$	$p = 0.132$
Coleoptera	$r_p = 0.280$ $t = 6.380$	abundance	$r_p = 0.0001$ $t = 0.003$	$r_p = - 0.008$ $t = - 0.177$
	$p < 0.001$	richness	$p = 0.997$	$p = 0.859$
Diptera	$r_p = 0.222$ $t = 4.988$	$r_p = 0.200$ $t = 4.468$	abundance	$r_p = 0.007$ $t = 0.151$
	$p < 0.001$	$p < 0.001$	richness	$p = 0.880$
Lepidoptera	$r_p = 0.109$ $t = 2.409$	$r_p = 0.279$ $t = 6.348$	$r_p = 0.263$ $t = 5.965$	abundance
	$p = 0.016$	$p < 0.001$	$p < 0.001$	richness

For the Microlepidoptera assemblages in salt marshes under short-term grazing experiments, a change in dominance from species feeding on herbaceous plants in the ungrazed towards grass-feeding species in the intensively grazed salt marshes was apparent. This shift in dominance patterns from ungrazed to grazed salt marshes was more pronounced in the lower salt marshes of the Sönke-Nissen-Koog.

In Friedrichskoog, all assemblages of Microlepidoptera (Fig. 47), except for the intensively grazed salt marsh, were dominated by *Crambus perlella*, feeding on grasses. In the ungrazed treatments, *Coleophora adjunctella* was the only other species reaching dominant levels. The low intensively grazed salt marsh was dominated by only three grass-feeding species, *C. perlella* being eudominant and *P. aridella* and *A. selasella* dominant. In the extensively and moderately grazed marsh, *C. perlella* and *P. aridella* reached eudominant values. Only *P. aridella* was eudominant in the intensively grazed plots, *C. perlella*, *A. selasella* and *Elachista* sp. were all dominant.

In the lower salt marsh of the Sönke-Nissen-Koog, a well-defined change from the *Aster tripolium*-feeding species *Bucculatrix maritima* and *Eucosma tripoliana* to the grass-feeding species *Pediasia aridella* from the ungrazed to the intensively grazed treatments is apparent (Fig. 48).

B. maritima was eudominant in the ungrazed, low intensively and moderately grazed salt marsh, whereas the moth assemblage of the extensively grazed treatment was dominated by *Coleophora deviella*, with *P. aridella* and *Scrobipalpa instabilella* having dominant values as well. In the intensively grazed salt marsh *P. aridella* reached eudominant status, while *C. deviella* and *B. maritima* were dominant. No clear effect of different grazing intensities was recognisable in the dominance pattern of spider, beetle and fly assemblages in the salt marshes of Friedrichskoog and the Sönke-Nissen-Koog.

Spider assemblages (DIERBEN et al. 1994a, b) of the higher salt marshes of Friedrichskoog were dominated by *Erigone longipalpis* (eudominant) in all grazing intensities accompanied by *Oedothorax fuscus* (dominant) in the low intensively and extensively grazed salt marsh. In the lower salt marshes of the Sönke-Nissen-Koog, spider assem-

blages of the ungrazed, the low intensively and the moderately grazed marsh were dominated by *Baryphyma duffeyi*, whereas *Erigone longipalpis* reached dominant values in the extensively and intensively grazed plots. There, *Baryphyma duffeyi* received lower values. The spider assemblages of the low intensively and moderately grazed salt marshes showed a heterogeneous dominance structure. The ungrazed, extensively and intensively grazed treatments, however, were dominated by a single eudominant species (*Baryphyma duffeyi* e.g. *Erigone longipalpis*) that, in the case of the intensively grazed marsh, was only accompanied by subdominant species.

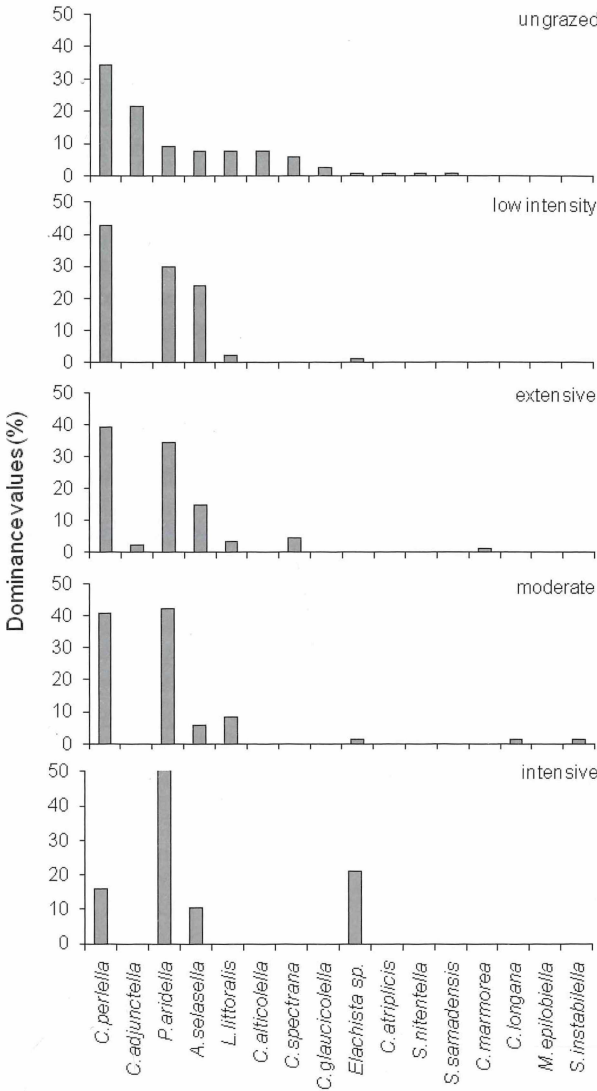


Fig. 47: Dominance values of moth species in the different grazing intensities of the Friedrichskoog salt marshes.

The coleopteran assemblages (DIERßEN et al. 1994a, b) of Friedrichskoog showed a differentiated response to grazing, but without a clear change in dominance structure from ungrazed to intensively grazed salt marshes. *Dicheiostichus gustavii* reached the highest dominance values in the ungrazed, extensively and intensively grazed salt marsh, *Phyllobius vespertinus* was the dominant species in the low intensively and moderately grazed plots. The coleopteran communities of the Sönke-Nissen-Koog were in all levels of grazing intensity dominated by *Dicheiostichus gustavii*, *Dyschirius calceus* and *Bembidion minimum* with little changes in dominance values.

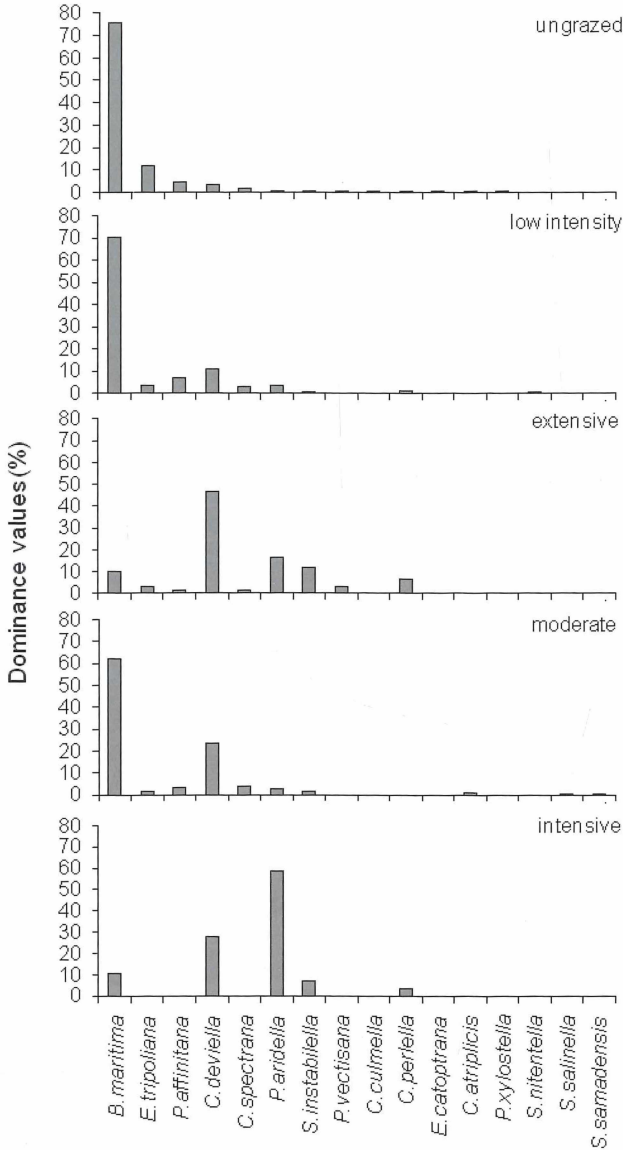


Fig. 48: Dominance values of moth species in different grazing treatments in the salt marshes of the Sönke-Nissen-Koog.

Dipteran assemblages (DIERËN et al. 1994a, b) of the Friedrichskoog showed a similar distribution of dominant species for all levels of grazing intensity, with *Lestodiplosis* sp. being the eudominant species, followed by *Micaria alba* (dominant). Only in the intensively grazed salt marsh, *Symplecta stitica*, *Mayetiola puccinelliae* and *Nemotelus notatus* reached higher dominance values than *Micaria alba*. In the salt marshes of the Sönke-Nissen-Koog, only the intensively and extensively grazed plots were slightly different from the others by higher dominance levels of *Nemotelus notatus* and *Hydroecea oceanus*. All assemblages showed a similar level in heterogeneity of dominance structure with rather low overall dominance levels.

4.4 Species composition and ecological indication

To analyse whether the species distribution of Microlepidoptera in differently managed parts of the salt marshes was based on habitat preferences, and whether a shift in species composition from ungrazed to intensively grazed salt marshes occurred, all data obtained by photoeclector and light traps were analysed according to the Compositional Indicator Species Analysis (ROBERTS 2010)(see chapter Methods). It combines a species' relative abundance with its relative frequency of occurrence in a group of sites.

4.4.1 Microlepidoptera in intermediate-term grazing treatments

Due to their highly specific ties to their host plants, it can be expected that a number of halobiontic species show distinct preferences for either grazing type, which is reflected in the plant species composition in different parts of the salt marsh.

The analysis of variance based on dissimilarities (ADONIS) gives statistical evidence to the difference in species composition between the grazed and the ungrazed salt marshes of Westerhever and the Hamburger Hallig (Tab. 9).

Tab. 9: Results of the ADONIS for the impact of grazing on the distribution of Lepidoptera obtained by photoeclector and light traps in the salt marshes of Westerhever and the Hamburger Hallig based on 999 permutations, bold characters indicating a significance level of $p < 0.005$. Bonferroni corrected.

Years	Hamburger Hallig				Westerhever	
	Light traps		Photoeclector traps		Light traps	
	F.Model	Pr(>F)	F.Model	Pr(>F)	F.Model	Pr(>F)
2006	3.864	0.001	-	-	1.650	0.090
2007	3.924	0.001	10.11823	0.001	2.148	0.007
2008	3.389	0.002	22.48011	0.001	3.922	0.001
2009	6.991	0.001	32.12602	0.001	-	-
all	11.608	0.001	59.14954	0.001	4.500	0.001

Significant differences in the species composition between the grazing treatments were found in 2007 and 2008, and when considering the whole sampling period of 2006-2008 in Westerhever and for all years in the salt marshes of the Hamburger Hallig.

A difference in species composition for differently grazed salt marshes supports the assumption that a number of halobiontic moths with distinct habitat preferences showed a distinct response to the impact of grazing and therefore qualify as indicator species for salt marsh management.

With the means of a Compositional Indicator Species Analysis of the data obtained with light traps in Westerhever, six moth species could be identified as potential indicator species for the effect of grazing on the species distribution (Tab. 10).

Tab. 10: Indicator Species Values (ISV) of Lepidoptera caught with light traps in the salt marshes of Westerhever according to different grazing intensities. Underlined characters indicate suitable indicator species and their ISV ($p < 0.05$, based on 999 permutations). X indicates occurring species with non-significant ISV. Occurrences < 5 individuals were excluded from analysis.

Species	ungrazed	moderate grazing	intensive grazing
<i>Agdistis bennetii</i>	<u>0.594</u>	.	.
<i>Agriphila straminella</i>	x	x	<u>0.660</u>
<i>Bucculatrix maritima</i>	0.301	x	.
<i>Chrysoteuchia culmella</i>	0.364	x	<u>0.487</u>
<i>Clepis spectrana</i>	0.280	X	x
<i>Coleophora atriplicis</i>	x	.	.
<i>Coleophora salicorniae</i>	0.474	x	x
<i>Crambus perlella</i>	0.229	0.305	<u>0.468</u>
<i>Eucosma catoptrana</i>	<u>0.398</u>	0.198	.
<i>Eucosma lacteana</i>	0.233	<u>0.387</u>	.
<i>Eucosma tripoliana</i>	<u>0.278</u>	x	.
<i>Ostrinia nubilalis</i>	0.303	.	.
<i>Pediasia aridella</i>	0.226	0.307	<u>0.337</u>
<i>Phalonidia affinitana</i>	0.238	x	.
<i>Scrobipalpa instabilella</i>	0.212	0.332	<u>0.495</u>
<i>Scrobipalpa salinella</i>	0.207	<u>0.371</u>	x
Mean ISV = 0.155			

In the ungrazed salt marsh, *Agdistis bennetii* reached the highest indicator species value of 0.594, followed by *Eucosma catoptrana* and *Eucosma tripoliana*. *Ostrinia nubilalis* also qualified as indicator species in the ungrazed salt marsh, since it was only caught in these plots. Because it must be considered a 'tourist species' not developing in the salt marsh it had to be considered unsuitable nevertheless.

Suitable indicator species for the moderately grazed salt marsh were *Eucosma lacteana*, feeding on *Artemisia maritima*, and *Scrobipalpa salinella* feeding on *Suaeda maritima*. In the intensively grazed plots mainly grass-feeding species (*Agriphila straminella*, *Chrysoteuchia culmella*, *Crambus perlella* and *Pediasia aridella*) reached high and significant indicator values, though also occurring in the moderately and ungrazed salt marsh. Of these, only *Pediasia aridella* and *Agriphila straminella* could be considered halobiontic, whereas both other species are occurring in all grasslands abundantly. Additionally *Scrobipalpa instabilella* qualified as an indicator species. All other caught species did not qualify as indicator species due to low ISVs or their occurrences in both grazing treatments.

The analysis of data obtained by light traps on the Hamburger Hallig yielded slightly different results with five species suitable as indicators for the impact of grazing in salt marshes. *Coleophora salicorniae*, *Eucosma catoptrana* and *Agdistis bennetii* showed a signifi-

cant preference for ungrazed salt marshes. *Eucosma tripoliana* and *Phalonidia vectisana* reached a higher indicator species value in the extensively grazed salt marsh (Tab. 11). According to the analysis for the photoelector samples, seven species can be considered suitable as indicators for the impact of grazing in salt marshes.

Tab. 11: Indicator Species Values (ISV) of Microlepidoptera caught with photoelector (mean = 0.212) and light traps (mean = 0.124) on the Hamburger Hallig in the four different grazing intensities. Underlined characters indicate suitable indicator species and their ISV ($p < 0.05$, based on 999 permutations). Occurring species with non significant ISV are indicated with an X.

Species	Photoelector traps				Light traps			
	Un-grazed	Extensive	Moderate	Intensive	Un-grazed	Extensive	Moderate	Intensive
<i>Agdistis bennetii</i>	.	x	.	.	<u>0.306</u>	x	.	.
<i>Bucculatrix maritima</i>	0.344	0.379	x	X	0.338	0.338	x	.
<i>Chrysoteuchia culmella</i>	.	.	x	X	x	x	0.322	x
<i>Clepis spectrana</i>	0.327	0.345	x	.	0.272	0.233	0.276	x
<i>Coleophora artemisiella</i>	x	.	x	.	.	x	x	.
<i>Coleophora atriplicis</i>	<u>0.432</u>	x	.	.	x	.	.	.
<i>Coleophora salicorniae</i>	<u>0.514</u>	x	X	.	<u>0.433</u>	0.276	.	.
<i>Crambus perlella</i>	.	.	1.000	x	0.307	0.245	0.257	x
<i>Eucosma catoptrana</i>	<u>0.335</u>	x	x	.	<u>0.320</u>	0.259	x	.
<i>Eucosma lacteana</i>	.	x	<u>0.563</u>	.	0.319	<u>0.376</u>	0.264	x
<i>Eucosma tripoliana</i>	0.401	<u>0.546</u>	.	.	0.249	0.304	x	.
<i>Lobesia littoralis</i>	x	x	.	.	x	x	.	.
<i>Pediasia aridella</i>	x	x	.	.	x	0.226	0.212	x
<i>Phalonidia affinitana</i>	0.298	<u>0.332</u>	x	.	0.289	<u>0.292</u>	0.278	.
<i>Phalonidia vectisana</i>	x	x	x	X	0.289	<u>0.381</u>	x	.
<i>Scrobipalpa instabilella</i>	0.360	0.327	x	x	0.287	0.289	0.368	0.417
<i>Scrobipalpa salinella</i>	<u>0.370</u>	.	x	.	<u>0.267</u>	0.253	0.243	x
<i>Scrobipalpa samadensis</i>	.	.	.	.	x	x	.	.
	mean ISV = 0.212				mean ISV = 0.124			

While the Tortricide *Eucosma lacteana*, feeding on *Artemisia maritima*, occurred more often in the moderately grazed salt marshes, *Eucosma catoptrana*, which feeds on *Aster tripolium*, showed a distinct preference for ungrazed salt marshes.

