

Stiftung Alfred-Wegener-Institut für Polar- und Meeresforschung

Wattenmeerstation Sylt

**Ecological functions of intertidal seagrass beds for fishes and
mobile epibenthos in the northern Wadden Sea**

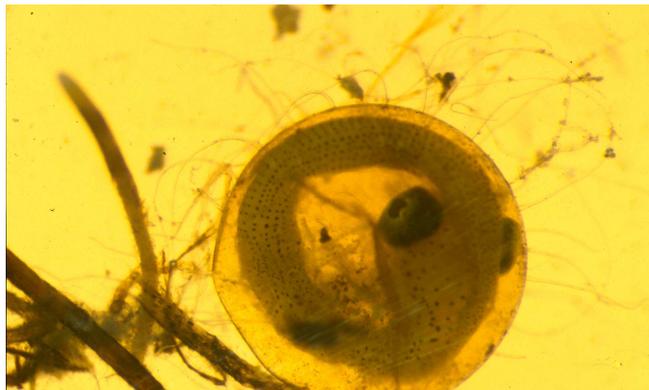
Dissertation

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Titelbild:

Ei des Hornhechts (*Belone belone* L.),
angeheftet an Blätter des Zwergseegrases (*Zostera noltii* Hornem.)

Garfish egg (*Belone belone* L.),
attached to leaves of the dwarf seagrass (*Zostera noltii* Hornem.)

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Summary

Seagrass beds are worldwide known to represent important habitats and nursery grounds for fishes and invertebrates. They mostly harbour a higher biodiversity and density of individuals compared to adjacent substrates without a complex structure. Most investigations of the role of seagrass beds as habitats for animal assemblages were carried out in subtidal zones, whereas only little information is available on intertidal seagrass beds. However, different ecological functions are to be expected between both systems.

Since the substantial loss of subtidal eelgrass (*Zostera marina* L.) by the “wasting disease” during the 1930`s, in the northern Wadden Sea extended meadows are exclusively limited to the intertidal zone, where they are dominated by the dwarf seagrass (*Zostera noltii* Hornem.).

This study was conducted to investigate whether intertidal seagrass beds fulfil vital ecological functions for common North Sea fishes and -crustaceans although they are exposed to air during long emersion periods within the tidal cycle.

To answer this question quantitative sampling strategies were combined with field experiments on vegetated and unvegetated tidal flats in the Sylt-Rømø Bight (German-Danish Wadden Sea, North Sea). Results of sampling at high tide showed that abundances as well as secondary production of juvenile shore crabs (*Carcinus maenas* L.), brown shrimps (*Crangon crangon* L.) and common gobies (*Pomatoschistus microps* Krøyer) were significantly higher on vegetated tidal flats during the main growth period of *Z. noltii*. Furthermore mobile epibenthos was found abundant within seagrass beds during ebb tide when a thin layer of residual water remains within the canopies. The faunal density was consistently higher in the canopy water layer than in experimentally installed tide pools although the content of dissolved oxygen dropped drastically at night.

As a result the preference of intertidal *Z. noltii* beds by mobile epifauna is not limited to high tide. The meadows also provide extended ebb tide refuges and allow juvenile epibenthic animals for avoiding tidal migration to deeper waters where predation pressure is probably increased. Thus the presence of seagrass in the upper intertidal zone is supposed to support the nursery function, generally attributed to tidal flats, for epibenthic key species of the Wadden Sea food web.

Juveniles of larger fishes showed low densities in the intertidal zone and the species composition was found strictly subjected to season. However, during their temporary residence on inundated tidal flats fish species showed distinct preferences for either vegetated or unvegetated flood habitats. Among 0-group fishes visiting the intertidal zone three groups could be identified by cluster analysis: (i) species almost exclusively found in the *Z. noltii* bed, (ii) species primarily found in the seagrass bed but also on bare sand flats in lower numbers and (iii) species almost limited to sand flats. According to the results it can be concluded that *Z. noltii* beds qualitatively structure the distribution of transient fishes temporary visiting tidal flats.

For some fish species that periodically enter shallow Wadden Sea waters as adults it could be demonstrated, that the preference of *Z. noltii* beds was directly linked with spawning. Species such as the herring (*Clupea harengus* L.) and the garfish (*Belone belone* L.) attached their demersal eggs to the seagrass leaves or, as the three-spined stickleback (*Gasterosteus aculeatus* L.), constructed camouflaged nests within the canopy. Although it is a widespread paradigm that seagrass beds represent important spawning grounds fish species using plants as spawning substrate are relatively rare in marine environment. This study gave empirical evidence that *Z. noltii* beds were important for fish reproduction despite long emersion periods. The role of alternative structures, such as e.g. the dominant macro algae (*Fucus vesiculosus*, L.) for reproductive success was of minor relevance.

The species composition of fishes was studied in different intertidal habitats, such as mussel beds (*Mytilus edulis* L.), sand flats and *Z. noltii* beds and compared to a bare sand area in the shallow subtidal where dense *Z. marina* beds have been reported to exist in the 1930's. On the basis of historical data the effects of substantial seagrass loss on the fish assemblage were reconstructed. Results indicate that ecological functions were basically kept by present Wadden Sea habitats since mussel beds and intertidal seagrass meadows prevent a substantial loss of fish species. However, since these residual habitats still continue to decrease, consequences of former habitat losses might become pronounced with a delay of decades. In case of a re-establishment of subtidal vegetation, the residual habitats act as distribution centres and provide good conditions for resilience of biodiversity.

Zusammenfassung

Seegraswiesen gelten weltweit als bedeutende Lebensräume und Kinderstuben für Fische und Wirbellose. Gegenüber unstrukturierten Meeresböden zeichnen sie sich zumeist durch eine größere Biodiversität und Individuendichte aus. Die meisten Untersuchungen bezüglich der Rolle von Seegraswiesen als Habitat für Tiergemeinschaften wurden im Sublitoral durchgeführt, während über die Funktionen der Seegraswiesen im Gezeitenbereich nur wenige Informationen vorhanden sind. Es ist jedoch zu erwarten, dass sich beide Systeme hinsichtlich ihrer ökologischen Funktionen unterscheiden.

Seit dem schwerwiegenden Verlust sublitoraler Bestände des großen Seegrases (*Zostera marina* L.) durch das „Wasting Disease“ in den 1930er Jahren sind ausgedehnte Seegraswiesen im nördlichen Wattenmeer ausschließlich auf den Gezeitenbereich beschränkt, wo sie vom Zwergseegras (*Zostera noltii* Hornem.) dominiert werden.

Die vorliegende Studie ging der Frage nach, ob die Seegraswiesen des Eulitorals grundlegende, ökologische Funktionen für heimische Nordseefische und -Krebse erfüllen, obwohl sie während des Tidenzyklus für lange Zeit trocken fallen. Um diese Frage zu beantworten wurden auf bewachsenen und unbewachsenen Watten in der Sylt-Rømø Bucht (deutsch-dänisches Wattenmeer) quantitative Beprobungen mit Freiland-Experimenten kombiniert. Die Ergebnisse der Beprobungen bei Hochwasser zeigten, dass sowohl die Abundanz als auch die Sekundärproduktion juveniler Strandkrabben (*Carcinus maenas* L.), Nordseegarnelen (*Crangon crangon* L.) und Strandgrundeln (*Pomatoschistus microps* Krøyer) während der Vegetationsperiode des Seegrases in den Wiesen signifikant höher waren. Darüber hinaus fanden sich in den Seegraswiesen hohe Dichten mobiler, epibenthischer Fauna bei Ebbe, wenn die Blätter der Pflanzen eine dünne Restwasserschicht auf dem Wattboden zurückhielten. Die Individuendichte der Epifauna in dieser Restwasserschicht war durchweg höher als die gemessen in experimentell angelegten Gezeitentümpeln, obwohl der Gehalt an gelöstem Sauerstoff in der Restwasserschicht während der Nacht drastisch absank. Demzufolge stellen Seegraswiesen nicht nur während der Wasserbedeckung einen bevorzugten Lebensraum im Gezeitenbereich dar, sondern dienen auch als ausgedehnte Ebbrefugien. Sie erlauben, das Abwandern in tiefere Zonen zu vermeiden und dem

dort vermutlich höheren Prädationsdruck zu entgehen. Demnach verstärkt die Anwesenheit von Seegraswiesen im oberen Eulitoral die Kinderstuben-Funktion für Schlüsselarten des Wattenmeer-Nahrungsnetzes, die dem Gezeitenbereich generell zugesprochen wird.

Jungfische größerer Arten fanden sich in geringer Dichte im Eulitoral und ihre Artenzusammensetzung variierte stark saisonal. Während ihres vorübergehenden Aufenthaltes auf überfluteten Wattflächen zeigten diese Fischarten jedoch ausgeprägte Präferenzen für bewachsene oder unbewachsene Flut-Habitats. Die Fische der 0-Gruppe, die den Gezeitenbereich aufsuchten, ließen sich mittels Clusteranalyse in drei Gruppen aufteilen: (i) Arten, die nahezu ausschließlich im Seegras gefangen wurden, (ii) Arten, die vorwiegend im Seegras, jedoch in geringeren Mengen auch auf Sandwatten gefangen wurden, und (iii) Arten, deren Vorkommen nahezu auf Sandwatten beschränkt war. Die Ergebnisse zeigen, dass *Z. noltii* Wiesen die Verteilung der im Gezeitenbereich vorübergehend anwesenden Jungfische qualitativ beeinflussen.

Für einige Fischarten, die als ausgewachsene Tiere in das Wattenmeer einwandern, wurde gezeigt, dass ihre Vorliebe für Seegraswiesen direkt mit dem Laichvorgang zusammenhängt. Arten wie der Hering (*Clupea harengus* L.) und der Hornhecht (*Belone belone* L.) heften ihren Laich an die Seegraspflanzen, während der Dreistachelige Stichling (*Gasterosteus aculeatus* L.) gut getarnte Nester in die Seegraswiese baut. Obwohl Seegraswiesen oft im Zusammenhang mit Laichgründen genannt werden sind im marinen Bereich konkrete Beispiele für Fischarten, die Pflanzen als Laichsubstrat nutzen, selten. Diese Untersuchung weist experimentell nach, dass *Z. noltii* Pflanzen trotz langer Phasen des Trockenfallens direkt für die Reproduktion mancher Arten von Bedeutung sind. Die Rolle anderer potentieller Laichsubstrate hingegen, wie z. B. die der dominanten Makroalge (*Fucus vesiculosus* L.), ist diesbezüglich zu vernachlässigen.

Die Artenzusammensetzung der Fischfauna wurde in verschiedenen Lebensräumen des Eulitorals wie Muschelbänken (*Mytilus edulis* L.), Sandwatten und *Z. noltii* Wiesen beprobt und mit der Fischfauna einer Sandfläche im flachen Sublitoral verglichen, auf der die Existenz einer dichten Seegraswiese (*Z. marina*) für die 1930er Jahre dokumentiert ist. Auf der Grundlage historischer Daten wurden die Auswirkungen des umfangreichen Seegrassterbens der Vergangenheit auf die

Fischgemeinschaft rekonstruiert. Die Ergebnisse legen nahe, dass ökologische Funktionen weitgehend von den existierenden Lebensräumen wie Muschelbänken und Seegraswiesen des Gezeitenbereichs aufrechterhalten wurden. Da diese Restlebensräume jedoch kontinuierlich zurückgehen, können diese Funktionen nicht weiter aufrechterhalten werden und somit werden die Auswirkungen früherer Lebensraumverluste erst Jahrzehnte später sichtbar.