Coleophora atriplicis, feeding mostly on *Atriplex portulacoides* and *Suaeda maritima*, *Coleophora salicorniae*, feeding solely on *Salicornia europea*, and *Scrobipalpa salinella*, feeding on *Aster tripolium*, *Salicornia europea* and *Suaeda maritima*, also showed a preference for ungrazed salt marshes, although their feeding plants frequently occurred in grazed marshes. Finally, *Eucosma tripoliana* and *Phalonidia affinitana*, both feeding on *Aster tripolium*, indicated ungrazed or extensively grazed salt marshes, seemingly with a slight preference for a low grazing intensity.

4.4.2 Invertebrates in short-term grazing experiments

An ADONIS was computed on the Araneae, Coleoptera and Diptera data determined during the Ecosystem Research Wadden Sea Project (DIERBEN et al 1994a, b) as well as on

the newly determined data on Lepidoptera, to compare the response of the four groups to grazing. The results suggest an impact of grazing on the species composition of Lepidoptera in the salt marshes of Friedrichskoog, although only the analysis for the complete time period of research showed a significant influence of grazing (Tab. 12). The results of the ADONIS for the sampled Coleoptera and Araneae showed a significant effect of grazing on the composition in the years 1990 to 1993 as well as over the whole sampling period, whereas the variation in the distribution of Diptera only showed a significant impact of grazing in 1993 and over the whole sampling period.

Tab. 12: Results of the ADONIS for the impact of grazing on the species composition of Coleoptera, Diptera, Araneae (DIERBEN et al. 1994a & b), and Lepidoptera in the salt marshes of Friedrichskoog based on 999 permutations, underlined values indicate a significance level of $p < 0.005$, Bonferroni corrected.

Year	Lepidoptera		Coleoptera		Diptera		Araneae	
	F.Model	Pr(>F)	F.Model	Pr(>F)	F.Model	Pr(>F)	F.Model	Pr(>F)
1990	1.32151	0.211	1.57088	0.056	1.07600	0.315	0.96185	0.477
1991	1.41706	0.164	<u>2.08024</u>	<u>0.001</u>	1.5648	0.007	<u>1.99707</u>	<u>0.002</u>
1992	1.58973	0.074	<u>1.91777</u>	<u>0.001</u>	1.25790	0.180	<u>4.81696</u>	<u>0.001</u>
1993	2.50367	0.009	<u>1.75333</u>	<u>0.002</u>	<u>1.79025</u>	<u>0.003</u>	<u>2.79394</u>	<u>0.001</u>
<u>1990-93</u>	<u>3.26196</u>	<u>0.001</u>	<u>3.70706</u>	<u>0.001</u>	<u>1.92807</u>	<u>0.002</u>	<u>4.39793</u>	<u>0.001</u>

Tab. 13: Results of the ADONIS for the impact of grazing on the species composition of Coleoptera, Diptera, Araneae (Dierßen et al. 1994a & b) and Lepidoptera in the salt marshes of the Sönke-Nissen-Koog based on 999 permutations, underlined characters indicate a significance level of $p < 0.005$, Bonferroni corrected.

Year	Lepidoptera		Coleoptera		Diptera		Araneae	
	F.Model	Pr(>F)	F.Model	Pr(>F)	F.Model	Pr(>F)	F.Model	Pr(>F)
1990	1.02630	0.398	0.66733	0.888	<u>1.95321</u>	<u>0.005</u>	<u>2.98661</u>	<u>0.001</u>
1991	<u>2.96934</u>	<u>0.002</u>	<u>2.61153</u>	<u>0.001</u>	1.49055	0.024	<u>3.28767</u>	<u>0.001</u>
1992	2.24707	0.013	1.75492	0.011	1.59216	0.028	<u>3.86007</u>	<u>0.001</u>
1993	<u>4.88907</u>	<u>0.001</u>	1.48784	0.026	<u>3.17788</u>	<u>0.001</u>	<u>3.58698</u>	<u>0.001</u>
<u>1990-93</u>	<u>8.13856</u>	<u>0.001</u>	<u>2.36909</u>	<u>0.001</u>	<u>3.69756</u>	<u>0.001</u>	<u>7.27958</u>	<u>0.001</u>

Results of an ADONIS on the species composition of Araneae, Coleoptera, Diptera and Lepidoptera in the salt marshes of the Sönke-Nissen-Koog support the hypothesis of an impact of grazing on the species composition of Lepidoptera and show a significant impact of grazing intensity on the distribution of moths for the years 1991, 1993 and for all years combined, but no significant effects in 1990 and 1992 (Tab. 13). A similar impact of grazing on the species composition could be found in the samples of Coleoptera, Diptera and Araneae, although the results for Coleoptera were less distinct than for Lepidoptera. Araneae showed a significant response to grazing in all years.

These differences in species composition especially for beetles and spiders in the higher salt marshes of Friedrichskoog, and for moths, flies and spiders in the lower salt marshes of the Sönke-Nissen-Koog imply a possible suitability of halobiontic invertebrates as indicator species for salt marsh management.

Tab. 14: ISV of Araneae caught with photoeclector traps in the salt marshes of Friedrichskoog and the Sönke-Nissen-Koog (DIERBEN et al 1994a & b) according to different grazing intensities. Underlined characters indicate suitable indicator species and their ISV ($p < 0.01$, based on 999 permutations). Occurrences < 10 individuals were excluded from analysis (un: ungrazed, ext.: extensive, mod.: moderate, int.: intensive).

Species	Friedrichskoog					Sönke-Nissen-Koog				
	Grazing management									
	un.	low	ext.	mod.	int.	un.	low	ext.	mod.	int.
<i>Araneoncus humilis</i>	.	.	.	.	0.339	.	.	.	.	.
<i>Baryphyma duffeyi</i>	.	.	.	.	.	0.283	0.274	0.291	0.270	0.323
<i>Bathypantes gracilis</i>	0.347	0.327	0.239	0.285	0.305	0.190	0.307	0.297	0.291	0.333
<i>Clubiona stagnatilis</i>	.	.	<u>0.329</u>	.	.	.	.	.	.	.
<i>Erigone arctica</i>	0.317	0.275	0.256	0.327	0.303	.	.	.	.	.
<i>Erigone atra</i>	0.323	0.297	0.260	0.308	0.308	0.307	0.301	0.322	0.316	0.337
<i>Lepthyphantes tenuis</i>	0.307	0.285	0.265	0.285	0.354	.	.	.	.	.
<i>Lepthyphantes ericaeus</i>	.	.	.	.	.	.	.	.	.	<u>0.357</u>
<i>Oedothorax apicatus</i>	.	0.267	.	.	.	.	0.291	.	0.316	<u>0.356</u>
<i>Oedothorax fuscata</i>	0.311	0.288	0.270	0.305	0.289	.	.	.	.	.
<i>Oedothorax retusus</i>	0.346	0.346	0.293	0.323	0.298	0.271	0.374	.	0.316	0.328
<i>Pachygnatha clercki</i>	0.282	0.280	0.261	0.309	.	0.322	0.343	0.399	0.325	0.380
<i>Pachygnatha degeeri</i>	.	0.283	<u>0.343</u>	.	.	0.274	<u>0.305</u>	.	<u>0.296</u>	.
<i>Pardosa agrestis</i>	0.339	0.280	0.313	0.290	0.339	0.349	0.321	0.337	0.276	.
<i>Porrhomma errans</i>	.	.	.	.	.	0.228	.	0.339	0.293	0.366
<i>Porrhomma microphthalamum</i>	0.356	0.287	0.268	0.321	0.300	.	<u>0.348</u>	0.339	.	0.360
<i>Porrhomma montanum</i>	.	.	.	.	.	.	<u>0.440</u>	0.355	.	.
<i>Silometopus ambiguus</i>	0.301	0.288	0.261	0.332	0.284	.	.	.	.	.
	mean ISV = 0.148					mean ISV = 0.147				

Results of the Indicator Species Analysis (ISA)(see chapter 3.2.2), computed on the spider, beetle and fly data (DIERBEN et al 1994a, b) as well as on the moth data showed significant values for most spider species occurring in higher abundances in the salt marshes of Friedrichskoog and the Sönke-Nissen-Koog, although most species reached low values due to their occurrence in all grazing intensities. No clear pattern could be derived. According to its distribution, only *Clubiona stagnatilis* and *Pachygnatha degeeri* qualified as indicator species for low grazing intensities for the *Festuca rubra*-dominated salt marshes of Friedrichskoog (Tab. 14). The spider communities found in the lower salt marshes of the Sönke-Nissen-Koog were more easily distinguishable according to their indicator values, with *Lepthyphantes ericaeus* and *Oedothorax apicatus* indicating higher grazing intensities, and *Pachygnatha degeeri*, *Porrhomma microphthalamum* and *Porrhomma montanum* indicating salt marshes of low grazing intensities. Overall, results of the ISA showed a small variation in indicator species values, with numerous species showing significant values in the grazing intensities, and thus only minor variations in species composition for the differently grazed paddocks. Most species that reached high indicator values in any of the management types are not halobiontic. The species are able to

cope with the extreme conditions in salt marshes, but reach their peak of occurrence mostly in terrestrial habitats like bogs, heathlands, wet meadows or fields. Most typical halobiontic spider species, like *Bathyphantes gracilis* or *Baryphyma duffeyi*, did not qualify as indicator species for either management type.

Tab. 15: ISV of Coleoptera caught with photoeclector traps in the salt marshes of Friedrichskoog and the Sönke-Nissen-Koog (DIERBEN et al 1994a & b) according to different grazing intensities. Bold characters indicate suitable indicator species and their ISV ($p < 0.05$, based on 999 permutations). Occurrences < 5 individuals were excluded from analysis (un.: ungrazed, ext.: extensive, mod.: moderate, int.: intensive).

Species	Friedrichskoog					Sönke-Nissen-Koog				
	Grazing management									
	un.	low	ext.	mod.	int.	un.	low	ext.	mod.	int.
<i>Atomaria fuscata</i>	.	.	.	.	.	0.214	0.353	0.219	0.259	0.298
<i>Atomaria puncticollis</i>	.	.	.	.	.	0.286	.	0.305	0.241	0.302
<i>Bembidion minimum</i>	0.199	0.206	0.196	0.178	0.183	0.217	0.265	0.277	0.229	0.231
<i>Bembidion normannum</i>	.	.	.	.	.	.	0.359	.	.	0.274
<i>Bledius tricornis</i>	0.256	0.229	0.216	0.222	0.243	.	.	.	.	.
<u><i>Cantharis fulvicollis</i></u>	.	.	.	.	.	.	.	.	.	<u>0.390</u>
<i>Cantharis rufa</i>	.	.	.	.	.	0.295	.	.	0.334	.
<u><i>Corticaria fuscata</i></u>	<u>0.373</u>	0.162	.	.	.	0.272	0.285	<u>0.348</u>	0.207	.
<i>Ceutorhynchus assimilis</i>	.	.	0.262	.	.	.	.	.	.	.
<i>Clavina fossor</i>	0.148	.	.	.	.	.	.	.	.	.
<u><i>Corticarina gibbosa</i></u>	.	.	.	<u>0.253</u>	.	.	.	.	.	.
<i>Dicheirotichus gustavii</i>	0.189	0.213	0.240	0.220	0.215	0.381	0.199	0.285	0.311	.
<i>Dyschirius calceus</i>	.	.	.	.	.	0.321	0.297	0.347	0.283	0.301
<u><i>Dyschirius salinus</i></u>	.	.	.	.	<u>0.278</u>	.	.	.	.	.
<i>Enicmus transversus</i>	0.195	0.232	0.247	0.213	.	.	.	.	.	.
<i>Harpalus rufa</i>	.	.	.	.	.	0.255	0.237	.	0.227	.
<i>Heterocerus maritima</i>	.	.	.	.	.	0.250	0.332	0.324	0.248	0.294
<i>Heterocerus flexuosus</i>	0.247	0.208	0.223	0.202	0.272	.	0.218	0.253	0.253	0.299
<u><i>Lasiotrechus discus</i></u>	.	.	.	.	.	.	.	.	.	<u>0.257</u>
<i>Longitarsus plantagomartini</i>	0.380	0.203	0.269	0.213	0.302	.	.	.	.	.
<i>Ochtebius auriculatus</i>	0.351	0.212	0.202	0.237	0.274	.	.	.	.	.
<i>Otiorhynchus frisius</i>	0.271	0.241	0.258	0.221	0.277	0.261	0.206	0.427	0.302	0.324
<i>Phyllobius verspertinus</i>	0.290	.	0.247	0.259	0.385	.	.	.	.	.
<i>Phytobius zumpti</i>	0.280	0.274	0.200	0.187	0.247	0.318	.	.	0.269	0.231
<i>Polydrusus pulchellus</i>	0.196	0.229	.	0.245	.	.	.	.	.	0.242
<i>Psylliodes chrysocephala</i>	.	.	.	.	.	0.281	0.185	.	.	0.252
mean ISV = 0.113						mean ISV = 0.131				

A similar pattern is apparent for the indicator species values of beetle communities in salt marshes, with low but significant values for most species that occurred in higher

abundances. Only *Lasiotrechus discus* and *Cantharis fulvicollis*, occurring in the salt marshes of the Sönke-Nissen-Koog, and *Dyschirius salinus*, occurring in the salt marshes of Friedrichskoog, seemed to indicate grazed salt marshes. *Corticarina gibbosa* that qualified as indicator for moderate grazing intensities, and *Cantharis fulvicollis* are common species with main occurrences in many terrestrial habitats (Tab. 15). According to the ISA, all other Coleoptera that occurred in higher abundances in the salt marshes of Friedrichskoog or the Sönke-Nissen-Koog were unsuitable as indicators for grazing management in salt marshes and their distribution seemed to be influenced rather by other environmental factors such as soil compaction, sand content or vegetation height.

Tab. 16: ISV of Diptera caught with photoeclector traps in the salt marshes of Friedrichskoog and the Sönke- Nissen-Koog (DIERBEN et al 1994a & b) according to different grazing intensities. Bold characters indicate suitable indicator species and their ISV (p < 0.05, based on 999 permutations). Occurrences < 5 individuals were excluded from analysis (un.: ungrazed, ext.: extensive, mod.: moderate, int.: intensive).