Im Falle einer Wiederbesiedlung mit sublitoraler Vegetation, würden die genannten Resthabitats Verbreitungszentren darstellen und damit gute Voraussetzungen für eine Erholung der biologischen Vielfalt bieten.

General Framework

1 General Introduction

1.1 Habitat functions attributed to seagrasses

About 58 seagrass species are distributed from coastal waters of the tropical zones to polar areas (Den Hartog, 1970; Philips & Meñez, 1988). They represent the only group of flowering plants (angiosperms) successfully adapted to a submerged marine environment (Kuo & McComb, 1989).

The entire diversity of coastal biotopes provided by numerous seagrass species worldwide is generally used as an important example for positive impacts of complex habitat architecture on faunal composition. Several studies dealing with the impact of vegetation on faunal communities point out that complex seagrass habitats increase species diversity and individual numbers of epibenthic crustaceans and fish (e.g. Orth et al., 1984; Isaksson & Pihl, 1992; Boström & Bonsdorff, 1997; Mattila et al., 1999). Faunal diversity and species abundance is further supposed to be correlated with seagrass density and sediment composition (Virnstein et al., 1983; Pihl, 1986).

Some fundamental, ecological functions widely attributed to seagrasses in coastal waters are (a) representing refuge from predators by increased habitat complexity (Nelson & Bonsdorff 1990, Mattila, 1992, Hindell et al. 2001), (b) promoting larval pre- and post settlement processes (e.g. Pile et al., 1996; Boström & Bonsdorff, 2000; Moksnes, 2002), (c) reducing currents and thus enhancing accumulation of fine sediment and organic matter (Fonseca, 1996; Asmus & Asmus, 2000) and (d) providing important nursery habitats for fishes and invertebrates (e.g. Perkins-Visser et al., 1996; Scott et al., 2000; Beck et al., 2001). The latter has been viewed more critically recently. Various studies considered the nursery role of seagrass canopies to be less on ecosystem level compared to higher fish abundance and -diversity in other marine habitats as e.g. mangroves, oyster beds and even bare sand bottoms (Nagelkerken et al., 2002; Jenkins et al., 1997; Hemminga and Duarte, 2000; review in Heck et al., 2003). Consequently modern research is in progress to define more exact scales to overcome inaccurate generalisation. Earlier studies already showed that habitat function differ between seagrass species coexisting within a particular geographic locality: As the extent of habitat complexity provided by plants is due to the morphology of a certain species, faunal composition, especially size classes of

inhabitants varies according to seagrass species and their assemblages. MacArthur & Hyndes (2001) found that preferences of different species of the teleost family Odacidae were linked to plant and meadow structure of three seagrass assemblages in south-western Australia. They documented that species with a larger body size preferred seagrass habitats formed by *Amphibolis griffithii* with open spaces below a dense canopy, whereas smaller species were more abundant within meadows of *Posidonia sinuosa* densely covering the substrate. Furthermore the authors found lower species richness and individual densities in shallow, nearshore seagrass beds than in meadows located further offshore.

Numerous publications describe differing impacts of seagrass on marine fauna due to geographic region, particular plant morphology, dimensions and “patchiness” of meadows. By evaluating habitat functions of bottom vegetation caution is necessary as results received from different seagrass biocoenoses might not be suitable to make comparisons (Den Hartog, 1983). Especially vertical distribution of seagrasses might induce differences with respect to ecological functions. Thus intertidal meadows periodically exposed to air are likely to fulfil habitat roles different from those attributed to sublittoral beds. Exemplarily the nursery function provided for fishes is assumed to be more pronounced in seagrass beds situated in deeper water (Jenkins et al., 1997). Since shallow waters and intertidal zones are known to act as nurseries per se (Horn et al., 1999), the factor of water depth might be superimposed to the presence of bottom vegetation. In general less attention is paid to functional roles of intertidal seagrasses in the temperate zones of the northern hemisphere. The majority of studies on this subject were conducted in Australian waters (e.g. Edgar & Shaw, 1995; Jenkins et al., 1997). Along the Atlantic coast of Europe, the dwarf seagrass *Zostera noltii* presents the dominant species occurring in intertidal areas. While the distribution of *Z. noltii* is exclusively limited to the intertidal zone in the Wadden Sea, it occurs also submerged in shallow, sheltered waters in the Mediterranean, in Portugal and in the Kattegat (Den Hartog, 1983). However, functional roles of intertidal *Z. noltii* beds for faunal communities received less scientific attention in the past. For the Wadden Sea area this knowledge gap is even wider, as *Z. noltii* is the only remaining seagrass species forming extended meadows after the severe loss of *Z. marina* stocks during the “wasting disease” in the 1930`s.

1.2 Global effects of seagrass loss on faunal composition and fisheries

Events of substantial seagrass loss, consistently occurring around the world (Short & Wyllie-Echeverria, 1996), may display distinct impacts of vegetated habitats on the composition of coastal fish assemblages.

As a consequence of major eelgrass (*Zostera marina*) loss in coastal waters of southern New England, Massachusetts, U.S.A., Hughes et al. (2002) found significant declines in species richness, abundance and biomass of fishes.

Unfortunately quantitative pre-impact data of associated fauna are rare and while reconstructing consequences of seagrass loss most studies compare faunal diversity and species abundance found in present seagrass beds with those on adjacent unvegetated areas.

However, investigations of fish assemblages in Western Australia 25 years after a severe seagrass loss according to Vanderkliff & Jacoby, (2003) showed little evidence for essential differences in fish composition directly linked to the presence of seagrass but rather to water depth and amount of drifting matter. Jenkins et al. (1997) stated that seagrass loss in South Australia would generally cause a decrease of species richness which is more emphasised by the loss of subtidal beds of *Heterozostera tasmanica* than by that of intertidal beds of *Zostera muelleri*. Edgar & Shaw (1995) found higher abundances of small fishes in intertidal beds composed by the same species found in southern Australia but only few specimens were juveniles of commercially important fishery species. Correlated with the production of crustacean prey, they found however the production of small fishes twice as high within seagrass compared to unvegetated areas.

During the “wasting disease” in the 1930`s sublittoral seagrass beds (*Zostera marina*, L.) drastically declined in the North Atlantic ocean but failed to cause major impact on the fishery (Rasmussen, 1977). In contrast Gemp & Bryzova (1968) as well as Wechov (1987) documented a significant decline of Herring stocks in the White Sea (Russia) attributed to the loss of spawning grounds provided by *Z. marina*. However, impacts of seagrass occurrence on commercially important species are often important on a regional scale (see review in Jackson et al., 2001).

The impact of geographic latitude on faunal diversity is supposed to be of general importance. As species richness is decreasing from southern to northern latitudes

(Virnstein et al. 1984, Virnstein 1995, Macpherson & Duarte 1994, Mattila et al. 1999), environmental impacts on single species stocks might induce major economical and ecological consequences in temperate and arctic ecosystems.

1.3 Seagrass biotopes in the Wadden Sea: What is lost and what is left?

About 70 years after the exhaustive seagrass loss in the North Atlantic area, *Z. marina* stocks recovered along various European coasts, whereas extended, subtidal meadows remained absent within the whole Wadden Sea area (van Katwijk et al., 2000; Schanz & Asmus 2003). The processes leading to the collapse of seagrass stocks as well as the reasons for the failure of their re-establishment until today are still discussed controversially (De Jonge & Ruiter, 1996; van Katwijk et al., 2000; de Jonge et al., 2000). The disappearance of *Z. marina* is attributed to an infection caused by the parasitic slime mould *Labyrinthula zosterae* in combination with exceptional climatic conditions (Giesen et al., 1990; de Jonge et al., 2000). A consensus, however, exists about general changes of faunal composition due to the drastic habitat loss (Reise et al., 1989; Reise, 1994; Ducrotoy et al., 2000).

Changes of fish fauna were on the one hand limited to a few small and “cryptic” species, predominantly pipe fishes (*Entelurus aequoreus*, *Sygnathus typhle*) and the sea stickleback (*Spinachia spinachia*) (Nijssen & De Groot, 1987; Asmus & Asmus 2000; Wolff, 2000), which are assumed to inhabit shallow water zones as residents almost permanently. On the other hand migratory species seem to be affected by the loss of spawning grounds. Wohlenberg (1935) documented that the loss of *Z. marina* beds may have caused a drastic decline of spring spawning herring stocks in the northern Wadden Sea as it did in the White Sea (see citation above). Most of those spawning guests are still immigrating Wadden Sea coasts during their spawning season.

Intertidal seagrass beds were not affected by the “wasting disease” to this extent (Vergeer & Den Hartog, 1991; Philippart & Dijkema, 1995). Although their stocks were declining at the south (NL) and central (D) Wadden Sea coast during the past four decades (Den Hartog & Polderman, 1975; Michaelis, 1987; Kastler & Michaelis, 1999), they extensively recovered in the northern parts of the Wadden Sea (Reise, 2003). To our knowledge less information is available about habitat functions of

intertidal *Z. noltii* beds nowadays and in former times when they coexisted with subtidal *Z. marina* meadows. In the Wadden Sea intertidal meadows reveal drastic seasonal fluctuations. Although the dwarf seagrass is a perennial plant, grazing by water fowl, ice drift and water turbulence increased by winter storms in addition to seasonal leaf loss, lead to the almost complete absence of above ground plants on tidal flats during winter (Nacken and Reise, 2000; Ganter, 2000; Schanz and Asmus, 2003). Additionally *Z. noltii* beds are exposed to long emersion periods within the semi-diurnal tidal cycle and therefore might represent only temporarily available habitats for the majority of fishes.

1.4 Aims of the present study

As *Z. noltii* beds represent the majority of seagrass stocks left in the Wadden Sea, this study focuses on ecological functions they might provide for mobile, epibenthic macrofauna and migratory fishes. Additionally the role of mussel beds (*Mytilus edulis*) is discussed in terms of providing residual habitats for resident fishes in the northern Wadden Sea potentially lowering the effect of habitat loss by seagrass extinction on fish diversity. A combination of field experiments and quantitative faunal sampling was conducted between the years 2001 and 2003. Furthermore historical descriptions of shallow water fish communities were consulted to reach the following aims:

- 1) To present a first overview of the influence of vegetation on distribution patterns of fish immigrating tidal flats during the seagrass growth period.
- 2) To prove whether the presence of *Z. noltii* beds increases density and production of mobile epibenthos compared to sand flats bare of vegetation.
- 3) To investigate if intertidal seagrass cover contributes to the nursery function of tidal flats by providing refuges for mobile epifauna during ebb tide.
- 4) To demonstrate empirically the role of *Z. noltii* beds for reproduction of common North Sea fishes by providing suitable spawning grounds.
- 5) To reconstruct effects of seagrass loss in the Wadden Sea on shallow water fish assemblages and to evaluate the role of residual habitats, as e.g. mussel beds, to preserve fish diversity on ecosystem level.