Species	Friedrichskoog					Sönke-Nissen-Koog				
	Grazing management									
	un.	low	ext.	mod.	int.	un.	low	ext.	mod.	int.
<i>Campsicnemus armatus</i>	0.165	0.207	.	.	0.182	.	.	.	.	.
<i>Cerodontha denticornis</i>	0.177	0.199	0.178	0.223	0.259	0.209	0.160	0.324	0.265	0.255
<i>Chersodromia cursitans</i>	0.273	0.268	0.244	0.214	0.221	.	.	.	.	.
<i>Dolichopus clavipes</i>	0.228	0.242	0.238	0.183	0.237	0.303	0.373	0.320	0.307	0.215
<i>Dolichopus diadema</i>	.	.	.	.	.	0.310	0.319	0.362	0.342	0.288
<i>Dolichopus plumipes</i>	.	.	0.194	.	.	.	.	.	.	.
<i>Hydrophorus oceanus</i>	0.183	0.236	0.186	.	0.199	0.202	0.252	0.266	0.254	0.256
<i>Jaapiella schmidtii</i>	.	.	0.197	.	.	.	.	.	.	.
<i>Lestremia cinerea</i>	.	0.241	0.168	0.251	.	0.169	0.229	.	0.270	.
<i>Mayetiola agrostivora</i>	0.238	0.253	.	0.175	0.217	.	.	.	.	.
<i>Mayetiola puccinelliae</i>	0.188	0.242	0.234	0.200	0.189	0.202	0.253	0.262	0.236	0.236
<i>Micromorphus albipes</i>	0.239	0.249	0.207	0.248	0.191	0.247	0.274	0.330	0.304	0.273
<i>Nemotelus notatus</i>	0.256	0.255	0.261	0.238	0.217	.	0.291	0.315	0.277	0.304
<i>Nemotelus uliginosus</i>	.	0.248	.	0.227	.	0.281	.	.	.	.
<i>Parepidopsis argentifera</i>	0.216	0.186	0.185	0.342	0.217	.	.	.	.	.
<i>Campiglossa plantaginis</i>	.	.	.	.	.	0.278	.	.	.	.
<i>Rhamphomyia florum</i>	.	.	.	.	.	0.186	0.302	.	0.303	.
<i>Rhaphium riparium</i>	.	.	.	.	.	0.183	0.261	0.410	0.218	.
<i>Rhamphomyia simplex</i>	.	.	.	.	.	0.236	0.211	X	X	.
<i>Stilpon nubila</i>	.	0.232	0.223	0.213	.	.	.	.	.	.
<i>Symplecta stictica</i>	0.215	0.293	0.188	0.222	0.185	0.223	0.227	0.263	0.358	0.263
<i>Syntormon filiger</i>	0.191	0.224	0.194	0.230	0.190	.	.	X	.	0.230
<i>Syntormon pallipes</i>	.	.	.	.	.	0.218	0.216	0.232	0.236	0.256
mean ISV = 0.103						mean ISV = 0.133				

Concerning Diptera species in salt marshes, indicator species values were generally low and only *Campiglossa plantaginis* indicated ungrazed lower salt marshes dominated by *Puccinellia maritima*. *Symplecta stitica* was linked to low grazing intensities in Friedrichskoog, but received higher indicator values in the moderately grazed lower salt marshes of the Sönke-Nissen-Koog (Tab. 16). *Rhaphium riparium*, *Dolichopus clavipes* and *D. diadema* indicated low to extensive grazing in *Puccinellia maritima*-dominated salt marshes.

For the communities of Araneae, Coleoptera and Diptera, the indicator species values for all species occurring in higher numbers exhibited a narrow margin range, and possible indicator species qualified only due to their occurrence in different parts of the salt marshes with different grazing intensities.

Tab. 17: ISV of Lepidoptera caught with photoeclector traps in the salt marshes of Friedrichskoog and the Sönke-Nissen-Koog according to different grazing intensities. Bold characters indicate suitable indicator species and their ISV ($p < 0.05$, based on 999 permutations). Occurrences < 5 individuals were excluded from analysis (un.: ungrazed, ext.: extensive, mod.: moderate, int.: intensive).

Species	Friedrichskoog					Sönke-Nissen-Koog				
	Grazing mangement									
	Un.	low	ext.	Mod.	Int.	Un.	low	ext.	mod.	Int.
<i>Agriphila selasella</i>	X	X	X	X	X	.	.	.	.	.
<i>Bucculatrix maritma</i>	.	.	.	.	.	0.359	X	0.389	X	X
<i>Clepis spectrana</i>	X	.	X	.	.	0.410	X	0.523	.	.
<i>Coleophora adjunctella</i>	X	.	X	.	.	.	.	.	.	.
<i>Coleophora atriplicis</i>	X	.	.	.	.	X	.	X	.	.
<i>Coleophora alticolella</i>	X	.	.	.	.	.	.	.	.	.
<i>Coleophora deviella</i>	.	.	.	.	.	0.269	0.444	0.448	X	X
<i>Coleophora glaucicolella</i>	X	.	.	.	.	.	.	.	.	.
<i>Crambus perlella</i>	X	X	0.561	X	X	X	X	.	X	.
<i>Eucosma catoptrana</i>	.	.	.	.	.	X	.	.	.	.
<i>Eucosma tripoliana</i>	.	.	.	.	.	0.341	X	X	X	.
<i>Lobesia littoralis</i>	X	X	X	X	.	.	.	.	.	.
<i>Phalonidia affinitana</i>	.	.	.	.	.	0.291	X	X	.	.
<i>Phalonidia vectisana</i>	.	.	.	.	.	X	.	.	X	.
<i>Scrobipalpa instabilella</i>	.	.	.	X	.	X	.	X	X	X
<i>Pediasia aridella</i>	X	0.644	0.556	X	X	X	X	0.571	X	X
mean ISV = 0.487						mean ISV = 0.374				

The pattern of the indicator values for the Lepidoptera communities was distinctly different, however. In the high marshes of Friedrichskoog, significance levels varied considerably, and only the grass-feeding species *Crambus perlella* and *Pediasia aridella* showed significant ISVs for the low to moderately grazed salt marshes. Of these, *C. perlella* is a eurytopic species that occurs in numerous habitats. Therefore, its indicator quality is questionable. In the lower salt marshes of the Sönke-Nissen-Koog, six lepidopteran species could be identified as indicator species. *Phalonidia affinitana* and *Eucosma tripoliana*

liana showed a clear linkage to ungrazed salt marshes, *Clepis spectrana*, *Coleophora deviella* and *Bucculatrix maritima* to extensively grazed plots, and *Pediasia aridella* mostly occurred in moderately grazed salt marshes (Tab. 17).

5 Discussion

Effects of grazing and succession in salt marshes have been under critical discussion for several years (BAKKER 1985, BAKKER 1989, IRMLER & HEYDEMANN 1986, IRMLER et al. 1987, STOCK et al. 1997, PÉTILLON & GARBUTT 2008a) but invertebrates have received surprisingly little attention (but see MEYER & REINKE 1996, ANDRESEN et al. 1990, PÉTILLON et al. 2005).

They have been studied more thoroughly in other grazing ecosystems, and sometimes large responses by insects and spiders were found, despite small changes in the plant communities (MORRIS 1971, GIBSON et al. 1992, MILCHUNAS et al. 1998, MYSTERUD et al. 2005).

Moths and especially Microlepidoptera have remained largely neglected in these studies because of feared difficulties in identification and a lack of knowledge in their distribution and life history (GIBSON et al. 1992), although a strong response of this mostly specialised group of herbivores to grazing can be expected. This is the first time the response of Microlepidoptera to grazing management in salt marshes has been investigated, and results show a sensitive response to different types of management.

5.1 Microlepidoptera in salt marshes of Schleswig-Holstein

Although Lepidoptera belong to the best collected and studied orders of insects (GASTON 1991, VAN SWAAY et al. 2008), the focus of research has always been on Macrolepidoptera and the more numerous Microlepidoptera have been largely ignored (NEW 2004a). Therefore, gaps of knowledge in their recent occurrences and distributions exist and literature has remained scattered. A lack of information on the diversity, life history and distribution of specialised invertebrates remains one of the challenges in ecological research (SUMMERVILLE & CRIST 2005). Studies in salt marshes mostly focused on spiders and beetles and their distribution along an inundation gradient or the impact of an increase of *Elymus athericus* (REINKE & MEYER 1999, REINKE et al. 2000, IRMLER et al. 2002, PÉTILLON et al. 2005a, FINCH et al. 2007, PÉTILLON et al. 2008). Only few studies dealt with moth diversity (HEYDEMANN 1938, STÜNING 1980, JANSEN 2005).

Habitat diversity and plant species composition are factors influencing species richness and abundance of invertebrate communities (DESENDER & MAELFAIT 1999, KORICHEVA et al. 2000), and the diversity of Lepidoptera is expected to be correlated with plant diversity in all vegetation types (ERHARDT & THOMAS 1991). Additionally, their abundance was found to be positively correlated to warm and dry summers (HOLYOAK et al. 1997, ROY et al. 2001). Because of their small body size, Microlepidoptera are especially affected by climatic conditions and their activity is, to a large extent, influenced by temperature and wind, since their ability to fly is limited to a narrow range of body temperature (WIKSTRÖM et al. 2008). Thus, salt marshes, which are often exposed to strong winds, inundation and a high variation in temperature, form an extreme habitat, to which only few moths are adapted. In Northern Europe about 40 halobiontic Microlepidoptera are known which mainly occur on salt marshes or inland salt pans.

Between 2006 and 2009 87 species were caught in the mainland salt marshes of Schleswig-Holstein of which 29 are considered to be exclusively or mostly occurring on salt marshes (see Tab. 3).

The high number of non-halobiontic species (58) has to be ascribed to so called 'tourist species' (GASTON et al. 1993), which most likely dispersed into the salt marsh from surrounding habitats like seawalls and agricultural fields and gardens behind the seawall, and to polyphagous species mostly feeding on grasses. Especially with light-trapping high numbers of 'tourist species', moths as well as water beetles and water bugs, were attracted, which did not necessarily develop in the salt marsh. These species were recorded in very low numbers, but count for a high proportion of the overall recorded species richness. Twenty-eight of the recorded species were exclusively caught by light traps and had to be considered 'tourists' to the salt marsh habitat.

Photoeclector traps on the contrary, exclusively catch those species fulfilling their life-cycle in the sampled site, and allow a conclusion on the indigenous moth community of the investigated salt marsh to be made (REINKE & MEYER 1999, FRANK et al. 2009). On the Hamburger Hallig, 25 different moth species were trapped by this means of which two, *Crambus perlella* and *Chrysoteuchia culmella* are not considered halobiontic, but are able to develop in salt marshes depending on the occurrence of grasses. In contrast to the light trap catches, even those species caught in low abundances or as single specimens are indigenous to the salt marsh, and had to be considered rare in the habitat.

Most trapping methods are biased either by not applying an equal lure to each species and thus not attracting all species to the same extent (light traps) (MCGEACHIE 1989) or by only trapping a part of the occurring population by excluding migrant or 'tourist' species (photoeclector traps) (REINKE & MEYER 1999). Additionally, sampling artefacts can occur, because rare species are less likely to be observed than abundant species (Vazquez & Aizen 2003). The calculation of species accumulation curves for the quantitative data obtained by light-trapping and with photoeclector traps allowed an estimation of the completeness of sampling and it was assumed, that a representative part of the moth community was recorded (THOMPSON et al. 2003, THOMPSON & THOMPSON 2007). Qualitative measurements by net sweeping, searching for larvae and attraction with a Mercury-Vapour-Lamp led to additional records of species, which had not been caught otherwise due to their distinct life history and flight period. These species were under-represented in the quantitative data sets and could not be included in the statistical analysis. Fluctuations in species abundances in different years had to be explained by climatic conditions, which are known to have a high impact on moths (KUCHLEIN & ELLIS 1997) leading to sampling errors especially with light trap samples (HOLYOAK et al. 1997, ROY et al. 2001). Additionally, different sampling intensities in different years depending on weather conditions lead to sampling artefacts for light trap samples.

Most species recorded abundantly by means of trapping with light and photoeclector traps (Fig. 23) were halobiontic species, such as *Scrobipalpa instabilella*, *Bucculatrix maritima* and *Eucsoma catoptrana*, or eurytopic species, such as the already mentioned *Chrysoteuchia culmella* and *Crambus perlella*. The majority of eurytopic species, however, was caught only infrequently and could not be considered resident. A considerable number of halobiontic species were infrequently distributed as well. *Aristotelia brizella* for example, was infrequently recorded and could only be caught by net sweeping. Larval stages could not be found in spite of intensive searching. The moth's rareness might be explained by the patchy distribution of the host plant (*Armeria maritima*), mostly in extensively and moderately grazed areas which are scarce along the mainland coast.

Coleophora atriplicis, *C. asteris* and *C. artemisiella* however, were hardly recorded by light traps or photoeclector traps but larval stages were found frequently. They are therefore under-represented in trapping data, although they should be considered fairly common in Schleswig-Holstein salt marshes.

This research was executed in acknowledgement of studies on Lepidoptera in the supralittoral of Schleswig-Holstein from 1968 to 1975 (STÜNING 1980). During this time, due to intensive grazing on and drainage of most mainland salt marshes, plant species diversity on fore-land marshes was poor, consisting mostly of short swards of *Puccinellia maritima* or *Festuca rubra* accompanied by only few grazing resistant species (KIEHL 1997). Consequently, research by STÜNING (1980) was mainly restricted to two main observation sites in the Meldorf Bight and the Hauke-Haien-Koog. Here, small grazing enclosures and biotopes in recently embanked polders and on seawalls were sampled, adding to a high number of species. Additionally, few biotopes on the Halligen, close to the Hindenburgdamm to Sylt, in Schobüll near Husum and on the Baltic on Fehmarn were sampled infrequently. It was expected that the cessation or extensification of grazing on 55% of the mainland salt marshes (STOCK et al. 2005) would lead to an increase in species richness of moths and especially halobiontic species. During the study of STÜNING (1980), altogether 79 species of Microlepidoptera, with 24 species considered to be halobiontic were recorded. Of these, 21 were caught in salt marsh habitats. Unfortunately, no conclusion on the total amount of specimens found only in salt marsh habitats can be drawn from the former work, leaving major uncertainties on the commonness and rarity of some species.

In comparison, more halobiontic as well as eurytopic species were recorded in the salt marsh habitats from 2006 to 2009. On the one hand, a possible explanation could be a constantly changing and highly variable environment, where extinction and colonisation occur frequently, depending on the existence of suitable source populations (BLOMQVIST et al. 2003). This often leads to differences in species richness in each location and year. On the other hand, in both studies various salt marsh habitats along the coast of Schleswig-Holstein had been sampled, minimising regional effects. An increase in species richness thus can be ascribed to the cessation or extensification of grazing in the last 25 years, leading to a higher heterogeneity of habitats and a higher abundance of host plants (KIEHL et al. 2003, STOCK et al. 1997). This reasoning is supported by the fact that all of the species found by STÜNING (1980) but one (*Scrobipalpa obsoletella*, known to occur in the salt marshes of Schleswig-Holstein) were also caught during this study whereas no extinction could be detected. Five species were identified, which had not been recorded in Germany before (*Goniodoma limoniella*), had only been found infrequently (*Agdistis bennettii*, *Aristotelia brizella* and *Eucosma catoptrana*) or had not been recorded for decades (*Whittleia retiella*).

These results illustrate the importance of knowledge on life histories of species and emphasise, that simple trust in standardised methodology and counted data might lead to false conclusions. Additionally, insects have a reputation for high inter-annual population variation due to their climatic dependency (HOLYOAK et al. 1997), therefore relationships to habitat types have to be tested across multiple years (HUGHES et al. 2000a). The importance of a combined application of expert knowledge, standardised methods and a careful analysis pursuing trustworthy results can not be overrated.

5.2 Life history of halobiontic Microlepidoptera

The knowledge of life history traits is often essential in understanding species distribution and their conservation needs. For many Lepidoptera their life histories have been

thoroughly studied and, as in the case of *Maculinea alcon*, have led to further understanding on the rarity and endangerment of species (MAES et al. 2004). Populations of *Maculinea alcon* were recognised to be declining even though their larval host plants (*Gentiana pneumonanthe*, *Gentiana cruciata*, *Gentiana asclepiadea*) were protected and plant populations considered stable. Only when the symbiotic dependency of *Maculinea alcon* on ants (*Myrmica ruginodis* and *Myrmica rubra*) as hosts for larvae was understood (ELMES et al. 2001) and site characteristics were considered in conservation management, butterfly populations slowly recovered (MAES et al. 2004). But although the necessity of the knowledge on life histories were recognised a crucial factor in species conservation, many details are still unknown, especially when regarding the moths which are smaller and less conspicuous.

With respect to the halobiontic moths, information on life histories was scattered throughout literature, sometimes missing, and no comprehensive description with illustrations of larval stages existed. The results on life histories synthesise all known details, complement missing information and give illustrations of larval stages as well as the adult moths, if possible.

In the following, quintessential information on the life histories of species, which appeared to be of relevance for ecological monitoring and grazing management are discussed to underline the importance of the knowledge of their life histories.

Whittleia retiella, which was found in MAY 2007 in the salt marshes of Westerhever, had not been recorded in Germany since 1959, where only few specimens were caught by Rill (situated in the collection of the Zoological Institute and Museum Hamburg). Even though the Psychide was considered to be very rare (BINOT et al. 1998), it was found in high abundances in all investigated salt marshes except heavily grazed plots, where its host plants *Puccinellia maritima* and *Festuca rubra* occurred (RICKERT et al. 2009). It is most likely that the species had not been found since the late 1950s since most authors mentioned a flight period of late May to early June (KAABER 1982, HÄTTENSCHWILER 1985), whereas older records in Germany as well as all new records were collected during a short period in the beginning of May. Nevertheless, since *W. retiella* had not been recorded by STÜNING (1980), it was apparently not abundant due to intensive grazing, and populations could recover only after extensification or abandonment after 1985. Notwithstanding, no conclusions on the quality of a habitat could be drawn from the occurrence of *W. retiella*, since it was mostly found in grassy vegetation and occurred abundantly in the moderately grazed areas on the Hamburger Hallig as well as in the ungrazed patches in Westerhever. However, it was not found in the intensively grazed salt marshes and might prove to be a good indicator for overgrazing in future studies.