The present study is based on the hypotheses:

- a) Seagrass cover promotes abundance and secondary production of mobile, 0-group epibenthos on tidal flats
- b) Tidal migration of fishes is influenced by the existence of bottom vegetation
- c) Intertidal *Z. noltii* beds provide relevant spawning structures for common, migratory fish species
- d) Impact of substantial habitat loss by the disappearance of subtidal *Z. marina* stocks on fish diversity was attenuated by the presence of mussel beds and intertidal *Z. noltii* meadows.

2 Study sites

Investigations were carried out at the east coast of the island of Sylt in the western part of the Sylt-Rømø Bight (54°50'–55°10' N, 8°20'–8°40' E), a shallow tidal basin located in the northern Wadden Sea (North Sea). The lagoonal character of the semi-enclosed system was established by the construction of causeways connecting the island of Sylt (1927) and the Danish island of Rømø (1947) with the mainland. Total water exchange of the Sylt-Rømø Bight with the open North Sea takes place through one single tidal inlet of 2 km width between the islands. The maximum velocity of the tidal currents within this tidal inlet is about 1.3 m s^{-1} . From the inlet to the inner bight, the gully branches and current velocities are abated. The tides are semi-diurnal with a mean tidal range of about 2 m. Salinity varies seasonally between 28 and 32 psu. Mean annual water temperature is 9°C with a seasonal variation of about 19°C in summer and 0°C in winter. The bight encloses an area of 404 km^2 of which one third comprises tidal flats. The sediments within the intertidal area of 135 km^2 are composed of sand flats (75 %), muddy sand (10 %) and mud flats (3 %) (Reise & Lackschewitz, 1998). About 12 % (15.6 km^2) of the intertidal area is covered by seagrass beds (Asmus and Asmus 2000), dominated by the dwarf seagrass (*Zostera noltii*). The latter is growing predominantly on upper parts of tidal flats close to the mean high tide line. These seagrass beds are exposed to emersion periods of 4–6 h per tidal cycle (Fig. 1, shaded areas). Mussel beds (*Mytilus edulis*) represent 0.28 % of the tidal basins intertidal area (Gätje & Reise, 1998), whereas subtidal mussel beds are almost absent due to overexploitation. Mussel beds are located in the lower intertidal zone close to the mean low tide line, exposed to emersion periods from 1–3 h during ebb tide (Asmus, 1987; Buschbaum & Saier, 2001). About half of the mussel beds are densely covered by the macroalga *Fucus vesiculosus*. Intertidal sampling sites, including seagrass beds, bare sand flats and mussel beds were influenced by the regime of the same tidal gully. Investigated seagrass beds and adjacent sand flats (publ I,II,III) were situated on the same tidal level were subject to flood waters from NE- direction (Fig. 1, red cycle). For some analyses study sites were extended up to the southern tidal basin (Hörnum Deep) (see publ. III). Mean water depth at high tide was 0.7–1 m. At low tide the investigation areas were emerged for 4–6 hours per tidal cycle. Investigation periods were dominated by south-westerly winds with a mean velocity of $4\text{--}5 \text{ m s}^{-1}$.

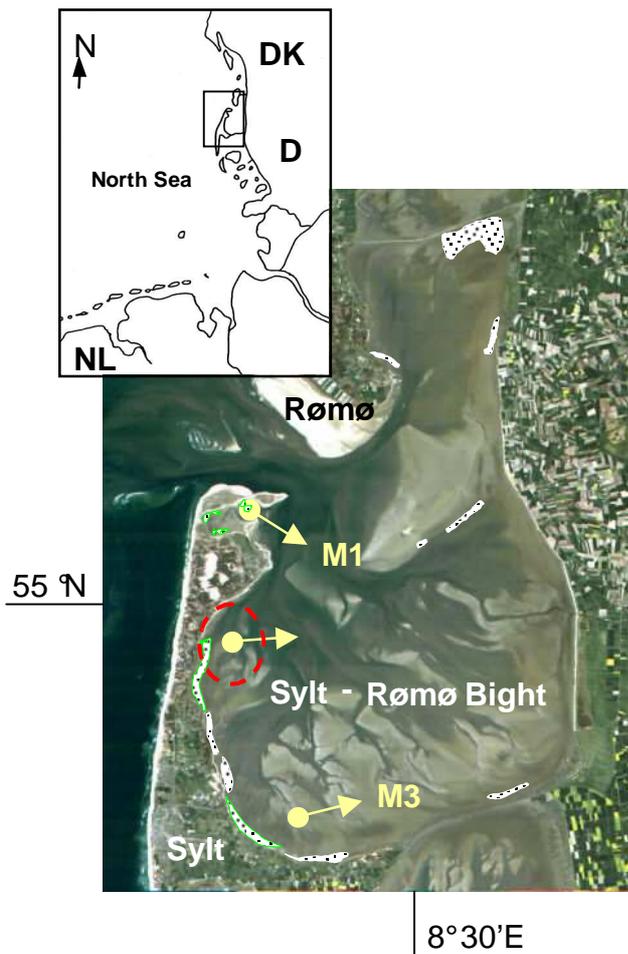


Fig. 1 The Sylt-Rømø Bight located in the northern Wadden Sea. The tidal basin is composed by the islands Sylt (G) and Rømø (DK) connected to the main land by artificial causeways. Study sites included intertidal seagrass beds, bare sand flats and mussel beds located within the same tidal regime (red cycle). Along the east coast of the Island of Sylt additional seagrass beds (green shades) and mussel beds (M) were involved in comparative investigations in respect of fish spawning (pub. III).

3 Materials and Methods

3.1 Seagrass density and-biomass

The shoot density of *Zostera noltii* was determined monthly from May to September during the years 2002 and 2003. Sampling was carried out by using a metal frame of 25 x 25 cm area randomly placed on the seagrass canopy with six replicates. Shoots were counted from a subunit (12.5 cm²) and extrapolated to 1 m² (publ. I, III). Mean number of leaves per plant, mean length and width of leaves were measured of randomly chosen plants ($n= 139$) (publ. III).

Calculations of seagrass above ground biomass (publ. III) were based on box corer sampling (100 cm² area, $n= 6$). Plants were cut off at the substrate surface and washed to remove sediment, adherent fauna and algae. Afterwards plants were dried at 80 °C to constant dry weight (DW) and ashe d at about 500 °C for 14 h. Finally ash-free dry weight (AFDW) was calculated.

3.2 Physical characteristics

Simultaneously to every faunal high tide sampling, surface water temperature was measured on tidal flats at daytime. At ebb tide oxygen content and temperature were measured *in situ* using a Microprocessor Oxymeter (Mod.OXI 196, WTW) within tide pools and the residual seagrass water layer at day and night (publ. I). Parameters were taken for each of the tide pool replicates and also for six randomly chosen areas within the seagrass water layer. Additionally water samples were taken to the laboratory and were analysed for salinity using an AUTOSAL salinometer (Mod. 8400A Guildline Intr.).

3.3 Seine fishing on tidal flats

For quantitative records of fishes on inundated tidal flats (publ. II; III) a 20 m wide and 1.5 m high beach seine was used (mesh size 10 mm). In the centre of the seine a 2 m long bag (mesh size 4 mm) was fixed. The upper fringe of the net was kept at the water surface by buoys and the bottom line contained rounded weights for a better gliding on the ground. The beach seine was lowered by a small boat, while

both wings of the seine were connected with the shore by towropes over a distance of 80 m (Fig.2). After a period of 10 minutes the seine was hauled to the beach by two people and closed after a distance of 60 m by people walking towards each other. The investigation area of 900 m² was determined by the seine opening (15 m) and the haul distance (60 m).



Fig. 2. Beach Seine sampling on inundated tidal flats. The seine was hauled by two people over a total distance of 80 m while the opening (15 m) was closed after 60 m.

In the laboratory fishes were identified to species level, counted, divided into size-classes and preserved by freezing at $-18\text{ }^{\circ}\text{C}$. Two hauls were taken monthly from Mai to September on vegetated and unvegetated tidal flats, respectively, while the distance between both hauls was a 100 m minimum to avoid negative sampling effects.

Sampling on different habitat types was carried out on following days during the same period during flood tide (one hour before high tide to one our afterwards).

3.4 Tidal migration of whiting (*Merlangius merlangus* L.)

The intensity of tidal migration of the whiting (*Merlangius merlangus*) was studied using light traps (Fig. 3), which has been placed, on different tidal levels on vegetated and unvegetated tidal flats (publ. II). The traps consisted of round bow

nets with a diameter of 60 cm and 1.2 m length (6 mm mesh size). One trap was installed at both sampling sites, in the lower intertidal part close to the mean low tide line and one in the upper part close to the mean high tide line. A white, cold, chemical light (8 h OMNIGLOWTM) was placed within each trap at the raising flood, when high tide happened to take place at nighttime. Traps were emptied for fishes in the following ebb tide period, before the tide was entirely out. Traps on bare sand and in seagrass were set at the same time over a period of four days. The numbers of individuals caught with each trap was pooled over the sampling period and given as mean number of individuals per trap and day.



Fig. 3. Light trap consisting of a rounded net body (length: 1.2 m, diameter: 60 cm), equipped with cold, chemical light fixed in the centre.

3.5 Sampling of mobile epibenthos on inundated tidal flats

For quantitative sampling of mobile epibenthos on inundated tidal flats (publ. I, II) a portable drop trap (modified after Pihl Baden and Pihl, 1984) was used monthly during the vegetation period of *Z. noltii* from May to September. Six random replicates were taken at daytime in *Z. noltii* beds and adjacent bare sand flats on succeeding days during the same period at the rising flood (one hour before high tide to one hour afterwards). The drop trap consisted of a 1.20 m high aluminium frame with a sampling area of 0.5 m² and was mounted at the bow of a small boat (Carolina Skiff, 4.16 m x 1.65 m) powered by an outboard motor (Fig. 4). The engine of the boat was turned off and after a short drifting period the boat was stopped by an anchor carefully dropped at the stern. The trap was quickly lowered and got stuck

into the ground by its own weight. The trap was emptied for epifauna using a hand net (1 mm mesh size) attached to a 1.5 m long handle (Fig.2). The frame of the hand net was composed of solid metal suitable to plough through the sediment surface. After six hauls through sediment surface and water column the trap was considered to be empty. Animals were taken to the laboratory and preserved by freezing in sea water at $-18\text{ }^{\circ}\text{C}$. Organisms were identified to species level, counted and divided into size classes. For analyses of secondary production (publ. I) 0-group individuals of dominant species were dried at $80\text{ }^{\circ}\text{C}$ and ashed at about $500\text{ }^{\circ}\text{C}$ for 14 h to estimate ash-free dry weight (AFDW). Secondary production was estimated by the change of individual numbers and weight during two subsequent dates. Secondary production was given per month or over the entire vegetation period of the investigated seagrass bed.



Fig.4 Drop trap sampling for quantities of dominant, mobile epifauna on inundated seagrass beds and adjacent bare sand flats. After lowering the trap (bottom area: 0.5 m^2 ; height: 1.2 m) by a “quick-release”-hook. Animals were removed using a hand net (1 mm mesh size). The trap was considered to be empty for animals after six hauls by the hand net.