Goniodoma limoniella could be verified as a new record for Germany in 2006 (RICKERT 2009a). Since *G. limoniella* was only known from France, Belgium, Great Britain and the Netherlands, but so far had not been found in Germany or Scandinavia, its occurrence raised the question of a recent expansion. The Coleophoridae occurred in great abundances in the salt marshes of Westerhever and St. Peter-Ording but could only be found with a few specimens in the Hamburger Hallig, despite the frequent occurrence of its host plant *Limonium vulgare*. Intensive investigations north of the Hamburger Hallig on Hallig Gröde, Hallig Langeness, the isle of Sylt and the mainland salt marshes as well as on Skallingen and the isle of Rømø in Denmark in autumn 2006 and spring 2007 lead to no further proof of occurrence, although larvae are easily detectable. A first record for Denmark was noted in 2008 on the isle of Rømø (Gregersen & Szyska 2009), which suggests that the species might be spreading north. No statement on whether this range expansion is related to climate change or rather determined by chance of colonisation

can be made. Unfortunately, the first appearance of *G. limoniella* in Germany is unknown, since records on the distribution of Microlepidoptera especially on salt marshes are scarce (ROWECK & SAVENKOV 2002). Like *W. retiella*, it had not been caught during the comprehensive studies of STÜNING (1980). Its food plant *Limonium vulgare* is known to react sensitively to grazing (KIEHL et al. 2003), and could spread only after abandonment. Hence, it can be assumed that colonisation by *G. limoniella* started after extensification or cessation of grazing following the establishment of the Wadden Sea National Park (1985). The abundant occurrence of *G. limoniella* and the easy detection of its larvae in combination with its linkage to the grazing-sensitive *L. vulgare* would suggest the suitability as an indicator species in ecological monitoring. However, the species was not caught sufficiently in the salt marshes of the Hamburger Hallig and was only seldomly attracted by light. Assumptions on the sensitivity of *G. limoniella* towards grazing are so far mostly based on the larval hibernation in the easily breaking stems of *L. vulgare*, which suggest a high influence of disturbances, but need to be validated in further studies.

Agdistis bennetii is the second species whose larvae feed exclusively on *Limonium vulgare*, and which therefore can be expected to have benefited from changes in grazing management, since many monophagous butterflies are sensitive to changes that affect their host plants (NELSON 2007). In contrast to the two species mentioned before, *A. bennetii* has to be considered rare with only two specimens caught in 2007, 42 in 2008 and 19 in 2009. A possible reason for low abundances might be the hibernation as larvae affixed to leaves of the food plant and they thus were affected by cold winters and storm tides (DESCHKA 1998). Both *Gonidodoma limoniella*, whose larvae hibernate in the stem of *L. vulgare* and *Whittleia retiella*, whose larvae hibernate in the larval case on the ground sheltered by grass tussocks, are likely to be less affected. The occurrence of *A. bennetii* thus seems to be more determined by climatic conditions than affected by grazing and the suitability as an ecological indicator has to be disregarded.

Recorded equally infrequently was *Aristotelia brizella*, whose larvae feed on the seeds of *Armeria maritima*, a salt marsh plant especially in moderately grazed, grass dominated higher salt marshes which have become scarce along the mainland coast. The occurrence of *A. brizella* in the salt marshes of Westerhever and St. Peter-Ording but not on the Hamburger Hallig or any of the other visited locations suggests that fragmentation might have led to isolated populations (ÖCKINGER et al. 2010) because of site fidelity of moths and limited dispersion abilities (ZSCHÖKKE et al. 2000). An upper limit in dispersal distance of approximately 1 km was recognised for many moth (Macrolepidoptera) species (RICKETTS et al. 2002, SUMMERVILLE & CRIST 2004), hampering the colonisation possibilities of small and remote salt marsh patches. Therefore, due to a spatial isolation those remaining scattered areas with populations of *A. brizella* might not function as source habitats (DENNIS et al. 1998a). However, rareness of recording might be a sampling artefact. The moths are most active during the early evening hours and therefore not attracted by light (BLAND et al. 2002), which leads to an underestimation of abundance in comparison to other species. Nevertheless, the species was only caught by net sweeping above stands of its host plant on few occasions, which suggests that it is one of the less common species on Schleswig-Holstein salt marshes. This assumption is supported by only infrequent findings in the Netherlands and Denmark (pers. communication M. Jansen). The hibernation as larvae in the flower heads of *A. maritima*, which easily break, might be a further explanation for the species rarity. Additional trapping especially with pheromone traps (ALBERT et al. 1984) might reveal new insights into the distribution and abundance of *A. brizella*. A suitable lure, however, is yet unknown.

By contrast, the frequent distribution of *Eucosma catoptrana* on all sampled salt marshes during 2006 to 2009 but only few records before 1980 (GÄDICKE & HEINICKE 1999) suggests a positive effect of the abandonment. The recovery of populations of *Aster tripolium*, host plant of *E. catoptrana*, throughout the salt marshes of Schleswig-Holstein after the cessation of grazing (KIEHL et al. 2003, STOCK et al. 2005) supports this hypothesis. *E. tripoliana*, the second *Eucosma*-species feeding on *Aster tripolium*, however, had already been recorded during the studies of STÜNING (1980). The only apparent difference is a slightly earlier flight period of *E. catoptrana*, with a peak in June and again in August, whereas *E. tripoliana* shows highest abundances in late July. Additionally, *E. tripoliana* is slightly smaller than *E. catoptrana*. Unfortunately, no information on the abundance of *E. tripoliana* during the earlier studies was made, and therefore it is difficult to draw conclusions from the appearance of *E. catoptrana* after the abandonment of grazing. Nevertheless, during the recent studies both species reacted sensitively to grazing, *E. catoptrana* being more abundant in the ungrazed salt marsh, *E. tripoliana* in the extensively grazed marsh, and both only infrequently recorded in the moderately and intensively grazed plots. This could be explained by denser inflorescences and thus more seeds in *Aster*-stands in the ungrazed salt marsh, whereas the plants tend to grow with shorter stems and less flowers in the grazed marsh, likely due to its high palatability. Since both species depend on the shelter of spinnings in the inflorescence from which they feed, it is reasonable that the lower density of flowers reduces the possibility of hatching. Their high abundance, their distribution in all researched salt marshes and their sensitivity towards grazing suggests that *E. catoptrana* and *E. tripoliana* are suitable candidates for ecological monitoring in salt marshes.

Larval specificity and hibernation stage are determinant factors influencing distribution and extinction risk (MATTILA et al. 2008). Hibernation as larvae, which has been found in all occurring microlepidopteran species in salt marshes could be an adaptation to the extreme conditions, and seems to be a crucial factor determining their abundance. DESCHKA (1998) showed that hibernation is the major determinant for survival of leaf-miners throughout the year. In salt marshes, the most common species were found to be those hibernating in a cocoon in the ground or inside a plant (*Scrobipalpa instabilella*, *Eucosma catoptrana*, *Eucosma tripoliana*, *Phalonidia affinitana*), whereas those hibernating outside on the plant or in exposed parts of the plant seemed to be more affected by climatic effects and inundation (*Agdistis bennetii*, *Aristotelia brizella*).

Additionally, habitat fragmentation and the availability of suitable source habitats seem to be crucial factors influencing colonisation possibilities especially in the smaller moths (ÖCKINGER et al. 2010).

The response of these species to climatic conditions or disturbances can therefore be explained by their specific life history and highlights the necessity of basic knowledge to complement ecological research and to understand responses of species to environmental change and disturbance (NOSS 1990).

5.3 Response of plant and invertebrate communities to grazing

Salt marshes are narrow ecotones between terrestrial and marine systems which harbour a comparatively species poor but highly specialised biota, dominated by halobiontic or even 'halophilic' invertebrates (DESENDER & MAELFAIT 1999). While cessation of grazing was believed to be favourable for diversity and the conservation of rare species (BALMER & EHRHARDT 2000), a number of studies have described an impoverished plant community in late successional stages (BAKKER 1985, ESSELINK et al. 2002) and favour an extensive grazing management (KRUESS & TSCHARNTKE 2002a, DENNIS et al. 2001, PÉTILLON et

al. 2007, PÉTILLON & GARbutt 2008a) proposing higher species diversity in plants as well as insects. It is questionable however, whether hypotheses coined on extensive grazing in semi-natural grasslands (GIBSON et al. 1987, DENNIS et al. 1998b, SWENGEL & SWENGEL 1999, KRUESS & TSCHARNTKE 2002a, HENDRICKX et al. 2007) are applicable in salt marshes. Unlike most terrestrial grasslands, their appearance is not only determined by climatic factors but also influenced especially by site conditions such as salt content and inundation frequency (POTT 1996), which leads to an azonal ecosystem. Stages of bushes and trees are missing.

Many invertebrates are susceptible to changes in microclimatic conditions and can thus perceive changes in habitat heterogeneity at finer scales than larger organisms (DENNIS et al. 2001, COLE et al. 2010), but knowledge on the relationships between plant species richness, structural heterogeneity and arthropod diversity is still rudimentary (PÖYRY et al. 2005), and the question on the relevance of a stabilising effect in mature salt marshes remains unresolved (FRITZ et al. 2008).

5.3.1 Effects of grazing on the vegetation of salt marshes

The impact of grazing on plant species richness and vegetation structure in salt marshes has been the topic of numerous studies during recent decades (BAKKER 1985, JENSEN 1985, BAKKER 1987, DIERBEN et al. 1994a, KIEHL 1997, ESSELINK et al. 2000, GETTNER 2002, BAKKER et al. 2003, KIEHL et al. 2003). Most investigations led to the result that a cessation of grazing is beneficial for plant species richness as well as heterogeneity of vegetation structure during the first few years after intensive grazing (JENSEN 1985, KIEHL 1997, GETTNER 2002) but that eventually plant species such as *Elymus athericus* and *Atriplex portulacoides* will gain dominance (JENSEN 1985, ESSELNIK et al. 2000, BAKKER et al. 2003). Although taller vegetation results in a more stable microclimate potentially important to arthropods (DENNIS et al. 1998b, COLE et al. 2010), a decline in plant species richness would most likely lead to a consequent decrease in the associated herbivore species. Most salt marshes of the mainland in Schleswig-Holstein were intensively grazed until the establishment of the Wadden Sea National Park (1985) and remained ungrazed only for the last 20 to 25 years. Successional processes are still proceeding and concluding statements on the direction of development can only be based on assumptions.

However, vegetation mapping of salt marshes of the Hamburger Hallig showed a spreading of *Elymus athericus* in the ungrazed parts of the salt marsh as well as in the extensively grazed parts from 2001 to 2006 (STOCK & PETERSEN 2008). This recent increase of salt marshes occupied by *Elymus athericus* enforce the impression that a succession towards dominance in most parts of the ungrazed salt marshes of Schleswig-Holstein is likely, since the exclusion of grazers was found to promote tall grasses sensitive to frequent defoliation and trampling (MAYER et al. 2009).

Even when excluding plots dominated by *E. athericus* from analysis, corresponding to former studies (LITTLEWOOD 2008, KIEHL et al. 2003) on salt marsh vegetation, a positive effect of extensive grazing on plant species richness combined with a reduction of plant height was found. This led to a significantly different vegetation structure than in either ungrazed or intensively grazed areas. Contrary to former studies (MORRIS 1978), grazing had no effect on plant cover as well as the thickness of the litter layer. Only in the intensively grazed salt marshes was the area of bare soil significantly higher than in the ungrazed salt marsh.

The ordination plot displayed that the extensively and ungrazed plots were characterised by similar plant communities, while those of moderately and intensively grazed patches differed widely in comparison (Fig. 24). This proved the hypothesis that grazing

herbivores alter the structural heterogeneity of vegetation within a particular successional stage more than plant species composition (DENNIS et al. 2001, KIEHL et al. 2003).

Therefore, though not affecting the composition of plant communities considerably compared to ungrazed salt marshes, extensive grazing promoted plant species richness in salt marshes by delaying succession and facilitating a re-establishment of pioneer species in high marshes (ESSELINK et al. 2000).

5.3.2 Influence of grazing on moth assemblages

Apart from the monitoring of plant communities in salt marshes, most studies mainly focused on the distribution of spiders, beetles and flies and the impact of grazing by cattle or sheep (IRMLER & HEYDEMANN 1986, ANDRESEN et al. 1990, REINKE & MEYER 1999, PÉTILLON et al. 2005, PÉTILLON et al. 2008). Moths and especially Microlepidoptera remained largely unnoticed (but see HEYDEMANN 1938, STÜNING 1980, JANSEN 2005) due to a lack of knowledge about their distribution and life history, as well as difficulties with determination in some groups. Nevertheless, specialised moths are adapted to survive in salt marshes, and as vegetation-associated insects they can be expected to be vulnerable to anthropogenic impacts such as grazing (DEBANO 2006, SAMWAYS & LU 2007).

Species richness and abundance

High grazing intensities lead to a homogenisation of vegetation structure and absence of flowers (BERG et al. 1997, GETTNER 2002). As an extreme effect of overgrazing, intensively managed salt marshes were characterised by species poor plant communities (KIEHL 1997, GETTNER 2002), having little attraction for insects (SJÖDIN et al. 2008). Studies researching the effect of continual successional development in fresh grasslands recorded highest species richness and abundance of butterflies and moths in abandoned sites (PÖYRY et al. 2005) and found no significant difference between intensively and extensively grazed grasslands (WETTSTEIN & SCHMID 1999, KRUESS & TSCHARNTKE 2002a). Recent studies, though, identified low grazing pressures to enhance plant species richness as well as structural heterogeneity (DENNIS et al. 2001, LITTLEWOOD 2008). Additionally, the effects of grazing on butterflies and moths varied greatly depending on environmental conditions, intensity and timing of management (EHRHARDT & THOMAS 1991, WALLISDEVRIES & RAEMAKERS 2001, SAARINEN & JANTUNEN 2005). MYSTERUD et al. (2005) suggested that grazing by large herbivores may make plants more vulnerable to insect herbivory and thus benefit herbivore diversity. Specialised herbivorous invertebrates such as moths proved to be highly sensitive to disturbances (STERLING et al. 1992), yielding additional information on structural heterogeneity not obtained by the monitoring of plants alone (LITTLEWOOD 2008), since different parts of a plant are utilised for different developmental stages. Minor changes in plant architecture might affect their development.

Hence, moth communities of extensively grazed salt marshes were expected to be the most species rich, whereas ungrazed areas were thought to harbour less species. Intensively grazed salt marshes could undoubtedly be considered species poor (LITTLEWOOD 2008, COLE et al. 2010).

The present study in mid-term grazed salt marshes of Westerhever and the Hamburger Hallig showed that significantly less species and individuals were found in the moderately and intensively grazed salt marshes, though the results in moderately grazed marshes were less distinct. While species accumulation curves of Westerhever suggested that moderately grazed salt marshes only slightly contribute to overall species richness (Fig. 26), results on the Hamburger Hallig showed that grazing intensities of

four to five sheep per hectare (moderate grazing) can contribute to overall species richness in a habitat network with ungrazed and extensively grazed plots (Fig. 26). These differences were possibly related to difficulties determining the exact grazing intensity of the factual moderately grazed salt marshes of Westerhever. In moderately grazed salt marshes of the Hamburger Hallig more moth species were caught than in intensively grazed marshes and in some years harboured as many species as the ungrazed and extensively grazed marsh (Fig. 29, 30). This supports findings by DOLEK & GEYER (1997) that grazing does not have to be as detrimental on the diversity of Lepidoptera as formerly thought, depending on pasture size, management intensity and the surrounding habitats. Though plant species richness differed significantly between extensively grazed and ungrazed salt marsh plots, species richness of moths did not. However, a trend (though not significant) towards overall higher species richness in the extensively grazed salt marsh was discernible for light trap data (Fig. 29). While this trend in species richness was not observed in the photoeclector samples on the Hamburger Hallig (Fig. 30), more individuals (though not significant) were caught in the extensively grazed salt marsh (Fig. 33). Therefore, a beneficial influence of extensive grazing was identifiable in both data sets, which corresponds with the hypothesis that low grazing intensities facilitate a high herbivore richness by enhancing plant species richness and vegetation heterogeneity (SAARINEN & JANTUNEN 2005, LITTLEWOOD 2008).