3.6 Sampling of mobile epibenthos from ebb tide pools

Young of the year individuals of dominant, mobile epibenthos, including plaice (publ. II), common gobies, brown shrimps and shore crabs (publ. I) were sampled from

natural (publ. II) and artificial (publ. I) tide pools during ebb tide (see below, tide pool experiments). For quantitative sampling a 30 cm high, aluminium frame with a bottom area of 0.5 m² was used (Fig. 5). From a distance of about 2 m the frame was thrown into the centre of the tide pool and got stuck into the sediment. Animals were removed using a hand net of 1 mm mesh size. Afterwards samples were treated as mentioned above in context with the drop trap sampling. On vegetated and unvegetated tidal flats six replicate pools were sampled during the same low tide period.



Fig. 5 Sampling of mobile epibenthos in artificial tide pools. A metal frame (50 cm x 50 cm x 30 cm) was thrown to the centre of the pool and emptied by a hand net (1mm meshsize).

3.7 Tide pool experiments

On bare sand flats soft bottom tide pools represent the only water resource available in the upper intertidal during low tide periods. To evaluate the functional role of water trapping seagrass canopies as alternative ebb tide refuges for mobile epifauna (publ. I), individual densities per m² of common gobies, brown shrimp and shore crabs in tide pools were compared with those found in the residual water layer trapped by seagrass leaves. Capture efficiency, however, might be affected by the degree of faunal accumulation according to tide pool dimensions. To avoid sampling artefacts caused by different tide pool diameter, artificial pools were created with a standardized diameter of 3 m (see publ. I for details). Pools were located in a seagrass bed and an adjacent bare sand flat on the same tidal level within the upper

intertidal zone. Six replicate pools were dug to a depth of about 10 cm and left unaffected over a one-week period. The phenomenon that natural tide pools located in the *Z. noltii* bed are bare of seagrass promoted the possibility to establish artificial pools without recreation of extended seagrass cover (see publ. I, Fig. 3, C). Sampling for epifauna was conducted in the seagrass water layer as well as in the artificial tide pools at day- and night time within the same tidal cycle ($n = 6$).

3.8 *In situ* spawning experiments

To prove the role of seagrass plants as spawning substrate for garfishes (*Belone belone*) alternative structures were offered to the fishes during the main spawning season (publ. III). PVC mats of 0.5 m² area were fitted with *Fucus vesiculosus* (Fig. 6, A) the dominant macro algal species (250 g fresh weight / 0.5 m²). Additional mats were covered with bast fibres (50 g / 0.5 m²) (Fig. 6, B) offering artificial, standardized substrate to figure out whether the type of structure is affecting the habitat choice. Six replicates of each structure were placed on a *Z.noltii* bed and the adjacent sand flat without vegetation. The surrounding area was taken as control and sampled for eggs using a metal frame of 0.5 m² area with 6 replicates. In respect of seasonal spawning peaks, mats and controls were examined for *B. belone* eggs on 4 dates from the beginning of June to the middle of July. To prevent accumulation of eggs from different spawning events, the eggs attached to experimental units were removed at each sampling day.

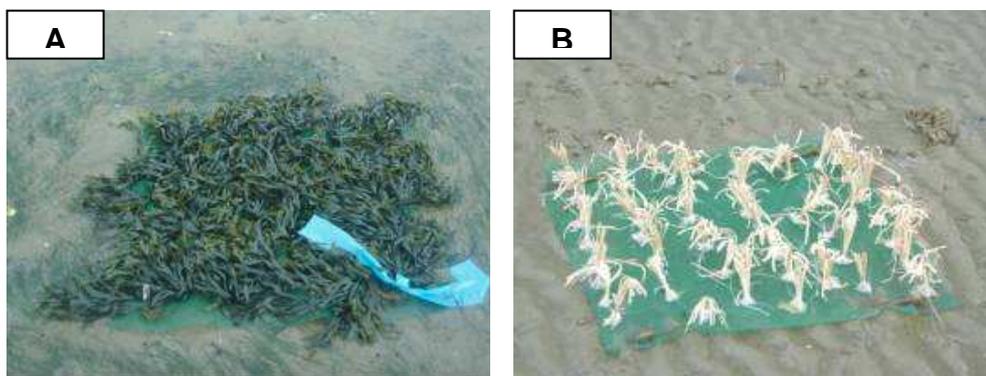


Fig. 6 Experimental units (0.5 m²) offered as spawning substrate to the garfish (*B. belone*) within *Z. noltii* beds and adjacent unvegetated tidal flats. Units were covered by *F. vesiculosus* (A) and bast fibre (B). Additionally the surrounding area was sampled for spawn with a metal frame (0.5 m²) randomly placed on the ground.

An additional spawning experiment was carried out to prove the indirect impact of seagrass cover on the hatching success of garfish larvae from eggs attached to green algae (*Enteromorpha spp.*) (publ. III). Clumps of *Enteromorpha* equipped with eggs were collected from the field. Eggs on each clump were counted and clumps were fixed by yarn obtaining their natural shape. Each clump was tied to an iron pole sticking in the ground. Six replicate algal clumps each on seagrass- and adjacent sand flats were installed in a distance of 1 m from each other. After five days algal clumps were controlled for egg numbers and - condition. The amount of eggs recovered on both habitats was documented and the percentage of damaged eggs was calculated.

3.9 Quantitative evaluations of different Herring (*Clupea harengus* L.) spawning grounds

During a spawning event in April 2002, extended *F. vesiculosus* beds associated with blue mussels (*Mytilus edulis*), single distributed algal aggregations associated with bed groynes and different seagrass beds were controlled for the presence of herring spawn in the intertidal zone along the east coast of the island of Sylt. Presence of spawn on algae and on seagrass (Fig. 7, A, B) was quantitatively compared according to egg numbers per unit plant biomass and according to the dimension of spawning zones. Above ground plant biomass and shoot density of those *Z. noltii* beds covered by herring spawn were compared with seagrass beds where no spawn could be found. Egg numbers were quantified by AFDW extrapolated on the basis of the average weight of a single egg (g AFDW, $n = 15$). The dimensions of spawning grounds were taken with a tape measure and plant biomass was calculated for the whole spawning area.

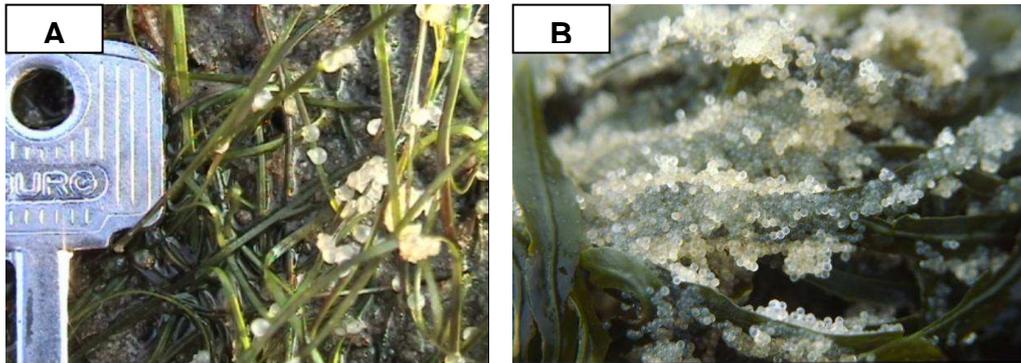


Fig. 7 Herring spawn attached to (A) *Z. noltii* leaves and (B) *F. vesiculosus* thalli during late April 2002.

3.10 Garfish (*Belone belone* L.) activity

The garfish (*B. belone*) is a highly mobile, epipelagic swimmer and thus extremely difficult to record quantitatively by current techniques. Former observations by fishermen describe garfishes tending to jump over flotsam drifting at the water surface. Due to this special behaviour a method was derived to compare garfish activity on different intertidal habitat types during the spawning season from early May to late July (publ.III). During the rising flood, one hour before high tide, a 20 m long rope (\varnothing 0.8 cm synthetic fibre) was fixed upon the water surface within a *Zostera noltii* bed and an adjacent sand flat. On nineteen days the number of adult garfishes jumping over the rope was counted over a 30 minutes time period. For a direct comparison of fish activity each site was sampled at the same time during the tide (for a detailed discription see publ. III). Afterwards data of sampling days were pooled for each site. This method is termed as jumping activity comparison (JUMP).

To estimate the occurrence of garfishes in different seagrass sites along the east coast of the island of Sylt, the JUMP method was used for a garfish mapping (publ. III). Five seagrass beds located in the Sylt-Rømø Bight and in addition one reference seagrass site in the intertidal of the southern basin (Hörnum Deep) were sampled for *B. belone* activity (see publ. III for particular locations). During the main spawning

period in June, 16 potential dates were given, where the tidal cycles allowed sampling at almost the same time of the day. As sampling success depends on weather conditions (strong easterly winds cause high water turbidity leading to reduced visibility) most of the sites were sampled once. Sampling of the first site was repeated at the end of the investigation period to prove seasonal effects.

3.11 Examination of fish spawn on mussel beds

Macroalgae (*Fucus vesiculosus*) associated with mussel beds were assumed to represent a potential alternative spawning substratum to seagrasses, quantitatively relevant in the Sylt-Rømø Bight. They were examined for eggs of garfish and herring within the particular spawning season parallel to investigations conducted in *Z. noltii* beds (results lead to a single conclusion presented in publ. III, general discussion). Intertidal parts of different mussel beds (Fig. 1; M1, M2, M3,) were sampled using a metal frame (0.5 m² area) randomly placed on the algal canopy ($n= 6$). *F. vesiculosus* thalli enclosed by the frame were controlled for eggs.

3.12 Sampling of fishes on mussel beds

An intertidal mussel bed (Fig. 1, M2) was sampled for fish composition monthly from June to November at high tide. Four replicate transects of 250 m length were fished with a 1 m wide dredge net (mesh size 10 mm) with a velocity of about 1.5 knots. On board of the research vessel (FS "MYA") fishes were separated from mussels and algae and stored in sea water. In the laboratory fishes were identified to species level, counted and divided into size classes according to total body length.

3.13 Determination of gobiid fishes (*Pomatoschistus spp*)

Gobies of the genus *Pomatoschistus* are generally difficult to identify to species level. The occurrence of *Pomatoschistus microps* and *Pomatoschistus minutus* occurring in shallow Wadden Sea waters is assumed to differ with tidal level and water depth, therefore one random sample of 100 individuals was supposed to adequately represent a general ratio of species in the intertidal zone.

As the present investigations dealt with young of the year juveniles with a body length less than 20 mm as well as a huge amount of individuals, problems in respect of identification were increased. Therefore individuals caught by drop trap sampling in the upper intertidal zone were kept in a fish tank for three month and fed until they reached a body length of 30 mm or more. Identification of 100 grown gobies showed a 100 % ratio of *P. microps*. According to that, results of gobiid fish density (publ. I) were attributed to *P. microps*.

Quantification of *P. minutus* was limited to Beach Seine samples (publ. II) including a relatively large investigation area (900 m²).

Publications

Publications

This thesis is cumulative including four publications listed below. My contribution to each publication is additionally demonstrated.

Publication I

Patrick Polte, Anja Schanz, Harald Asmus

The contribution of seagrass (*Zostera noltii*) to the nursery function of tidal flats for mobile epibenthos in the Wadden Sea.

Accepted for publication in *Marine Biology*

The basic hypothesis was conceived by all authors. I created the conceptual frame of this study, the sampling design and experimental set up. Sampling gear was to a large amount constructed by my own. I did all the faunal sampling in the field and all data analyses. The second author contributed data of plant densities and seagrass biomass. The third author refined the manuscript written by me and contributed to the orientation to currently important directions of research.

Publication II

Patrick Polte, Harald Asmus

Structuring influence of seagrass beds (*Zostera noltii*) on fishes temporarily visiting the intertidal zone of the northern Wadden Sea.

Submitted to Journal of Sea Research

The primary idea to investigate the influence of seagrass beds on fish distribution was developed by both authors. I developed the conceptual and methodological approach as well as the practical work and wrote the manuscript, which was reviewed by the co-author.

Publication III

Patrick Polte, Harald Asmus

Intertidal seagrass beds as spawning grounds for transient fishes in the Wadden Sea.

Submitted to *Marine Ecological Progress Series*

I developed the idea to investigate the function of intertidal seagrass beds as spawning ground for fishes in the Wadden Sea. I created the conceptual frame of the study; the experimental designs and quantitative sampling strategies as well as the entire field work. I conducted the data analyses and wrote the manuscript, which was constructively revised by the co-author.

Publication IV

Patrick Polte, Patrick Götz, Harald Asmus

Changes of Wadden Sea fish composition 7 decades after substantial losses of seagrass beds (*Zostera marina*) in the shallow subtidal zone.

To reconstruct the consequences of the former seagrass loss on Wadden Sea fish assemblages was a request of all authors. I contributed data of species composition in different intertidal areas including the field sampling required. I created the concept of the study, did the data analyses and wrote the manuscript, reviewed by the third author. The second author contributed the data of fish composition in the subtidal zones. Both co-authors contributed by analysing historical documents.

Publication I

**The contribution of seagrass (*Zostera noltii*) to the nursery
function of tidal flats for mobile epibenthos in the Wadden Sea**

Abstract

In the northern Wadden Sea, 0-group juveniles of dominant, mobile epibenthos were sampled by a portable drop trap on inundated intertidal seagrass beds (*Zostera noltii* Hornem) and adjacent bare sand flats during the summer months of 2002 and 2003. Despite inter-annual variations at the species level abundances of shore crabs *Carcinus maenas* (L.), brown shrimps *Crangon crangon* (L.) and common gobies *Pomatoschistus microps* (Krøyer) were significantly higher on vegetated tidal flats during the main growth period of *Z. noltii*. Accordingly epifaunal production was about three times higher within the seagrass habitat (621 mg AFDW m⁻²) than on bare sand flats (188 mg AFDW m⁻²) in the period from July to September 2003. The occurrence of seagrasses in the upper intertidal zone is supposed to support the nursery function of tidal flats for epibenthic key species of the Wadden Sea food web. As tidal flats are periodically emerged within the semi-diurnal tidal cycle the presence of ebb tide refuges is important for juvenile macrofauna to avoid migration to subtidal zones where predation pressure is increased. We compared different types of residual water resources in respect of their function as ebb tide refuge for the named epifauna species. During the day and night, faunal density was investigated in the water layer remaining between seagrass leaves at ebb tide, and it was compared to that of artificially installed tide pools. Simultaneously the level of dissolved oxygen was measured in both types of ebb tide refuges.

Faunal abundance were consistently higher in the extended residual water layer associated with seagrass coverage than in standardized tide pool units (Ø 3 m) located in vegetated and unvegetated habitats located on similar tidal levels.

The oxygen level dropped drastically at night especially within the seagrass water layer, but had no lowering consequences on individual densities. As a result habitat functions of intertidal *Z. noltii* beds are not limited to high tide inundation, they also provide important ebb tide refuges for juvenile, mobile epibenthos.

Introduction

The shallow waters of the Wadden Sea are generally considered as substantial nurseries contributing to the development of species stocks and faunal composition of the North Sea (Zijlstra 1972; Beukema 1992). The nursery function for fishes and epibenthic macrofauna is widely attributed to habitat diversity in the Wadden Sea, which is mostly discussed with respect to topographical properties, involving shallow water areas, tidal flats and gulleys, and to estuarine salinity gradients (Dankers et al. 1978; Pihl et al. 2002). The role of biogenic habitats is often underestimated, although they represent the majority of the few complex bottom structures within an ecosystem dominated by soft sediments. While the habitat role of seagrass beds received major attention in the neighbouring Baltic Sea region (Boström and Bonsdorff 1997, 2000) and in the Swedish Skagerrak (Pihl and Rosenberg 1982; Pihl Baden and Pihl 1984, Pihl 1986) it is less considered in the Wadden Sea today. This might be due to major seagrass loss during the 1930s when subtidal *Zostera marina* beds became extinct in the Wadden Sea area and failed to recover until today. A second seagrass die off began in the early 1970s, when intertidal *Z. noltii* beds declined drastically in the central- (German) and in the southern (Netherlands) part of the Wadden Sea (Michaelis et al. 1971; den Hartog and Polderman 1975; de Jonge and de Jong 1992; Reise 1994). Only little attention is paid to the ecological functions of the remaining intertidal *Z. noltii* beds in the northern Wadden Sea (Germany / Denmark) (Reise 1985; Schanz et al. 2000; Asmus and Asmus 2000) although they showed less fluctuation during the last decades representing about 90 % of seagrass stocks of the entire Wadden Sea today (Reise 2003).

Whereas subtidal seagrass beds are generally known to act as important refuges for several fishes and invertebrates increasing faunal diversity and species richness worldwide (e.g. Pihl Baden and Pihl 1984; Orth et al. 1984; Heck et al. 1995; Connolly 1994a; Edgar and Shaw 1995; Boström and Bonsdorff 1997), the faunal composition presently described for *Z. noltii* beds in the Wadden Sea does not differ from that found on unvegetated tidal flats (den Hartog, 1983). However, previous studies showed that presence of intertidal seagrasses promotes meiofaunal abundance (Hellwig-Armonies 1988) and potentially increases food availability for endo- and epibenthic organisms by acting as a sink for organic matter (Asmus and Asmus 2000). Due to grazing by water fowl (Nacken and Reise 2000; Ganter 2000)

and harsh weather conditions during winter, the occurrence of dense *Z. noltii* beds in the Wadden Sea is limited to the summer month (Schanz and Asmus 2003). Therefore temporarily vegetated tidal flats change their specific habitat functions within the course of the year. Simultaneously, with the major growth period of seagrass plants from June to October juvenile stages of brown shrimps (*Crangon crangon*), common gobies (*Pomatoschistus microps*) and shore crabs (*Carcinus maenas*) intensively use tidal flats as refuges avoiding predation pressure in the subtidal zone (Klein Breteler 1976a; Kuipers and Dapper 1984; Del Norte-Campos and Temming 1998; Temming and Damm 2002). High densities of juvenile brown shrimps can be found additionally in small tide pools and puddles (Berghahn 1983; Hinz 1989) outlasting the period of tidal emersion. All above-mentioned resources of residual water might allow organisms to prevent tidal migration and to remain in the intertidal zone during the ebb tide. Additionally juvenile brown shrimps and shore crabs are able to outlast ebb tide by burying into the ground and are not considered to perform extensive tidal migrations (Klein Breteler 1976b; Beukema 1992).

Dense *Z. noltii* beds may provide additional ebb tide refuges by retaining water on the tidal flats trapped between the leaves. However decreasing nocturnal oxygen contents due to plant respiration might induce unsuitable conditions for epifaunal organisms.

The aim of this study is to demonstrate the impact of vegetated tidal flats on the individual density of dominant epibenthic species, which are considered as most important within the food webs of the Wadden Sea (Kuipers et al. 1981; Asmus and Asmus 2000). Drop trap sampling together with field experiments involving artificially installed tide pools, might prove whether the existence of intertidal seagrass contribute to the nursery function of the intertidal zone.

The present investigation bases on the following hypotheses:

- 1) The presence of seagrass beds in the intertidal area promote the stock and secondary production of dominant, 0-group epibenthos during the vegetation period.
- 2) *Z. noltii* habitats provide extended ebb tide refuges for juvenile mobile epibenthos.

Materials and methods

Study sites

Investigations were conducted in the Sylt-Rømø Bight located in the northern part of the Wadden Sea (North Sea) (Fig. 1). A shallow tidal basin is composed by the islands Sylt (Germany) and Rømø (Denmark) almost enclosed by artificial causeways connecting the islands with the main land. The Sylt-Rømø Bight (54°50' - 55°10' N, 8°20' - 8°40' E) is connected with the open North Sea via one single tidal inlet of 2 km width. Tidal flats represent 1/3 of the 404 km² area of the bight and about 12 % of intertidal area is covered by seagrass beds. The mean range of semi-diurnal tides is about 2 m. Mean water temperatures varies seasonally between 0°C and 19°C. During the investigation period in July and August 2003 maximum temperatures of 27°C were measured in the upper intertidal zone. Salinity is also subjected to seasonal variations between 28 and 32. Seagrass stocks are dominated by *Zostera noltii* and are restricted to intertidal areas. Due to winter influences (e.g. storms and ice scouring) and grazing by ducks and brent geese (Ganter 2000; Nacken and Reise 2000) presence of above ground parts of seagrasses is restricted to the vegetation period from May to October.

Vegetated and unvegetated sampling sites were located within the same tidal level on the intertidal area at the east coast of the island Sylt (Fig. 1).

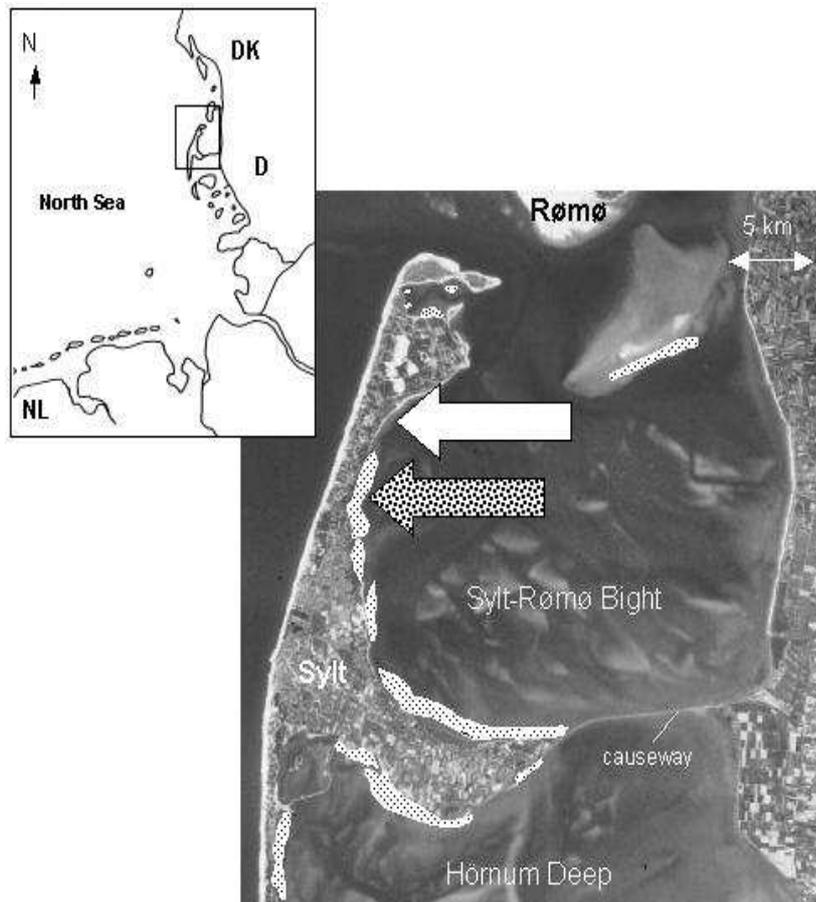


Fig.1 Rømø Bight (54°50' - 55°10' N, 8°20' - 8°40' E) and locations of intertidal seagrass beds along the east coast of the island of Sylt (spotted areas). Arrows indicates unvegetated (blank) and vegetated (shaded) sampling sites.