In context with the results of the now determined moths of the short-term grazing experiment in Friedrichskoog and the Sönke-Nissen-Koog (DIERBEN et al. 1994, a, b), this trend gains relevance.

Significantly higher species richness was only found in ungrazed or low grazing intensities compared to intensively grazed sites in the higher salt marshes of Friedrichskoog. In the Sönke-Nissen-Koog ungrazed, low and moderately grazed salt marshes were the species richest. Nevertheless, during the first years (1990 to 1993) after the establishment of the grazing experiment, more species and individuals were only recorded in the ungrazed salt marshes, whereas the sites with moderate, extensive or low intensities did not differ from each other. The moderately grazed sites in the *Puccinellia*-dominated marshes stand out with a higher species richness and abundance than in the extensively grazed plots. Whether this result was a response of moth communities to grazing or had to be attributed to exceptional site conditions as a sampling artefact could not be clarified. Often, exceptionally high species numbers are influenced by neighbouring, species-rich source habitats (DENNIS et al. 1998a). In this case however, a positive influence of neighbouring source populations seems unlikely. At the time of research, salt marshes in the vicinity of the grazing experiment were still intensively grazed. Although an airborne dispersion of moths from the low and ungrazed sites of the experiment seems possible, only those specimens developing in the sampled area are caught with photoeclector traps (FRANK et al. 2009). Recent research in salt marshes under intermediate grazing duration (Westerhever and Hamburger Hallig) as well as results from the Friedrichskoog area suggests that the higher species numbers in moderately grazed salt marshes were possibly influenced rather by exceptional site conditions than being a response to grazing intensity.

Total species richness as well as results of the GEE imply a positive effect of extensive grazing on moth communities, whereas higher grazing intensities can be expected to be detrimental. Additionally, differing grazing intensities seemed to contribute to overall species richness of the habitat, providing important microhabitats and vegetation structures to facilitate the occurrence of species not found elsewhere (DENNIS 2004). Findings of studies in grazed pastures, where a mosaic of different grazing intensities supported

highest species richness (WALLISDEVRIES & RAEMAKERS 2001, SAARINEN & JANTUNEN 2005), could thus be confirmed. The depletion in species richness in the intensively grazed salt marshes corresponded with former results (PÖYRY et al. 2005, PÖYRY et al. 2006). Studies during recent decades have reported a drastic decline in plant species richness with intensive grazing in grasslands leading to impoverished herbivorous insect communities as well (DOLEK & GEYER 1997, KRUESS & TSCHARNTKE 2002a, SJÖDIN 2007, BAKKER et al. 2008a, SJÖDIN et al. 2008).

Dominance structure of moth communities in salt marshes

According to THIENEMANN (1920, 1956), pioneer communities harbour few species in high abundances, whereas matured habitats are often characterised by: a high species richness which increases with age; being undisturbed; and the presence of source habitats in close vicinity. Therefore, in extreme habitats such as salt marshes, comparably few species with high abundances were expected. Differences in species richness and abundance due to disturbances often result in changes of species composition, which are reflected by variances in dominance patterns of communities in a habitat (NEW 1997). In undisturbed habitats one expects to find a diverse species community, whereas communities of disturbed habitats are expected to be more uniform, comprised of a few highly dominant species, but at least in early stages lacking the less abundant ones (MAGURRAN 2004).

Dominance levels of microlepidopteran communities in ungrazed and grazed salt marshes of Westerhever and the Hamburger Hallig showed a clearly visible change in dominance patterns of species assemblages (Fig. 34, 35, 36). In ungrazed salt marshes, halobiontic moths (*Bucculatrix maritima*, *Eucosma catoptrana* and *Eucosma tripoliana*), feeding on the grazing sensitive plant *Aster tripolium*, reached high dominance values, whereas their values decreased in the extensively and moderately grazed plots. Species linked to grazing sensitive plants were almost completely missing in the intensively grazed area. Contrarily, species feeding on grasses as larval host plants and developing in the roots exhibited higher dominance values in grazed salt marshes. The grass-feeding *Pediasia aridella*, *Crambus perlella* and *Chrysoteuchia culmella* dominated the moderately and intensively grazed plots. *Eucosma lacteana*, whose larvae feed on the herbaceous *Artemisia maritima*, reached highest dominance values only in the moderately grazed salt marsh. *Artemisia maritima*, which is considered unpalatable for livestock due to its high essential oil content (JENSEN 1985), was more abundant in moderately grazed parts but is sensitive to trampling and did hardly occur in intensively grazed marshes. The most common species, *Scrobipalpa instabilella*, feeding on *Atriplex portulacoides*, reached high levels of dominance in all salt marsh plots.

In summary, a distinct change in dominance patterns for moth communities from herbaceous- to grass-feeding species from the ungrazed to the intensively grazed salt marsh was recognisable in the mid-term grazing experiments, with an impoverished species assemblage in the heavily grazed plots.

Similar patterns were found in the moth assemblages of the short-term grazing experiment in Friedrichskoog and especially the Sönke-Nissen-Koog, but less pronounced. In ungrazed sites the moth assemblages consisted of more species with lower dominance values than the assemblages in the grazed salt marshes. With increasing grazing intensity, one species (*Pediasia aridella*) gained eudominant status and the moth community was poorer in species. Additionally, with increasing grazing intensity a shift in dominant species from the *Aster*-feeding *Bucculatrix maritima* to the grass-feeding *Pediasia aridella* was apparent in the lower salt marshes of the Sönke-Nissen-Koog. Therefore,

grazing resulted in a reduced diversity in high-intensity grazing sites, with generalists dominating (NICKEL & HILDEBRANDT 2003).

The response of moth assemblages to grazing was probably less distinct in the short-term grazing experiment, since both plant and moth assemblages need time to adapt to habitat changes (STERLING et al. 1992). Especially the cessation of grazing implied major successional development in those sites, and colonisation by moths occurred only slowly and was dependent on available source habitats (DENNIS et al. 2001).

The results of both the mid-term and short-term grazing experiments suggest a pronounced impact of grazing on the distribution of moths in salt marshes, leading to impoverished species assemblages in highly grazed sites. Monophagous species specialised on herbaceous plants were replaced by generalist species feeding on grasses with increasing grazing intensity. STERLING et al. (1992) & POHLUS et al. (2007) described this replacement as a general effect of habitat degradation and disturbance to natural communities in grasslands.

5.3.3 Comparative studies on the effect of grazing on invertebrates- re-evaluation of the Ecosystem Research Wadden Sea Project

Only few studies examined the effects of management intensity on several invertebrate groups simultaneously (ANDRESEN et al. 1990, DIERBEN et al. 1994b, KRUESS & TSCHARNTKE 2002a, SJÖDIN et al. 2008). In this study by application of the same statistical analysis to all data sets, results of the Ecosystem Research Wadden Sea Project on the response of beetles, spiders and flies to different grazing intensities (DIERBEN et al. 1994b, REINKE & MEYER 1999) were compared with the results of moths trapped during the same study, but determined 20 years later (see also chapter 6.3.2). Thus, the opportunity to recognise patterns in the response of different invertebrate groups to grazing was provided.

Effect of short-term grazing management on species richness and abundance of invertebrates

The importance of invertebrates for pollination, decomposition and food web structure in grassland ecosystems has been stated frequently, but only few studies dealt with the effect of livestock grazing on these assemblages (DEBANO 2006). Grazing can dramatically simplify vegetation diversity by reducing plant species richness and heterogeneity in plant architecture. Since plant diversity is considered a major determinant of diversity on higher trophic levels (GIBSON et al. 1987, STERLING et al. 1992), diversity of phytophagous insects is likely to decline with simplification of vegetation (KRUESS & TSCHARNTKE 2002a, LAWTON 1995, WETTSTEIN & SCHMID 1999). However, spider, beetle and fly assemblages showed no obvious response to grazing with respect to species richness and abundances. Species accumulation curves estimated an equally high expected number of species in each grazing management. However, no grazing intensity alone harboured all occurring species of the experimental sites (Friedrichskoog or Sönke-Nissen-Koog) and the total number of species of all grazing intensities combined was almost twice as high in each group. This suggests a species turn-over from the ungrazed to the intensively grazed marsh. Results could not support findings of DENNIS et al. (2001) that spider abundance was greater in ungrazed and taller, grazed swards. Possibly, a differentiation between airborne, web-building and predatory spiders would show more distinct responses (PÉTILLON et al. 2007). HOFMANN & MASON (2006) detected similar reactions for staphyliniid assemblages, which reacted quickly to the cessation of intensive grazing with a shift in dominance structure indicative of a less stressed environment. Species richness and abundance of staphyliniids in salt marshes was largely unre-

lated to management category. Soil temperature and vegetation height followed by soil compaction were recognised as the most important factors for their distribution. However, management categories could be clearly separated nevertheless (HOFMANN & MASON 2006). PÉTILLON & GARBUTT (2008a) and PÉTILLON et al. (2008) stated accordingly, that habitat structure was the major determinant of spider and beetle species richness. Habitat age and also management alone were of less importance.

In contrast, moths showed a very pronounced response to grazing with the most species and individuals found in the ungrazed salt marsh, intermediate numbers in the low intensity to moderately grazed plots and the lowest species richness in the intensively grazed sites (Fig. 39, 40). Corresponding to the results of photoeclector samples of the Hamburger Hallig in 2007-2009, none of the grazing intensities alone contained all of the species developing in the salt marshes of the Sönke-Nissen-Koog or Friedrichskoog, reinforcing the conclusion that no grazing management on its own can support overall species richness.

The statistical analysis (GEE) of species richness and abundance of moths as well as spiders, beetles and flies supported the impression of a more differentiated response to grazing for moth assemblages compared to any other group. In general, response to grazing in all groups was stronger in the lower salt marshes of the Sönke-Nissen-Koog than in the higher marsh of Friedrichskoog and increased with ongoing time after change of grazing management. Whereas a significant difference in species richness and abundance of moths between the grazing treatments was found, for none of the other investigated groups was a significant effect on species richness or abundance observed. This coincides with results of other studies, which found no significant response in species richness or abundance of beetles and spiders (HOFMANN & MASON 2006, PÉTILLON & GARBUTT 2008a). Instead, spider and beetle assemblages rather responded with a shift in species composition from species typical for open habitats in intensively grazed to e.g. web-building spiders in ungrazed sites (HOFMANN & MASON 2006, PÉTILLON & GARBUTT 2008a).

Studies in sites that were grazed during summer months only reported similar responses to grazing in wolf spiders, beetles, sawflies and lepidopteran larvae (COLE et al. 2010), suggesting a general pattern of invertebrate responses to grazing. In this case, one group could act as surrogate for another, rendering elaborate invertebrate monitoring unnecessary. However, in this study correlation between spiders, beetles, flies and moths were weak. Therefore, results by OLIVER & BEATTIE (1996) are confirmed which showed that no invertebrate group can serve as a surrogate for another concerning the response to grazing management.

Dominance patterns in invertebrate assemblages in salt marshes

In comparison with moth assemblages (chapter 6.3.2), spider, beetle and fly assemblages showed a less distinct reaction to grazing and no clear change in dominance pattern was recognisable. A shift in dominance from *Pardosa purbeckensis* to *Pirata piraticus* from grazed to ungrazed salt marshes found in earlier studies (HEYDEMANN 1961) was not apparent. Overall, in both locations spider assemblages in slightly grazed plots showed a more heterogeneous dominance pattern compared to the ungrazed and intensively grazed salt marshes. In the higher salt marshes of Friedrichskoog, *Erigone longipalpis* was the overall dominant species accompanied by *Oedothorax fuscus* in the low intensity and extensively grazed plots. *Erigone longipalpis* and *Oedothorax fuscus* are species from early successional stages in salt marshes (PÉTILLON & GARBUTT 2008a), suggesting that the disturbing impact of former intensive grazing was still considerable and the short-term

succession in the ungrazed sites did not have a strong influence on the spider assemblage. In the lower salt marshes of the Sönke-Nissen-Koog, the ungrazed and slightly grazed plots were dominated by *Baryphyma duffeyi* whereas *E. longipalpis* gained dominance in the intensively grazed sites only. Seemingly, in the lower salt marshes cessation of grazing led to a faster successional development than in the high marsh. In ungrazed and slightly grazed plots of the lower marshes, *Aster tripolium* was abundant and provided a microclimate similar to late successional stages (DIERSEN et al. 1994a), favouring *B. duffeyi*. Apart from *B. duffeyi*, dominant spider species in both salt marshes were eurytopic species not bound to salt marshes. Especially eurytopic spider species such as *O. fuscus* and *E. longipalpis* can withstand environmental changes well and are highly adaptable. Similar findings were reported by ZULKA et al. (1997), although his results, where spider assemblages of grazed sites in salt marshes were dominated by *Pardosa agrestis*, could not be supported. The dominance of these species implies that spider communities reacted slowly to changes and were more influenced by vegetation structure than plant species richness (MORRIS 1978, GRILL et al. 2005). Species richness of spiders seemed to be favoured by grazing due to the creation of a patchy and heterogeneous vegetation structure offering niches suitable for different trophic guilds. However, results presented in this thesis are based on photoeclector samples only. Alternative trapping methods such as suction-sampling or pitfall trapping would possibly yield different results. IRMLER & HEYDEMANN (1987) showed that *E. longipalpis* was more active in grazed salt marshes and thus more likely to be caught with pitfall traps, whereas it was occurring in higher abundances in the ungrazed salt marshes. It is likely that *E. longipalpis* in ungrazed salt marshes remains inactive in its web, but is forced to hunt in grazed salt marshes, which increases the likelihood of being trapped. Accordingly, a negative influence of grazing on large, web-building spiders and on diurnal predators associated with dense litter layers was reported by HORVÁTH et al. (2009). Furthermore, overgrazing was found to have a negative effect on species richness of spiders, mainly because of trampling effects due to a destruction of a sheltering litter layer and spider webs (BELL et al. 2001, PÉTILLON et al. 2007). Higher vegetation was found to provide suitable support for web-building spiders and refuges to hide from flooding for non-adapted spiders (PÉTILLON et al. 2005). The hypothesis that intermediate rates of grazing enhance the structural diversity of grasslands and maintain a higher diversity of arachnids was also refuted by DENNIS et al. 2001, since suction sampling detected greater diversity of arachnids in ungrazed grasslands, which was related to increased plant litter below the leaf stratum.

Coleopteran assemblages of the high marshes of Friedrichskoog were dominated by *Dicheiostichus gustavii*, a carnivorous ground beetle, though dominance values were lower in the low and moderately grazed sites. Similar to spider communities, coleopteran assemblages did not show a highly differentiated dominance pattern with increasing grazing intensity and a decline in species richness could not be recognised. These results are supported by studies in fresh grasslands, where no effects of grazing management on beetle abundance, species richness or evenness were found (WOODCOCK et al. 2005). *Dicheiostichus gustavii*, *Dyschirius calceus* and *Bembidion minimum* were the three most dominant species in all grazing intensities of the lower salt marshes in the Sönke-Nissen-Koog, with only slightly changing dominance values. No change of dominant species in response to grazing was apparent. This relates to results of IRMLER (2003) who found that a reduction in land use intensity had almost no effect on the species composition and that soil type was the major environmental factor determining ground beetle distribution. Results could not sustain propositions by MEIJER (1980), that carabid

beetles reflect the changes in the habitat more clearly, but rather supported the statement of SJÖDIN et al. (2008) that it is probably difficult to find universal responses to grazing for beetles.

Dipteran assemblages of the Friedrichskoog were dominated by *Lestodiplosis* sp. and *Micaria alba* in all grazing intensities and no distinct response to grazing could be recognised. Grazing in the lower salt marshes of the Sönke-Nissen-Koog, however, induced a different response. *Micaria alba*, *M. puccinelliae* and *Lestodiplosis* sp. reached high dominance values in all grazing intensities, while *Rhopalomyia florum* and *Campiglossa plantaginis* only reached considerable values in the ungrazed sites. *Nemotelus notatus* was only dominant in the intensively grazed marsh (see MEYER & REINKE 1996). Here, a change in dominant species was observable, although fly assemblages of the different grazing managements were similar in species richness. However, since species distributions of flies are known to be highly determined by soil properties (MEYER et al. 1997), an evaluation with respect to grazing seems difficult.

5.3.4 General conclusions on the response of invertebrates to grazing

Through comprehensive, replicated studies on the response of moth communities in short-term and mid-term grazing experiments, an appraisal of conclusions drawn from previous studies could be made.