Seagrass density

Shoot density of *Zostera noltii* was determined monthly from May to September 2003 (except June) in six replicate test areas. Sampling was carried out using a metal frame of 25 x 25 cm randomly placed on the seagrass canopy. Shoots were counted from subunits (156 cm²) and density was extrapolated to 1 m².

Sampling of mobile epibenthos

For quantitative sampling of mobile epibenthos on inundated tidal flats a portable drop trap (modified after Pihl Baden and Pihl 1984) was used at daytime during the main vegetation period of *Z. noltii* from July to September 2002 and during the whole vegetation period from May to September 2003. Six random replicates were taken monthly in *Z. noltii* beds and adjacent bare sand flats on following days during slack

water (one hour before high tide to one hour afterwards). The drop trap consisted of a 1.20 m high aluminium frame with a sampling area of 0.5 m² and was mounted at the bow of a small boat (4.16 m x 1.65 m) powered by an outboard motor. For sampling the engine of the boat was turned off and after a short drifting period the boat was stopped by an anchor carefully dropped at the stern. The trap was quickly lowered and stuck into the ground by its own weight. The trap was emptied for epifauna using a hand net (1 mm mesh size) attached to a 1.5 m long handle (Fig.2). The frame of the hand net was composed of solid metal suitable to plough through the sediment surface. Animals were taken to the laboratory and preserved by freezing in sea water. Organisms were determined to species level (isopods were determined to genus), counted and divided into size classes of 5 - 10mm steps respectively due to total body length (fishes and shrimps) or carapace width (crabs). Of each sample the amount of 0-group individuals of dominant species were separately dried at 80 °C and ashed at about 500 °C for 14 h to estimate biomass in ash-free dry weight (AFDW).



Fig. 2 Drop trap construction mounted on the bow of a small boat. Animals were removed using a hand net (1 mm mesh size) after lowering the trap by a quick release

Secondary Production

Secondary Production (P) of dominant 0-group individuals were estimated using the increment method (Crisp 1984). It was expressed in mg AFDW and was calculated for the period from July to September using the following formula:

$$P = \sum_{t=0}^{t=n} \frac{N_{t+1} + N_t}{2} \Delta \bar{W}$$

where ($\Delta \bar{W}$) means the mean individual weight and (N) the mean population density between to successive samplings (t , $t+1$) estimated by using the high tide abundances.

Production intervals from July to August and from August to September were pooled to demonstrate habitat specific differences of faunal production during the main seagrass vegetation period.

Artificial tide pools

The following field experiment was done in August 2002 to evaluate the functional role of seagrass canopies in comparison with other ebb tide refuges for mobile epifauna: Soft bottom tide pools are the only water resource available in the upper intertidal during low tide period. Due to strong variations of natural tide pool dimensions capture efficiency is affected by the degree of faunal accumulation. To avoid sampling artefacts due to different size of tide pools artificial pools were created with a standardized diameter of 3 m, (Fig. 3 A, B). Pools were located within the upper intertidal zone in a seagrass bed as well as on an adjacent unvegetated sand flat on the same tidal level. Six replicate pools were dug to a depth of about 10 cm and left unaffected during one week. Natural tide pools located in the *Z. noltii* bed are bare of seagrass and thus artificial pools were designed without seagrass cover (Fig. 3, B, C). Sampling for epifauna was conducted in the seagrass water layer and the artificial tide pools at day-and night time during low tide within the same tidal cycle ($n = 6$). For quantitative sampling an aluminium throw trap with a bottom area of 0.5 m² and walls 30 cm high, was used. From a distance of about 2 m the trap

was thrown into the centre of the tide pool respectively on the seagrass canopy and became stuck into the sediment. Animals were removed by using a hand net of 1 mm mesh size. Samples were treated as mentioned above (drop trap sampling).

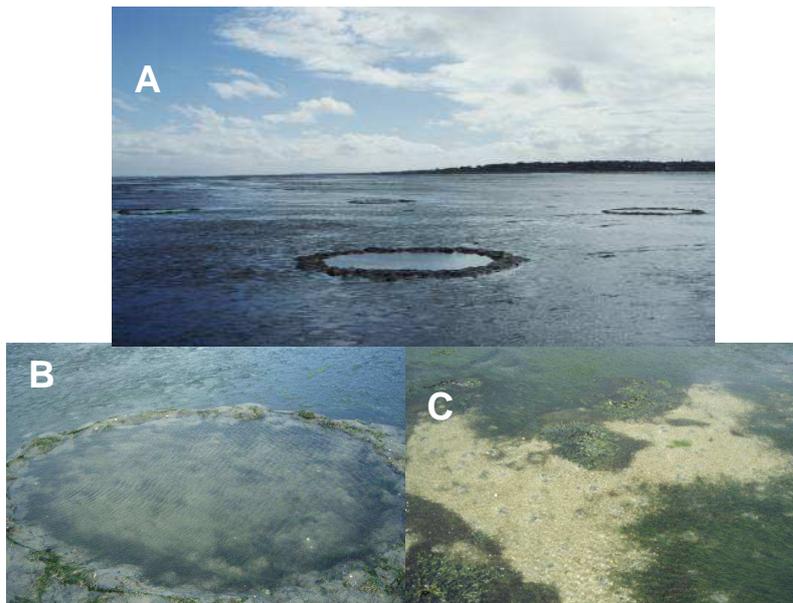


Fig.3 Artificial tide pools (A) installed within the canopy of an intertidal *Z. noltii* bed. The pools were left unaffected over a one-week period. Experimental tide pool unit (B) (\varnothing 3 m) and natural tide pool (C) within the *Z. noltii* meadow at low tide. Natural tide pools are similarly bare of seagrass cover.

Physical parameters

Simultaneously to faunal sampling physical parameters were measured within artificial tide pools and canopy water layer at low tide during day and night. Water samples were taken to the laboratory and analysed for salinity using AUTOSAL salinometer (Mod. 8400A Guildline Intr.). Oxygen content and temperature were measured *in situ* by Microprocessor Oxymeter (OXI 196, WTW). Salinity samples, temperature and oxygen measurements were taken for each of the six tide pool replicates and six randomly chosen areas within the canopy water layer.

Data analysis

Abundances of dominant species were calculated to 1 m² and presented as arithmetic mean \pm standard error (SE). Total abundances were calculated as sum of species abundances within each replicate. For annual comparison of faunal distribution high tide abundances of July and August were pooled. Results were statistically analysed by means of 1-way analysis of variance (ANOVA) additionally followed by a Tukey's honest significance (HSD) multiple comparison test (tide pool experiment). Data were tested for homoscedasticity of variances using Cochran's test and transformed by (log + 1) if necessary to fulfil the requirements of ANOVA. Statistical significance was assumed if the *p*-value was < 0.05. Statistical analyses were conducted using STATISTICA (StatSoft, Tulsa, Oklahoma).

Results

Habitat characteristics

The shoot density of *Zostera noltii* was 1088 m⁻² in May and increased during the summer 2003 up to 12000 shoots m⁻² in the main vegetation period in August (Table 1). Within the semi-diurnal tidal cycle investigated intertidal areas were emerged for 4-6 hours. While unvegetated tidal flats were completely exposed to air except of several sinks and soft bottom tide pools, *Z. noltii* beds retained water between the leaves forming extended water resources during low tide periods. The mean depth of these water layers was 6.2 cm (SE \pm 0.12, *n* = 6). Tidal phase and predominating wind directions influence the extension of water trapping seagrass area.

Table 1 Mean shoot density m⁻² (\pm SE) of *Z. noltii* during the vegetation period 2003.

season 2003	number of shoots m ⁻² (<i>n</i> = 6)
May	1088 (\pm 66)
Jun	no data
Jul	10944 (\pm 1395)
Aug	12000 (\pm 1145)
Sep	6261 (\pm 142)

Epifauna species composition

The mobile epibenthic fauna on investigated tidal flats was dominated by shore crabs (*Carcinus maenas*), brown shrimps (*Crangon crangon*), gobiid fish (*Pomatoschistus microps*) and isopods (*Idotea spp.*). Isopods were the only group restricted to vegetated areas whereas all decapod crustaceans and the gobiids were common in *Z. noltii* beds as well as on and bare sand flats (Table 2). Isopods were composed of the species *I. balthica* and *I. chelipes*. The mean abundance of both *Idotea spp.* found in the seagrass habitat was 64.3 (SE \pm 6.4) individuals m⁻² in July 2003. The following results will focus on the quantitative distribution of species principally found on both vegetated and unvegetated tidal flats.

Table 2 Dominant species of mobile epibenthos on *Z. noltii* flats and adjacent bare sand flats. Only the occurrence of *Idotea spp.* was limited to the seagrass bed.

taxon	habitat type	
	sand	seagrass
<i>Carcinus maenas</i>	+	+
<i>Crangon crangon</i>	+	+
<i>Pomatoschistus microps</i>	+	+
<i>Idotea spp.</i>	-	+

High tide abundance in different intertidal habitats

The distribution of most dominant epifaunal species was in general not limited to special habitat types. Drop trap sampling during the summer month of 2003 showed highest epifaunal abundances on the tidal flats in the end of June during the main recruitment period. In June only *C. maenas* showed a significantly higher abundance in the seagrass bed whereas abundances of *C. crangon* and *P. microps* showed no clear differences due to presence of seagrass (Fig. 4). Together with a decline of epifaunal abundances and increase of seagrass density from June to July (Table 1) the distribution of the three species shifted to vegetated tidal flats significantly (Table 3), and in the case of *P. microps* and *C. maenas* this ratio remained until the end of

Z. noltii vegetation period. The distribution of *C. crangon* showed a similar trend (Fig.4), but it was not significant in August and September (Table 3).