Although the studies of the Ecosystem Research Wadden Sea Project reflected only short-term changes in vegetation and invertebrate communities after cessation or extensification of grazing, moth assemblages in intermediately long (20 – 25 years) ungrazed and extensively grazed salt marshes of the Hamburger Hallig and Westerhever showed similar responses. The combined analysis of results suggests a general pattern in the reaction of moth communities with high species richness and abundances in ungrazed and extensively grazed salt marshes, whereas communities of intensively grazed sites were depleted and dominated by generalist species feeding on grasses. Results suggest that the trend towards higher species richness and abundance of moths in extensively grazed salt marshes would most likely gain significance in long-term (> 50 years) grazing experiments, consistent with studies on insect communities in calcareous and fresh grasslands (DOLEK & GEYER 1997, WETTSTEIN & SCHMID 1999, WALLISDEVRIES & RAEMAKERS 2001, PÖYRY et al. 2005). Absence of grazing, however, has been recognised as possibly detrimental to abundance and diversity of invertebrates (DEBANO 2006, LITTLEWOOD 2008). As a negative effect of abandonment and high sedimentation rates, invertebrate communities characteristic for salt marshes may eventually disappear and be replaced by common species from adjacent grasslands (ANDRESEN et al. 1990). Management practices such as sheep grazing, however, lead to early successional stages, which are known to benefit some halobiontic species (ZULKA et al. 1997, PÉTILLON & GARBUTT 2008a).

Since management effects on the faunistic and floristic composition of grasslands become only measurable after decades (KAHMEN 2003) and successional changes are proceeding endlessly, further changes in moth assemblages have to be expected. Therefore, results of the short-term grazing experiment of the Ecosystem Research Wadden Sea Project and even of the mid-term grazing duration on the Hamburger Hallig can not be considered conclusive for long-term grazing management. Rather, these results should be considered as a trend, suggesting higher species richness and abundance of moths in extensively grazed salt marshes with progressing successional development, and reinforce the hypothesis of beneficial effects of extensive grazing.

A comparison of the response of spider, beetle, fly and moth assemblages to grazing management in the two sampling locations of the Ecosystem Research Wadden Sea Pro-

ject (DIERËEN et al. 1994) leads to the conclusion that moth assemblages react more sensitively to grazing regarding species richness and abundance. Additionally, a distinct shift in the dominance structure of moth communities from herbaceous-feeding halobiontic species towards grass-feeding generalists was detected, which could not be derived with similar assuredness from the data on other groups. Moths are vegetation-associated and were found to react sensitively to livestock grazing (DEBANO 2006), whereas vegetation structure and not plant species composition determined arachnid species composition and abundance (DENNIS et al. 2001, PÉTILLON & GARBUTT 2008a). No general pattern in invertebrate responses to grazing management, as suggested by KORICHEVA et al. (2000), could be found. Although an increase in species richness is detectable in most undisturbed naturally developed terrestrial ecosystems with increasing maturity and source habitat availability (e.g. old beech forests) (MARTIKAINEN et al. 2000, MÜLLER 2008, IRMLER et al. 2010, SATTLER 2010), no evidence for an increasing insect diversity following abandonment of grazing as proposed by KRUESS & TSCHARNTKE (2002) and HENDRICKX et al. (2007) could be proven. In azonal habitats such as salt marshes, ageing might not be wholly beneficial, possibly due to dominance of single or a few plant species such as *Elymus athericus* and *Atriplex portulacoides*.

Overall, results suggest that a mosaic of extensively, moderately and ungrazed sites may facilitate the highest number of insect species and create a mosaic of marshes in different successional stages (KRUESS & TSCHARNTKE 2002a, DENNIS et al. 2001, ESSELINK et al. 2002, PÉTILLON & GARBUTT 2008a). This is in agreement with results from fresh and calcareous grasslands, where rotational grazing with at times moderately grazed pastures was recognised as the best option for butterfly richness (WALLISDEVRIES et al. 1999). SAARINEN & JANTUNEN (2005) and BENTON et al. (2003) postulated that different management intensities are needed regionally for the maintenance of grassland insect diversity and most closely resemble former natural conditions, where small grazers such as geese and hare created a patchy vegetation structure (STAHL et al. 2006) and older ungrazed salt marshes served as source biotopes. It seems important to adopt a flexible approach in salt marsh management for biodiversity, because practices relying on plant diversity only may not produce a corresponding benefit for arthropod and structural diversity.

5.4 Species composition and ecological indication

Communities are affected by disturbances not only by influencing species richness and overall abundances, but also by inducing changes in species composition. Whereas a loss of species is easily detectable when looking at species richness, shifts in community composition need further analysis and specialist knowledge to evaluate the consequences of grazing in a habitat. Since vegetation has repeatedly shown to be a poor surrogate for patterns of invertebrate diversity (CRISP et al. 1998, PANZER & SCHWARTZ 1998, EYRE & LUFF 2002, ANDERSEN et al. 2004) and research on community composition is time costly, the concept of ecological indication seems appealing (DUELLI & OBRIST 1998, CARROLL & PEARSON 1998).

DUFRENE & LEGENDRE (1997) developed the first analytical tool to predict the quality and suitability of a species as an indicator. The Indicator Analysis assigns an Indicator Value to each species of a community, integrating its frequency and abundance in a habitat (see chapter 3.2.2). In the following years, MCGEOCH (1998) and SAARINEN & JANTUNEN (2005) promoted the application of the species indicator analysis to validate the suitability of proposed indicators. A verification of their tolerance to disturbances by

testing the proposed indicators in different locations or time series is essential (LANGOR & SPENCE 2006).

A number of beetle, spider, fly and bug species were proposed as ecological indicators for the impact of grazing in salt marshes, derived from abundance data and occurrences (ANDRESEN et al. 1990, MEYER et al. 1997). However, they were never validated by an indicator analysis nor verified in other salt marshes. But indicator studies, particularly those involving invertebrates frequently fail to provide objectively determined indicator species or species subsets (MCGEOCH & CHOWN 1998a).

Within this thesis, possible indicator species of moths were validated, which appeared to be suitable according to their abundances and occurrences, using the indicator species analysis. Results were verified by application to different data sets from two different time periods (1989-1993 and 2006- 2009), four different localities (Westerhever, Hamburger Hallig, Friedrichskoog and Sönke-Nissen-Koog) and two different methods of collection (light traps and photoeclector traps). Additionally, the Indicator Species Analysis (ROBERTS 2010) was performed on the spider, beetle and fly data sets of photoeclector samples of the Ecosystem Research Wadden Sea Project (DIERBEN et al. 1994, b) to evaluate the suitability as indicators, though for those groups no additional data could be gathered within this study to verify the results.

5.4.1 Moths as ecological indicators for the impact of grazing in the salt marshes of Westerhever and the Hamburger Hallig

Recently, moth communities received an increasing conservation interest as a species rich, taxonomically tractable group, sensitive to environmental changes and disturbance (LUFF & WOIWOOD 1995, OOSTERMEIJER & VAN SWAAY 1998). According to Groenendijk et al. (2004), NEW (2004) and SCALERCIO et al. (2009) they are important indicator taxa, despite being a highly mobile group (ZSCHOKKE et al. 2000). Lepidopteran species are often host-specific and the species richness of butterflies or moths was found to be correlated with plant species richness (PEARMAN & WEBER 2007). They may not only indicate plant species richness, but also that of other phytophagous insects (RICKETTS et al. 2002) and many other terrestrial insect groups (THOMAS 2005).

Microlepidopteran assemblages SHOWED a clear response to grazing in species richness as well as abundances. They reacted with a distinct change from herbaceous-feeding to grass-feeding species with increasing grazing pressure (chapter 6.3.2). Therefore, they might be suitable ecological indicators for the impact of grazing in salt marsh communities.

According to the Indicator Species Analysis (ROBERTS 2010) of the data collected in Westerhever, four species (*Agdistis bennettii*, *Coleophora salicorniae*, *Eucosma tripoliana* and *E. catoptrana*) can be regarded as indicators for ungrazed salt marshes, whereas mainly grass-feeding species (*Agriphila straminella*, *Chrysoteuchia culmella*, *Crambus perlella* and *Pediasia aridella*) as well as *Scrobipalpa instabilella*, feeding on *Atriplex portulacoides*, were suitable indicators for intensively grazed salt marshes. The indicator potential of *S. instabilella* seems contradictory, since *Atriplex portulacoides* is known to react sensitively to trampling and to benefit from a cessation of grazing (KIEHL 1997, KIEHL et al. 2002). However, *Scrobipalpa instabilella* occurred in all plots abundantly. Its significant indicator value in intensively grazed plots should be considered in the context of only few other species co-occurring abundantly, whereas in the ungrazed and extensively grazed sites in comparison to other species *S. instabilella* was less abundant. In the moderately grazed sites, *Eucosma lacteana* feeding on *Artemisia maritima* and *Scrobipalpa salinella*, feeding on *Suaeda maritima* reached highest values.

The indicative values of these species were validated using datasets from the Hamburger Hallig. This comparison showed that not all selected moth species were suitable indicators and differences between light trap and photoeclector samples existed. In the ungrazed salt marsh, only *E. catoptrana* and *C. salicorniae* seemed to be generally suitable. *A. bennetii* (ungrazed), *Phalonia vectisana* (extensively grazed) and *S. instabilella* (intensively grazed) were only suitable using light trap samples. In the intensively grazed marsh no species qualified as an indicator. Regarding ungrazed and extensively grazed sites, *E. tripoliana* showed an affinity to extensive grazing, whereas *E. lacteana* indicated either moderately or extensively grazed sites.

Species that occur at multiple sites are more likely to be appropriate indicators than those present at single sites (BAKKER et al. 2008a). An evaluation of the results of Westerhever and the Hamburger Hallig combined revealed that an allocation of indicator suitability had to be implemented very cautiously. It was important to acknowledge the proposed indicator's life history, particularly host plant specificity and distribution, because changes in their population needed to be clearly related to the impact of grazing (PEARSON 1994, CARO & O'DOHERTY 1999). Mainly specialised species occurring in moderately abundant numbers and with a steady frequency are assumed to be reliable ecological indicators detectable in a brief survey (SAHLÉN & EKKESTUBE 2001), whereas eurytopic and highly abundant species as well as rare species are considered inappropriate (MCGEOCH 1998).

Although *A. bennetii* is specialised on the grazing sensitive *L. vulgare* and seemingly indicated ungrazed salt marshes, it was unsuitable as an indicator species, since its occurrence was highly variable between the years and seemed highly influenced by climatic conditions such as harsh winters and inundation rates (see chapter 6.2). An absence of *A. bennetii* therefore could not necessarily be attributed to overgrazing of salt marshes. The host plant for *P. vectisana* is the non-palatable *Triglochin maritimum*, which contains hydrogen cyanide (LODGET 1963). *T. maritima* is promoted by a heterogeneous vegetation structure due to a competition for light, but is sensitive to trampling and thus less frequently distributed in higher grazing intensities (JENSEN 1985, BOS et al. 2002, WAL et al. 2000). In spite of these promising characteristics, *P. vectisana* did not qualify as an indicator, since it is considered rare in most mainland salt marshes (M. Jansen, pers. communication). *Eucosma catoptrana*, *E. tripoliana*, *E. lacteana*, *Phalonia affinitana* and *C. salicorniae*, by contrast, occurred in high abundances if habitat features were suitable. Also, because of their distinct life history, these species appear suitable as ecological indicators.

Eurytopic grass-feeding species, on the other hand, yield little additional information on the quality of the habitat except a high percentage cover of grasses, which can be measured more easily. Nevertheless, mostly common, not specialised species (negative indicators) colonise habitats only after their degradation (CLAUSNITZER 2003). Thus, even though common species seemed unsuitable as indicators, the abundant occurrence of grass-feeding species and the absence of specialist species suggested a highly disturbed habitat, as already discussed in chapter 6.3.2.

Consequently, only *E. catoptrana* and *C. salicorniae* qualified as suitable ecological indicators for ungrazed salt marshes, *E. tripoliana* and *P. affinitana* for extensively grazed sites and *E. lacteana* indicated moderately grazed salt marshes. Co-occurrence of these species indicated a sustainably managed salt marsh with a high structural heterogeneity, where highly palatable plants such as *Aster tripolium*, pioneer species (*Salicornia europaea*) and species of the high marsh (*Artemisia maritima*) coincide.

However, these results were only based on data obtained during a comparably short time period from 2006 to 2009 in salt marshes under a mid-term (20-25 years) grazing management. After initial bioindicator identification, to derive a general applicable pattern, the validity of these indicator species needed to be tested for a different time period in similar habitats (DA MATA et al. 2008). This could be obtained by application of the Indicator Species Analysis (ROBERTS 2010) to the data sets on moths from the Ecosystem Research Wadden Sea Project from 1990-1993 (DIERBEN et al 1994).

Moths showed an obvious linkage to different grazing regimes, though in the higher salt marshes of Friedrichskoog only *Pediasia aridella* qualified as an indicator species for intermediate grazing intensities. In the lower salt marshes of the Sönke-Nissen-Koog, the response was more differentiated with two *Aster*-feeding species (*Phalonidia affinitana* and *Eucosma tripoliana*) indicating ungrazed salt marshes and *Bucculatrix maritima* and *Coleophora deviella* linked to low grazing intensities. Both *E. tripoliana* and *P. affinitana* were already mentioned as potential indicator species in the analysis of the mid-term grazed salt marshes in Westerhever and the Hamburger Hallig, where they qualified as indicators for extensively grazed salt marshes. This discrepancy is most likely explained by the short time period after cessation of grazing, during which vegetation rapidly changed with pioneer and herbaceous plant species peaking in their occurrences in the ungrazed salt marsh, whereas over time ungrazed salt marshes become more homogeneous in vegetation structure (JENSEN 1985).

Therefore, the Indicator Species Analysis (ROBERTS 2010) performed on the short-term grazing data of moths yielded comparable results to the mid-term grazing experiment on the Hamburger Hallig. This suggests that Microlepidoptera respond in a repeatable pattern to grazing in salt marshes and are suitable indicators for salt marsh monitoring, providing valuable additional information on habitat quality.

5.4.2 Species composition of invertebrates and ecological indication – The Ecosystem Research Wadden Sea Project

Similar to the results of species richness and abundance of invertebrates, the impact of grazing was more apparent in the lower salt marshes of the Sönke-Nissen-Koog than in the higher salt marshes of Friedrichskoog and the analysis of species composition (ADONIS) yielded more distinct results. This is most likely explained by faster changes in vegetation after cessation of grazing in the lower than in the higher marshes (DIERBEN et al. 1994a). In general, significant differences in species composition of moths were found in the later years of the grazing experiment, whereas differences in spider communities already existed at the beginning of the experiment. Beetle communities reacted more distinctly to grazing in the higher salt marshes than in the lower sites. This reaction can be explained by the low species richness in low salt marshes (Sönke-Nissen-Koog) due to high inundation rates in contrast to the species-rich higher salt marsh (Friedrichskoog). Thus, richness of beetle species in the low marsh is too low to detect differences between grazing intensities. Diptera showed the least distinct response in species composition to grazing and thus can be expected to have the lowest applicability as ecological indicators.

PÉTILLON et al. (2005) suggested a high potential for the bioindicator value of spiders in salt marshes, because higher vegetation in ungrazed salt marshes would provide suitable habitats for web-building spiders, refuges to hide from flooding for non-adapted, eurytopic spiders and more litter, which would provide hunting, resting and oviposition sites.

Most spider species, however, showed no clear tendency towards any grazing intensity and received low indicator values in all management schemes. All species with indicative value were eurytopic species living in different habitats (HÄNGGI et al. 1995). Their more frequent occurrence in higher (*Oedothorax apicatus* and *Leptyphantes ericaceus*) or intermediate grazing intensities (*Clubiona stagnatilis* and *Pachygnatha degeeri*) can be attributed to disturbance. According to the hypothesis of MEYER et al. (1997) eurytopic species should occur more in disturbed habitats. Only *Porrhomma microphthalamum* indicated low grazing intensities. Their applicability as indicators for salt marsh management is questionable, since eurytopic species give little information on the habitat, because they are able to cope with a high variety of conditions (ZULKA et al. 1997). No spider species could be identified to indicate undisturbed or ungrazed habitats. This result possibly accounts for the fact that changes in management had only occurred recently and changes in vegetation composition and structure continued. Recent studies suggest an indicative value of *Hypomma bituberculatum* and *Enoplognatha mordax* in extensively grazed salt marshes, whereas *Clubiona* sp. and *Pirata piraticus* seem to show a tendency towards undisturbed habitats (unpublished, pers. communication R. v. Klink). These suggestions relate to the hypothesis of PÉTILLON et al. (2005) that different functional groups can be used as indicator groups for assessing the change between natural and disturbed areas. However, these proposals still need verification prior to application in salt marsh management. During the analysis of the data from the short-term grazing experiment (DIERBEN et al. 1994b), the mentioned species either had no significant indicator value or were excluded due to rarity and therefore did not qualify as ecological indicators.