To show if distribution patterns of species are subordinated to annual variations, the years 2002 and 2003 were compared using pooled abundances of July and August. During the main vegetation period of two successive years a similar distribution of epifaunal abundances was found to be consistently higher on the seagrass site (Fig. 5). *Carcinus maenas* (2002: $p < 0.001$, $df = 1$, $F = 384.5$; 2003: $p < 0.001$, $df = 1$, $F = 24.4$) and *Crangon crangon* (2002: $p < 0.05$, $df = 1$, $F = 4.8$; 2003: $p < 0.01$, $df = 1$, $F = 14.1$) showed significantly higher abundances in association with seagrass cover, whereas individual densities did not vary between the years to a considerable amount. Despite huge inter-annual differences ($p < 0.05$, $df = 1$, $F = 6.6$) in the abundance of gobiids a trend for a higher individual density in the seagrass bed remained significant (2002: $p < 0.05$, $df = 1$, $F = 6.7$; 2003: $p < 0.01$, $df = 1$, $F = 15.9$).

Table 3 One-way ANOVA of mean (\pm SE) abundance of dominant epifaunal species in seagrass and bare sand habitats during *Z. noltii* vegetation period 2003. Significance level (p) set at 0,05. Degree of freedom (df) is 1 for each month.

		mean (\pm SE)		<i>F</i>	<i>P</i>
		seagrass	sand		
<i>C. maenas</i>	May	0	0	0	0
	June	711,3 (\pm 137)	46,3 (\pm 8,3)	73.88	< 0,001
	July	184,3 (\pm 36)	36,3 (\pm 11,3)	13.59	< 0,01
	August	99,3 (\pm 18,3)	7,7 (\pm 3)	20.84	0.001
	September	79,7 (\pm 20)	1,3 (\pm 0,7)	43.22	< 0,001
<i>C. crangon</i>	May	67,7 (\pm 14,6)	8,7 (\pm 3,6)	15.28	< 0,01
	June	181,0 (\pm 21,6)	256,0 (\pm 30,8)	3.00	0.11
	July	115,0 (\pm 8,7)	25,0 (\pm 8,2)	16.72	< 0,01
	August	58,0 (\pm 14,2)	26,3 (\pm 17,3)	4.92	0.05
	September	43,0 (\pm 23,5)	10,3 (\pm 3,9)	1.49	0.25
<i>P. microps</i>	May	0	0	0	0
	June	23,3 (\pm 7,8)	18,3 (\pm 3,5)	0.08	0.78
	July	10,7 (\pm 2,8)	2,0 (\pm 0,5)	16.41	< 0,01
	August	5,0 (\pm 1)	2,0 (\pm 0,9)	5.28	< 0,05
	September	2,3 (\pm 0,6)	0,3 (\pm 0,3)	8.86	< 0,05

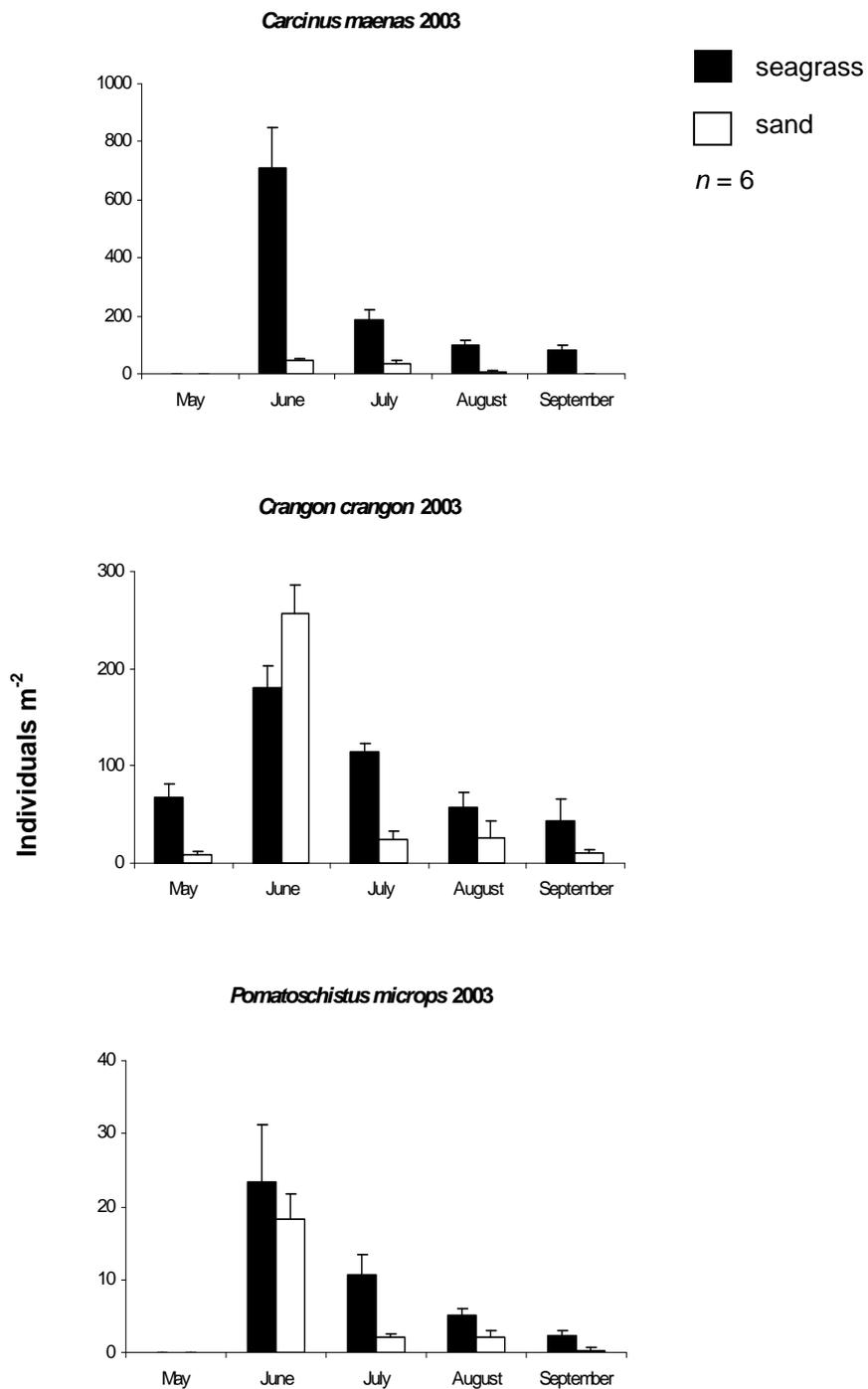


Fig. 4 Monthly abundances of dominant epifaunal species on vegetated and unvegetated tidal flats during *Z. noltii* vegetation period in 2003. After post larval recruitment in late June all species reached a higher abundance within the seagrass habitat.

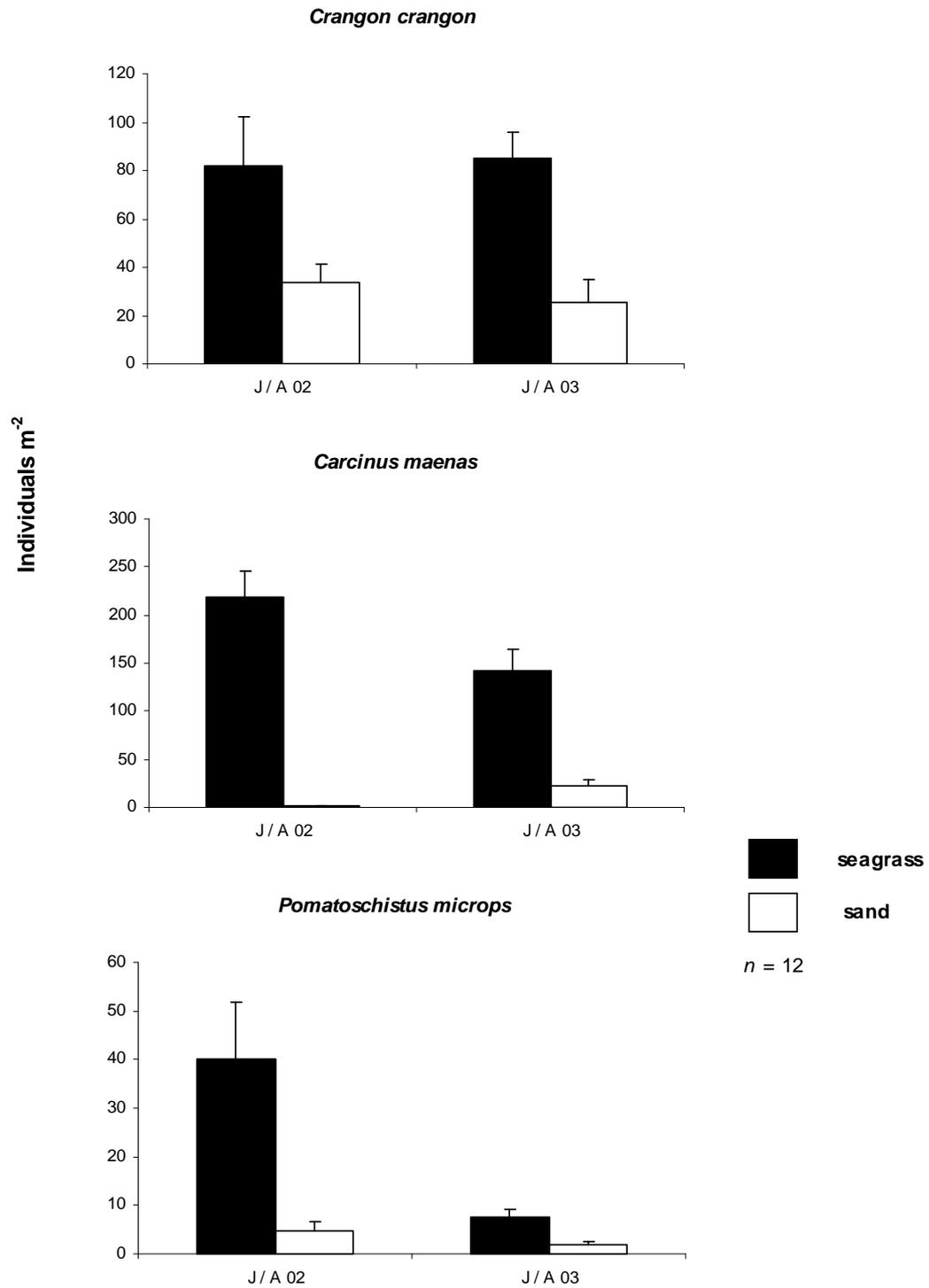


Fig. 5 Epifaunal abundance (pooled data July and August) compared between 2002 and 2003. In both successive years species showed significantly ($p < 0.05$) higher individual densities within the seagrass bed. Only gobiid (*P. microps*) abundances showed significant differences between the years.

Size class distribution

Separation into size classes revealed that the majority of individuals captured in the upper intertidal zone belong to the 0-group. In general, higher percentages of larger individuals were found on tidal flats without vegetation cover (Fig. 6). Due to a large amount of instar stages in June, most individuals of *C. maenas* were <5 mm (carapace width) in vegetated and unvegetated habitats. While the 5 mm cohort consistently represented the highest percentage in the seagrass bed during the whole vegetation period, size distribution of shore crabs shifted to larger individuals on tidal flats without seagrass cover.