Although species diversity of Carabidae was expected to increase with decreasing level of disturbance (VILLA-CASTILLO & WAGNER 2002) and beetles were recognised as valuable indicators for sites with high conservation interest (JANSSON et al. 2009), beetle assemblages gave an equally blurry picture as spiders regarding indicator values. Only *Dyschirius salinus*, which can be considered halobiontic, reached meaningful indicator values for intensively grazed plots in the high salt marsh. All other halobiontic species had low indicative values and their distribution in salt marshes seemed to be influenced by other factors than grazing. This coincides with findings of IRMLER (2003), that soil type is the major environmental factor determining ground beetle distribution. Some species exhibited high values in both the ungrazed and intensively grazed salt marshes, but did not occur or occurred less frequently in the intermediate grazing treatments (e.g. the leaf beetle *Longitarsus plantagomaritimus* and *Dicheirostichus gustavii*). Other species which gave high values were eurytopic species, not bound to salt marshes and therefore give little information on habitat quality. These results corresponded to other studies, where beetles were not significantly linked to land use (RYKKEN et al. 1997) or overall species richness (DUELLI & OBRIST 1998) and carabid beetles, especially generalist species, were not useful as an indicator group for different land management types (RYKKEN et al. 1997).

SOMMAGIO (1999) stated that Diptera, especially Syrphidae, possess three features that make them potentially good indicators: highly differentiated larvae, commonality and an easy identification due to a high documentation level. She found that Syrphidae were negatively affected by reduction in landscape diversity. But during this study, Diptera showed the least significant response to grazing and the tendency to intermediate grazing intensities was most likely influenced rather by a high soil compaction known to be beneficial for most dipteran species (MEYER et al. 1997) than by differences in plant species richness or vegetation structure. Most fly species were linked to intermediately

grazed salt marshes, though only *Rhaphium riparium* and *Dolichopus clavipes* received meaningful indicator values, while most species had very low and similar values in all grazing types. Only *Campiglossa plantaginis*, a halobiontic species, indicated ungrazed lower salt marshes though it did not occur in the upper salt marshes of Friedrichskoog, possibly due to a lack of its food plant *Aster tripolium* or colonisation limitations.

These results on the suitability of invertebrates in salt marsh monitoring, however, were only derived from data obtained by photoeclector traps. MEYER & REINKE (1996) found that photoeclector samples yielded the highest species richness, and abundances of species as well as dominance patterns were comparable to those caught with pitfall traps. Nevertheless, data obtained with different trapping methods (e.g. suction sampling, pitfall traps) might yield deviating results. Further validation of these results is therefore essential.

5.4.3 Conclusions on ecological indication

Ecological indicators are species or groups of species, which are able to act as a surrogate, if the identification of environmental gradients would be difficult or impossible (LANDRES et al, 1988). In this study however, potential indicator species were tested against known grazing gradients, to assess their utility as indicators rather than to identify environmental gradients (grazing intensity), which could have been recognised more easily (KREMEN 1994). Additionally, disturbances such as grazing often influence habitats in a variety of erratic and indiscernible ways, which can be detected by sensitive indicators but not distinguished purely by stocking rates (MORRIS 1978, FISHER 1998, MORRIS 2000). Furthermore, the hemerobic level always has to be considered in the evaluation of a habitat, since undisturbed habitats of a similar appearance are preferential to managed sites, since commonly harbouring a species-richer biocoenosis (KLOTZ & KÜHN 2002).

Drawing conclusions from short-term grazing experiments inevitably leads to great uncertainties since early years of succession are known to be the most variable regarding vegetation changes (GETTNER 2002, BAKKER et al. 1997). For a general applicability, these conclusions and recognised patterns need verification both in different localities as well as mid- and long-term grazing treatments.

Conclusions on the suitability of indicator species of spiders, beetles and flies in salt marshes, derived from the data on short-term grazing experiment and based on abundances (MEYER et al. 1997), were validated using the indicator species analysis. Spider, beetle and fly communities revealed only few grazing sensitive species providing limited information on the quality of salt marsh habitats. Only *Campiglossa plantaginis* indicated short-term ungrazed lower salt marshes, while one halobiontic beetle species (*Dyschirius salinus*) was linked to intensively grazed sites and eurytopic indicator species to intermediate grazing intensities. Spiders were regarded to be the most promising group for ecological indication (PÉTILLON et al. 2005a), but results of the short-term grazing experiment were weak. *Porrhomma microphthalamum* and *Porrhomma montanum* were the only eurytopic spider species linked to low grazing intensities, whereas other eurytopic species were linked to moderately or intensively grazed salt marshes. PÉTILLON et al. (2007) however, reported a decline of species such as *Pardosa purbeckensis* in grazed salt marshes, whereas species of high dispersal abilities such as *Erigone longipalpis* were positively affected by grazing. IRMLER & HEYDEMANN (1985) showed however, that the activity of *E. longipalpis* increased with grazing, but that the abundance decreased. Possibly, ongoing research in mid-term and newly established rotational grazing experiments will shed light on their applicability as indicators.

Moth communities however, seemed to respond more clearly to grazing and results from short-term (Ecosystem Research Wadden Sea Project) and mid-term (Hamburger Hallig) grazing experiments yielded similar results. Few especially sensitive herbaceous-feeding species indicated ungrazed (*Eucosma catoptrana* and *Coleophora salicorniae*) salt marshes or a sustainable management with low grazing intensities (*Phalonidia affinitana*, *Eucosma tripoliana* and *E. lacteana*), whereas grass-feeding species (*Pediasia aridella* and eurytopic species) indicated overgrazing. Hence, former suggestions on the adequacy of lepidopteran assemblages as indicators of habitat condition (NEW 1997, LUFF & WOIWOOD 1995, NEW 2004, SCALERCIO et al. 2009) were supported.

Their suitability to indicate species richness in other invertebrate groups, however, could not be proven and correlations between moth species richness and abundance with those of spiders, beetles and flies were weak. Findings for one species or species group could not straightforwardly be generalised to biodiversity (ÖSTER et al. 2008, STRIEN et al. 2009). GRILL et al. (2005) found similar results on butterflies and moths, which did not qualify as indicators for spider diversity and species richness and POCOCC & JENNINGS (2008) found contrasting results for Lepidoptera, Diptera and Carabidae. The lack of consistent patterns among most of the sensitive species casts doubt on the suitability of using a few species as indicators for the benefit of others (NOSS 1990, NIEMI et al. 1997) and highlights the importance of the application of more than one taxonomic group (CASTELLA et al. 1994, PAOLETTI 1999). Selecting these taxonomic groups on the basis of complementarities seems crucial. Since moths were associated with plant species richness while spiders were linked to vegetation structure (PÉTILLON et al. 2008), a combination seems reasonable to measure effects of disturbances in a habitat, when additionally considering the hemerobic level (ROWECK 1987).

Nevertheless, especially because the peak season of occurrence of moths is focused and connected to the growing season, monitoring effort would be low and improve the likelihood of a support for a long-term monitoring programme (MCGEOCH et al. 2002). Additionally, the five suitable moth indicator species are easily identifiable and their co-occurrence gives supplementary information on the structural heterogeneity of salt marshes.

For further validation of the applicability of halobiontic moths as ecological indicators in salt marsh monitoring, more data is needed (especially in long-term grazing experiments).

5.5 Implications for salt marsh management and monitoring

Salt marshes can serve as an example for natural azonal ecosystems that can be characterised by very low habitat-specific species numbers, but are still very important for national or global biodiversity by contributing specialised organisms, which cannot be found elsewhere (DUELLI & OBRIST 1998).

Through the establishment of the National Park (1985) and its declaration as a World Natural Heritage Site (2006), the uniqueness and value of the Wadden Sea including its salt marshes has been recognised. In German salt marshes, natural development and improvement processes were promoted. This resulted in either ungrazed or intensively grazed salt marshes along the West coast of Schleswig-Holstein and only few sites of intermediate grazing intensities were set up or remained for research purposes (e.g. Hamburger Hallig). But 25 years after the cessation of grazing, awareness is raising that abandonment most likely leads to dominant stands of *Elymus athericus* and/ or *Atriplex portulacoides* (JENSEN 1985, ESSELINK et al. 1998, BAKKER et al. 2010) and thus dense and high vegetation of low species richness. Breeding birds, focal objects of the trilateral

monitoring scheme, require low and patchy vegetation structures and tend to avoid ungrazed salt marshes (ESSELINK et al. 2000). Consequently, species richness of herbivorous invertebrates as well as important habitats for migratory and breeding birds are decreasing. Therefore, to maintain a typical landscape of species rich and flowering European salt marshes, a new management concept is needed. But meeting the requirements of plant, arthropod and bird communities is a demanding task. While many halophilic plants such as *Aster tripolium*, *Limonium vulgare*, *Plantago maritima* and *Triglochin maritima* are known to react sensitively to grazing (BOS et al. 2002), others (*Glaux maritima* and *Armeria maritima*) benefit from moderate grazing intensities. Breeding birds on the other hand were recorded more often in moderately grazed salt marshes which maintain young successional stages (ESSELINK et al. 2000). Breeding waders are heavily dependent on an abundant supply of their invertebrate food, with many species being generalist feeders (AUSDEN et al. 2003) and a decrease of arthropods poses a serious threat to bird breeding success (COLE et al. 2010, BUCHANAN et al. 2006, SCHEKKERMAN & BEINTEMA 2007).

Older studies in salt marshes suggested that there might be a species turnover from ungrazed to intensively grazed salt marshes concerning spider, beetle and fly species, but instead found a significant decrease of species richness in ungrazed sites (ANDRESEN et al. 1990, DIERBEN et al. 1994b, MEYER & REINKE 1996).

However, extensive grazing especially in wet grasslands is a widely used management tool to enhance plant and invertebrate diversity (LOUCOUGARAY et al. 2004, WALLIS-DEVRIES & RAEMAKERS 2001). Results of this study proved, that halobiontic moths show a clear response to grazing with significantly less species in the moderately and intensively grazed salt marshes, but a tendency towards higher species richness in extensively grazed sites. Overall, results correspond to recent studies in agricultural landscapes (WOODCOCK et al. 2005, LINDSAY & CUNNINGHAM 2009) and strongly suggest a mosaic of differently managed salt marshes including ungrazed, extensively and moderately grazed sites, which offer a variety of microhabitats to maintain species diversity of plants, insects and birds (KRUESS & TSCHARNTKE 2002a, ESSELINK et al. 2000). As an alternative, ANDRESEN et al (1990) suggested intermediate grazing intensities (2-3 sheep/ ha) on a large area as a suitable management practice to enhance plant species diversity and to create the equivalent of ungrazed areas in a grazed site due to the spatial heterogeneity of grazing impact (WALLISDEVRIES et al. 1999). Vegetation monitoring proved the increase of *E. athericus* especially in the ungrazed as well as in parts of the extensively grazed salt marshes (STOCK & PETERSEN 2008). Since parts dominated by *Elymus athericus* were deliberately excluded from this study it can be expected that the beneficial effect of grazing on invertebrate communities is even higher and that this research reveals a rather cautious estimate.

For evaluation and conservation planning in salt marshes, ideally a multi-species approach should be favoured combining groups of organisms (MAES & VAN DYCK 2005). The concept of monitoring indicator species seems to be an easy and appealing method, but caution is advisable against the (blind) application of ecological indicators that have not been validated in the context in which they are to be applied (GOLLAN 2010).

It was recognised that different moth species feeding on *Aster tripolium* depend on differently developed plants either in the ungrazed marsh (*E. catoptrana*) or the extensively grazed salt marsh (*Eucosma tripoliana* and *Phalonidia affinitana*). While *E. catoptrana* needs dense inflorescences to construct a sheltering spinning from a few blossoms, *P. affinitana* feeds on the pith of the stem and likely benefits from *Aster*-plants damaged by grazing (see MYSTERUD et al 2005). Possibly, the slightly smaller and later occurring *Eucosma*

tripoliana, which constructs a spinning of *Aster*-flowers as well, is disadvantaged in the competition with *E. catoptrana* and therefore occurs more frequently in the extensively grazed sites. The co-occurrence of both species therefore offers information on habitat structures which cannot be assumed by the occurrence of the host plant alone. Therefore, the integration of moth indicator species (*Eucosma catoptrana*, *Eucosma tripoliana*, *Phalonia affinitana*, *Coleophora salicorniae* and *Eucosma lacteana*) in combination with species richness of invertebrates, plants and birds (NICKEL & HILDEBRANDT 2003, RYKKEN et al. 1997) in salt marsh monitoring schemes is proposed. Ideally, these species should be complemented by easily identifiable spider and possibly beetle indicator species (Pétillon et al. 2008). More reliable information can be gained from studies of a set of species or one or more higher taxa measuring diversity, abundances and dominance than from focusing on a few indicator species. To make the overwhelming task of conservation planning more manageable, the combination of an invertebrate monitoring with the regular vegetation mapping in June, July and August is proposed, that being the peak time of moth activity.

This recommendation is supported by the recognition that insects are in many respects crucial organisms for maintaining and evaluating biodiversity (CLAUSNITZER 2003) leading to the demand of invertebrate groups as an integral part of biodiversity conservation (KIM 1993, TAYLOR & DORAN 2001, SAMWAYS & Lu 2007, JANSSON et al. 2009).

6 Acknowledgements

My "Doktorvater" Prof. Dr. H. Roweck gave me the great opportunity to write this thesis. He gave me freedom to explore; his advice and worthwhile comments especially in later stages of my thesis improved the outcome considerably.

I also thank Prof. Dr. H. Brendelberger, who kindly agreed to be my second supervisor, as well as all members of my examination board.

Writing and finishing this thesis would not have been possible without the kind support of N. Savenkov, P.D. Dr. M. Zimmer, Prof. Dr. U. Irmeler, Dr. A. Fichtner, M. Dahmen, Dr. M. Stock and the National Park Authorities, R. Rehm, S. Wagner, staff and trainees of the Amsinck House (Hamburger Hallig), the LKN Husum, the Schutzstation Wattenmeer e.V. and especially the crew at the Lighthouse Westerhever, M. Bahns, M. Schütz, H.-J. Voß, C.C.M. Lubos, F. Kroll, F. Krüger, J. Peyrat, the participants of the Coastal Ecology Workshops, J.P. Bakker, R. Van Klink, M. Schrama and the Cocon working group at Groningen University, my friends and family and all the people I possibly forgot to mention but were there for me, nevertheless. I would like to thank all of you; your help, ideas, and advice are invaluable to me!

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Appendix

Tab. A1: Species list of all Microlepidoptera caught in the salt marshes of Schleswig-Holstein with host plants.

IDKR	Species	Host plant
	<u>Incurvariidae</u>	
424	<i>Incurvaria masculella</i> (Denis & Schiffermüller, 1775)	<i>Crataegus</i> sp.
	<u>Tineidae</u>	
700	<i>Monopis rusticella</i> (Denis & Schiffermüller, 1775)	scavenger
708	<i>Monopis monachella</i> (Hübner, 1796)	scavenger
	<u>Psychidae</u>	
938	<i>Whittleia retiella</i> (Newman, 1847)	<i>Puccinellia maritima</i>
	<u>Bucculatricidae</u>	
1081	<i>Bucculatrix maritima</i> Stainton, 1851	<i>Aster tripolium</i>
	<u>Yponomeutidae</u>	
1348	<i>Yponomeuta padella</i> (Linnaeus, 1758)	<i>Prunus</i> sp.
	<u>Plutellidae</u>	
1525	<i>Plutella xylostella</i> (Linnaeus, 1758)	Cruciferen
	<u>Lyoniidae</u>	
1602	<i>Bedellia somnulentella</i> (Zeller, 1847)	polyphag
	<u>Depressariidae</u>	
1736	<i>Agonopterix heracliiana</i> (Linnaeus, 1758)	umbelliferous plants
	<u>Elachistidae</u>	
1863	<i>Elachista canapennella</i> (Clerck, 1759)	grasses
1883	<i>Elachista argentella</i> (Hübner, 1813)	grasses
	<u>Oecophoridae</u>	
2284	<i>Hoffmannophila pseudospetrella</i> (Stainton, 1849)	scavenger
	<u>Coleophoridae</u>	
2442	<i>Goniadoma limoniella</i> (Stainton, 1884)	<i>Limonium vulgare</i>
2686	<i>Coleophora adjunctella</i> Hodgkinson, 1882	<i>Juncus gerardii</i>
2689	<i>Coleophora glaucicolella</i> Wood, 1892	<i>Juncus</i> sp.
2692	<i>Coleophora alticolella</i> Zeller, 1849	<i>Juncus</i> sp.
2716	<i>Coleophora asteris</i> Mühlhig, 1864	<i>Aster tripolium</i> , <i>Achillea millefolium</i>
2729	<i>Coleophora versurella</i> Zeller, 1849	<i>Atriplex</i> sp., <i>Chenopodium</i> sp.
2733	<i>Coleophora vestianella</i> (Linnaeus, 1758)	<i>Atriplex</i> sp., <i>Chenopodium</i> sp.
2737	<i>Coleophora atriplicis</i> Meyrick, 1928	<i>Atriplex portulacoides</i> , <i>Suaeda maritima</i> , <i>Salicornia</i> sp.
2751	<i>Coleophora deviella</i> Zeller, 1847	<i>Suaeda maritima</i>
2816	<i>Coleophora artemisiella</i> Scott, 1861	<i>Artemisia maritima</i> , <i>Artemisia</i> sp.
2858	<i>Coleophora salicorniae</i> Heinemann & Wocke, 1876	<i>Salicornia</i> sp.
	<u>Momphidae</u>	
2892	<i>Mompha epilobiella</i> (Denis & Schiffermüller, 1775)	<i>Epilobium</i> sp.
	<u>Gelechiidae</u>	
3237	<i>Aristotelia brizella</i> (Treitschke, 1833)	<i>Armeria maritima</i>
3320	<i>Monochroa tetragonella</i> (Stainton, 1885)	<i>Glaux maritima</i>

3321	<i>Monochroa elongella</i> (Heinemann, 1870)	<i>Potentilla anserina</i>
3609	<i>Scrobipalpa instabilella</i> (Douglas, 1846)	<i>Atriplex portulacoides</i>
3616	<i>Scrobipalpa nitentella</i> (Fuchs, 1902)	<i>Suaeda maritima</i> , <i>Atriplex prostrata</i>
3620	<i>Scrobipalpa pauperella</i> (Heinemann, 1870)	<i>Cirsium palustre</i>
3628	<i>Scrobipalpa salinella</i> (Zeller, 1847)	<i>Salicornia europaea</i> , <i>Suaeda maritima</i> , <i>Aster tripolium</i>
3629	<i>Scrobipalpa samadensis</i> (Pfaffenzeller, 1870)	<i>Plantago maritima</i> , <i>Plantago coronopus</i>
3702	<i>Caryocolum marmorea</i> (Haworth, 1828)	<i>Cerastium</i> sp.
3865	<i>Brachmia inornatella</i> (Douglas, 1850)	<i>Phragmites australis</i>
	<u>Tortricidae</u>	
4256	<i>Phalonidia affinitana</i> (Douglas, 1846)	<i>Aster tripolium</i>
4263	<i>Phalonidia vectisana</i> (Humphreys & Westwood, 1845)	<i>Triglochin maritima</i>
4268	<i>Agapeta hamana</i> (Linnaeus, 1758)	<i>Carduus</i> sp.
4309	<i>Aethes smeathmanniana</i> (Fabricius, 1781)	<i>Achillea millefolium</i> , <i>Centaurea</i> sp.
4390	<i>Acleris variegana</i> (Denis & Schiffermüller, 1775)	Rosaceae
4474	<i>Cnephasia stephensiana</i> (Doubleday, 1849)	polyphagous
4477	<i>Cnephasia asseclana</i> (Denis & Schiffermüller, 1775)	polyphagous
4493	<i>Cnephasia longana</i> (Haworth, 1811)	polyphagous
4541	<i>Philedone gerningana</i> (Denis & Schiffermüller, 1775)	polyphagous
4581	<i>Pandemis dumetana</i> (Treitschke, 1835)	strawberries
4623	<i>Clepsis spectrana</i> (Treitschke, 1830)	polyphagous
4655	<i>Bactra lancealana</i> (Hübner, 1799)	<i>Juncus</i> sp., <i>Scirpus</i> sp.
4656	<i>Bactra furfurana</i> (Haworth, 1811)	<i>Juncus</i> sp., <i>Scirpus</i> sp.
4657	<i>Bactra lacteana</i> (Caradja, 1916)	<i>Carex</i> sp., <i>Juncus</i> sp.
4659	<i>Bactra robustana</i> (Christoph, 1872)	<i>Scirpus maritimus</i>
4673	<i>Endothenia quadrimaculana</i> (Haworth, 1811)	<i>Stachys palustris</i> , <i>Mentha spicata</i>
4714	<i>Hedya nubiferana</i> (Haworth, 1811)	<i>Crataegus</i> sp., <i>Prunus</i> sp.
4715	<i>Hedya pruniana</i> (Hübner, 1799)	<i>Prunus</i> sp.
4722	<i>Celypha striana</i> (Denis & Schiffermüller, 1775)	<i>Taraxacum officinale</i>
4806	<i>Lobesia littoralis</i> (Westwood & Humphreys, 1845)	<i>Armeria maritima</i> , <i>Lotus corniculatus</i>
4932	<i>Eucosma cana</i> (Haworth, 1811)	<i>Carduus</i> sp., <i>Centaurea nigra</i>
4935	<i>Eucosma hohenwartiana</i> (Dennis & Schiffermüller,	<i>Centaurea</i> sp.
4947	<i>Eucosma catoptrana</i> (Rebel, 1903)	<i>Aster tripolium</i>
4948	<i>Eucosma tripoliana</i> (Barrett, 1880)	<i>Aster tripolium</i>
4949	<i>Eucosma lacteana</i> (Treitschke, 1835)	<i>Artemisia maritima</i>
4985	<i>Gypsonoma dealbana</i> (Frölich, 1828)	polyphagous
4987	<i>Gypsonoma sociana</i> (Haworth, 1811)	<i>Populus</i> sp., <i>Salix</i> sp.
4989	<i>Gypsonoma aceriana</i> (Duponchel, 1843)	<i>Populus</i> sp.
5025	<i>Notocelia rosaecolana</i> (Doubleday, 1850)	<i>Rosa rubiginosa</i> , <i>Rosa</i> sp.
	<u>Pterophoridae</u>	
5348	<i>Agdistis bennetii</i> (Curtis, 1833)	<i>Limonium vulgare</i>
5381	<i>Alucita acanthodactyla</i> (Hübner, 1813)	polyphagous

Pyalidae

5661	<i>Endotricha flammealis</i> (Denis & Schiffermüller, 1775)	polyphagous
6086	<i>Phycitodes maritima</i> (Tengström, 1848)	<i>Achillea millefolium</i> , <i>Senecio jacobaea</i>
6112	<i>Ephestia elutella</i> (Hübner, 1796)	cereal, cacao, tobacco
6166	<i>Scoparia basistrigalis</i> Knaggs, 1866	<i>Mnium hornum</i>
6168	<i>Scoparia ambigualis</i> (Treitschke, 1829)	mosses
6222	<i>Chilo phragmitella</i> (Hübner, 1805)	<i>Phragmitis australis</i>
6235	<i>Calamatropha paludella</i> (Hübner, 1824)	<i>Typha</i> sp.
6241	<i>Chrysoteuchia culmella</i> (Linnaeus, 1758)	grasses
6253	<i>Crambus perlella</i> (Scopoli, 1763)	grasses
6258	<i>Agriphila tristella</i> (Denis & Schiffermüller, 1775)	grasses
6264	<i>Agriphila latistria</i> (Haworth, 1811)	grasses
6266	<i>Agriphila selasella</i> (Hübner, 1813)	<i>Puccinellia maritima</i> , <i>Festuca ovina</i>
6267	<i>Agriphila straminella</i> (Denis & Schiffermüller, 1775)	<i>Festuca ovina</i> and other grasses
6275	<i>Agriphila geniculea</i> (Haworth, 1811)	<i>Festuca ovina</i> and other grasses
6367	<i>Pediasia aridella</i> (Thunberg, 1788)	<i>Puccinellia maritima</i> , <i>Festuca rubra</i>
6416	<i>Elophila nymphaeata</i> (Linnaeus, 1758)	water plants
6421	<i>Acentria ephemerella</i> (Denis & Schiffermüller, 1775)	submersed aquatic angiosperms
6423	<i>Cataclysta lemnata</i> (Linnaeus, 1758)	<i>Lemna</i> sp.
6531	<i>Udea ferrugalis</i> (Hübner, 1796)	polyphagous
6538	<i>Udea lutealis</i> (Hübner, 1809)	polyphagous
6633	<i>Phlyctaenia perlucidalis</i> (Hübner, 1809)	<i>Cirsium</i> sp., <i>Carduus</i> sp.
6649	<i>Ostrinia nubilalis</i> (Hübner, 1796)	<i>Artemisia vulgaris</i> , <i>Zea mays</i>
6719	<i>Nomophila noctuella</i> (Denis & Schiffermüller, 1775)	<i>Trifolium</i> sp., grasses

Tab. A2: Species of Lepidoptera and their abundances caught with light traps in the different grazing intensities in the salt marshes of the Hamburger Hallig.

Species /Year	Grazing conditions															
	ungrazed				extensive				moderate				intensive			
	06	07	08	09	06	07	08	09	06	07	08	09	06	07	08	09
<i>Ephestia elutella</i>	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Eucosma catoptrana</i>	25	135	179	210	5	23	79	58	.	.	9	1	.	.	.	.
<i>Eucosam lacteana</i>	71	75	43	15	.	3	6	4	98	103	53	44	7	.	7	.
<i>Eucosam tripoliana</i>	40	127	215	144	52	34	14	23	1	15	3	1	.	.	.	.
<i>Hoffmannophila pseudospetrella</i>	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.
<i>Lobesia littoralis</i>	2	2	2	.	5	6	1	6	.	.	.	.	.	.	.	.
<i>Mompha epilobiella</i>	4	4	.	.	4	2	.	.	3	6	.	.	.	.	.	.
<i>Monopis monachella</i>	.	.	.	.	1	1	.	.	2	2	.	2	2	.	.	.
<i>Monopis rusticella</i>	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Monochroa tetragonella</i>	.	.	.	2	1	.	1	4	.	.	.	.	.	.	.	.
<i>Ostrinia nubilalis</i>	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1
<i>Pediasia aridella</i>	13	18	.	2	15	60	20	8	21	31	9	15	11	.	3	23
<i>Phalonidia affinitana</i>	1	17	50	33	3	16	79	113	.	3	17	13	.	.	.	.
<i>Phalonidia vectisana</i>	.	1	1	2	.	5	1	7	.	.	2	6	.	.	.	.
<i>Phlyctaenia perlucidalis</i>	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
<i>Plutella xylostella</i>	.	2	.	.	1	1	.	7	3	7	.	.	.	.	.	.
<i>Scrobipalpa instabilella</i>	18	118	148	213	5	59	117	204	.	17	42	26	.	5	31	35
<i>Scrobipalpa nitentella</i>	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.
<i>Scrobipalpa salinella</i>	30	38	35	25	32	9	35	19	7	9	3	.	.	.	10	2
<i>Scrobipalpa samadensis</i>	5	17	.	.	6	21	1	4	.	.	.	.	.	.	.	.
<i>Scrobipalpa sp.</i>	.	23	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Udea ferrugalis</i>	1	1	.	.	1	.	.	.	.	.	.	.	1	.	.	.
Number of Individuals	385	874	939	929	315	342	598	759	253	384	194	210	91	18	59	112
Sum	3127				2014				1041				280			

Tab. A3: Lepidoptera species and their abundances caught with photoeclector traps in the different grazing regimes of the Hamburger Hallig in the years 2007 to 2009.

Species /Year	Grazing intensity											
	ungrazed			extensive			moderate			intensive		
	07	08	09	07	08	09	07	08	09	07	08	09
<i>Agdistis bennetii</i>	.	.	.	.	2	1	.	.	.	.	.	.
<i>Bucculatrix maritima</i>	44	11	159	46	297	85	19	77	12	2	.	.
<i>Clepis spectrana</i>	.	14	3	2	9	2	.	.	5	.	.	.
<i>Coleophora adjunctella</i>	3	.	.	2	.	.	4	.	.	.	.	.
<i>Coleophora adpersella</i>	.	.	.	.	2	.	.	.	.	.	.	.
<i>Coleophora artemisiella</i>	.	.	1	.	.	.	.	.	3	.	.	.
<i>Coleophora atriplicis</i>	.	.	3	.	1	2	.	.	.	.	.	.
<i>Coleophora asteris</i>	14	1	.	2	.	.	2	.	.	.	.	.
<i>Coleophora glaucicolella</i>	.	.	.	1	.	.	.	.	1	.	.	.
<i>Coleophora salicorniae</i>	14	.	.	3	.	.	3	.	.	.	.	.
<i>Crambus perlella</i>	.	.	.	.	.	.	.	1	4	.	1	1
<i>Chrysoteuchia culmella</i>	.	.	.	.	.	.	.	.	1	.	.	1
<i>Eucosma catoptrana</i>	7	6	22	.	2	2	.	3	.	.	.	.
<i>Eucosma lacteana</i>	2	.	.	4	.	.	3	4	1	.	.	.
<i>Eucosma tripoliana</i>	15	1	9	5	.	2	.	.	.	.	.	.
<i>Goniodoma limoniella</i>	.	1	.	.	.	.	.	.	.	.	.	.
<i>Lobesia littoralis</i>	1	.	.	1	.	.	.	.	.	.	.	.
<i>Monochroa tetragonella</i>	.	.	.	.	1	1	.	.	.	.	.	.
<i>Pediasia aridella</i>	2	.	.	2	.	.	.	.	.	.	.	.
<i>Phalonidia affinitana</i>	.	8	16	2	21	22	3	5	1	.	.	.
<i>Phalonidia vectisana</i>	5	1	1	2	.	5	2	.	.	1	.	.
<i>Scrobipalpa instabilella</i>	27	28	72	21	8	143	3	67	.	1	4	5
<i>Scrobipalpa nitentella</i>	.	4	.	.	1	3	2	.	.	.	.	.
<i>Scrobipalpa salinella</i>	2	3	3	.	2	1	1	1	.	.	.	.
<i>Whittleia retiella</i>	.	.	.	.	1	.	.	.	.	.	.	.
Number of individuals	136	78	289	93	347	269	42	158	28	4	5	7
Sum	503			709			228			16		

Tab. A4: Species and individuals of Microlepidoptera caught by photoelector traps on the salt marshes of Friedrichskoog in the years 1990-1993 according to the different grazing intensities.

Species	Grazing intensity				
	ungrazed	low	extensive	moderate	intensive
<i>Agriphila selasella</i>	15	20	13	4	2
<i>Caryocolum marmorea</i>			1		
<i>Clepsis spectrana</i>	11		4		
<i>Cnephasia longana</i>				1	
<i>Coleophora adjunctella</i>	40		2		
<i>Coleophora alticolella</i>	13				
<i>Coleophora atriplicis</i>	1				
<i>Coleophora glaucicolella</i>	5				
<i>Crambus perlella</i>	65	37	34	29	6
<i>Elachista sp.</i>	1	1		1	4
<i>Lobesia littoralis</i>	16	4	4	6	
<i>Mompha epilobiella</i>	1				
<i>Pediasia aridella</i>	18	25	30	30	10
<i>Scrobipalpa instabilella</i>				1	
<i>Scrobipalpa nitentella</i>	1				
<i>Scrobipalpa smadensis</i>	1				
Sum	188	87	88	72	22

Tab. A5: Species and individuals of Microlepidoptera caught by photoelector traps on the salt marshes of Sönke-Nissen-Koog in the years 1990-1993 according to the different grazing intensities.

Species	Grazing intensity				
	ungrazed	low	extensive	moderate	intensive
<i>Bucculatrix maritima</i>	634	287	6	173	3
<i>Chrysoteuchia culmella</i>	2	0	0	0	0
<i>Clepsis spectrana</i>	15	11	1	11	0
<i>Coleophora atriplicis</i>	1	0	0	3	0
<i>Coleophora deviella</i>	28	45	28	65	8
<i>Crambus perlella</i>	2	4	4	0	1
<i>Eucosma catoptrana</i>	2	0	0	0	0
<i>Eucosma tripoliana</i>	99	15	2	4	0
<i>Pediasia aridella</i>	5	15	10	8	17
<i>Phalonidia affinitana</i>	39	28	1	9	0
<i>Phalonidia vectisana</i>	4	0	2	0	0
<i>Plutella xylostella</i>	1	0	0	0	0
<i>Scrobipalpa instabilella</i>	5	1	7	4	2
<i>Scrobipalpa nitentella</i>	0	1	0	0	0
<i>Scrobipalpa salinella</i>	0	0	0	1	0
<i>Scrobipalpa samadensis</i>	0	0	0	1	0
Sum	837	407	61	279	31