Most *C. crangon* recruits captured on tidal flats in May and June were of less than 10 mm in body length. Percentages of individuals of the <15 mm cohort increased in both habitats from July to September, whereas the occurrence of the <20 mm cohort was more pronounced on sand flats.

Recruitment of *P. microps* took place in June, when the percentage of the <10 mm cohort was higher on tidal flats without vegetation while individuals caught in the *Z. noltii* bed were larger. During July and August, the majority of individuals were grouped into the <20 mm cohort in both habitats. At the end of the investigation period in September, most of the gobiid fish caught in vegetated and unvegetated tidal flats were in the cohort <30 mm. Smaller individuals were limited to the seagrass bed.

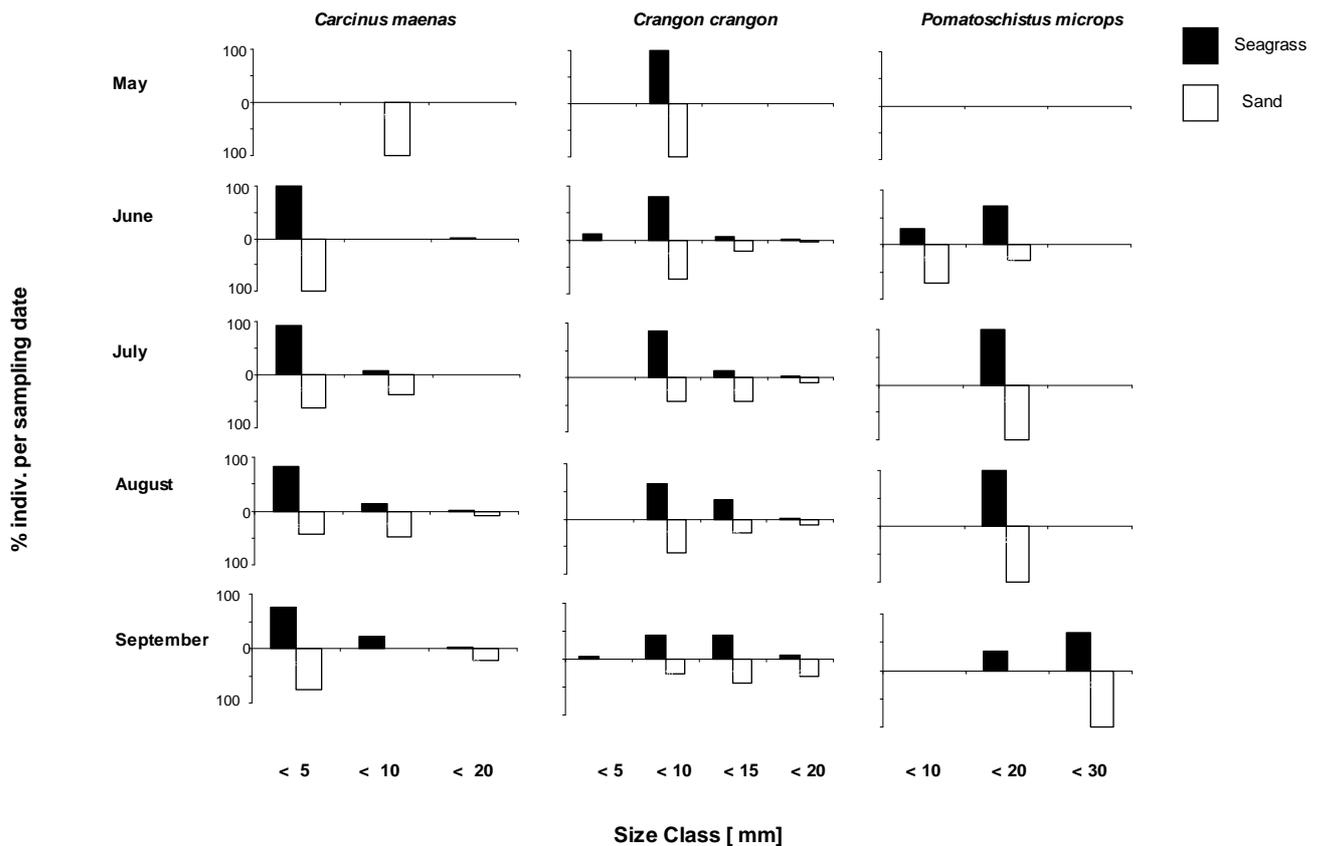


Fig. 6 Distribution of epifaunal size classes in vegetated (black bars) and unvegetated (white bars) tidal flats during summer 2003. Monthly amount of individuals caught was set at 100 % for each habitat. Size classes (mm) are due to carapace width at *C. maenas* respectively total body length at *C. crangon* and *P. microps*.

Production

Epifaunal production from July to September showed a significantly difference due to habitat type (Table 4). Crustaceans as well as gobiid fishes reached a higher production within the seagrass meadow than on adjacent bare sediments (Fig. 7). The total amount of the average production of the three species during the main vegetation period was 621 (SE \pm 30.1) mg AFDW m⁻² on seagrass covered tidal flats and 188 (SE \pm 21.2) mg AFDW m⁻² on sand flats. Accordingly the amount of total production in the seagrass habitat was about three times higher than that on bare sands (Fig. 7).

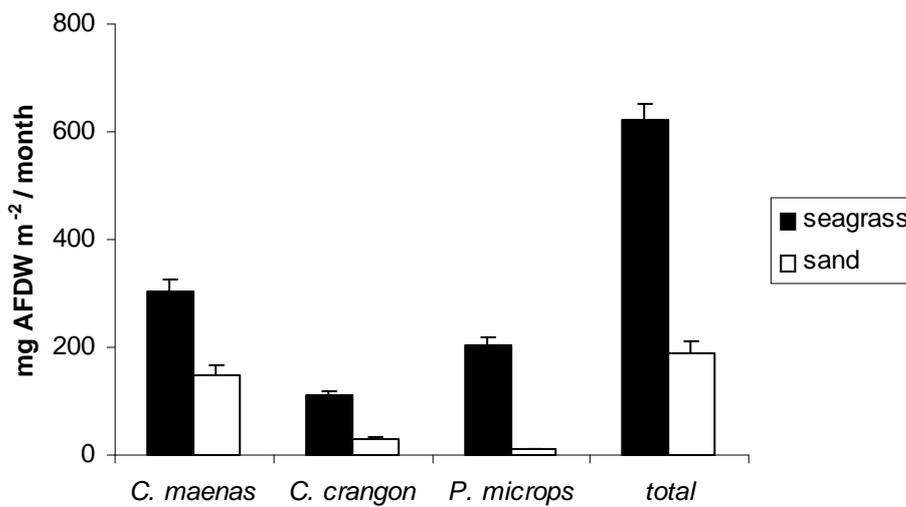


Fig. 7 Average production m^{-2} of dominant epibenthos by pooled time intervals from July to September 2003. All species reached a significantly higher production on vegetated tidal flats. As a result the total production of the three species was three times higher in association with seagrass cover than on bare sand flats.

Table 4 Significance level (p) of one - way ANOVA between epifaunal production on vegetated and unvegetated tidal flats. Pooled intervals from July to September 2003 showed a significantly higher production of each species within the seagrass habitat.

	<i>df</i>	<i>MS - effect</i>	<i>F</i>	<i>p</i>
<i>Carcinus maenas</i> ^a	1	2.0	5.9	< 0.05
<i>Crangon crangon</i>	1	20857.9	18.5	< 0.01
<i>Pomatoschistus microps</i> ^a	1	31.7	38.2	< 0.01
total ^a	1	5.4	17.8	< 0.01

^aLogarithmic transformation

Total epifaunal abundance within *Z. noltii* beds during flood and ebb tide

The mean total abundances composed of individual numbers of *C. crangon*, *C. maenas* and *P. microps* showed that 67 (SE \pm 3.0) individuals m^{-2} remained in the seagrass bed at low tide (Fig. 8). With a mean of 167 (SE \pm 7.2) individuals m^{-2} the

high tide abundance was found significantly higher at a factor of about 2.5 (ANOVA, $p < 0.001$, $df = 1$, $F = 48.41$).

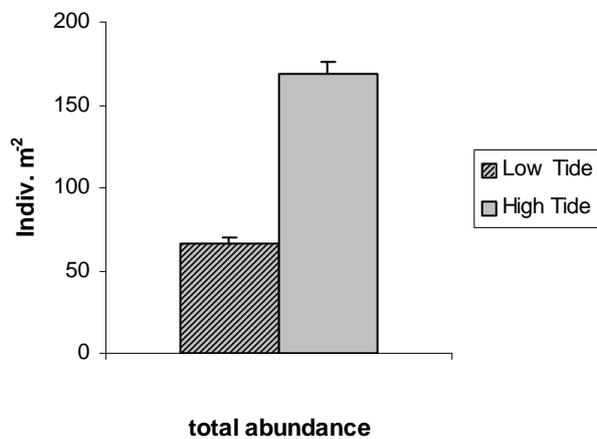


Fig. 8 Total abundance of shore crabs, brown shrimps and common gobies within intertidal seagrass beds subjected to tidal level. Although faunal density was clearly higher at high tide a considerable amount of individuals remained in the seagrass canopy when the tide is out.

Tide pool experiment

Most physical parameters within artificial tide pools and canopy water layer (CWL) were subjected to strong diurnal variations. With 8.5 ($SE \pm 0.06$) mg / l the mean oxygen level was high during day time on all investigation areas (Fig. 9) but reached a maximum of 9.7 ($SE \pm 0.2$) mg / l within the CWL. At night the oxygen content in the CWL dropped drastically to 1.5 ($SE \pm 0.04$) mg / l . The mean oxygen amount measured in the seagrass pools at night was 3.9 ($SE \pm 0.1$) mg / l and in the sand pools respectively 5.0 ($SE \pm 0.04$) mg / l . In August, water temperatures in the tide pools ($n = 6$) varied from $24^{\circ}C$ (± 0.01) in both habitats during the day to $19^{\circ}C$ on sand ($SE \pm 0.2$) and $17^{\circ}C$ on seagrass ($SE \pm 0.02$) in the night. Within the CWL ($n = 6$) temperatures varied from $24.5^{\circ}C$ (± 0.04) at day time low tide to $16^{\circ}C$ (± 0.02) at night. Salinity showed a constant mean amount of 28.5 (± 0.03 , $n = 18$).

Individuals of mobile epibenthos were consistently more frequent in the CWL than in artificial tide pools located in both habitat types (Fig. 9). ANOVA between abundances per m^2 of experimentally installed tide pools and the CWL showed significant effects during low tide period during the day ($p < 0.01$, $df = 2$, $F = 10$) and night ($p < 0.001$, $df = 2$, $F = 28$). While the utilization of tide pools by the epifauna in

vegetated and unvegetated habitats was influenced by diurnal variations, abundances were higher and more stable in the CWL (Tukey's test, $p < 0.05$). During the day time abundances did not differ between sand pools and seagrass pools (Tukey's test, $p = 0.4$) whereas at night faunal density was significantly higher in seagrass pools (Tukey's test, $p < 0.01$).

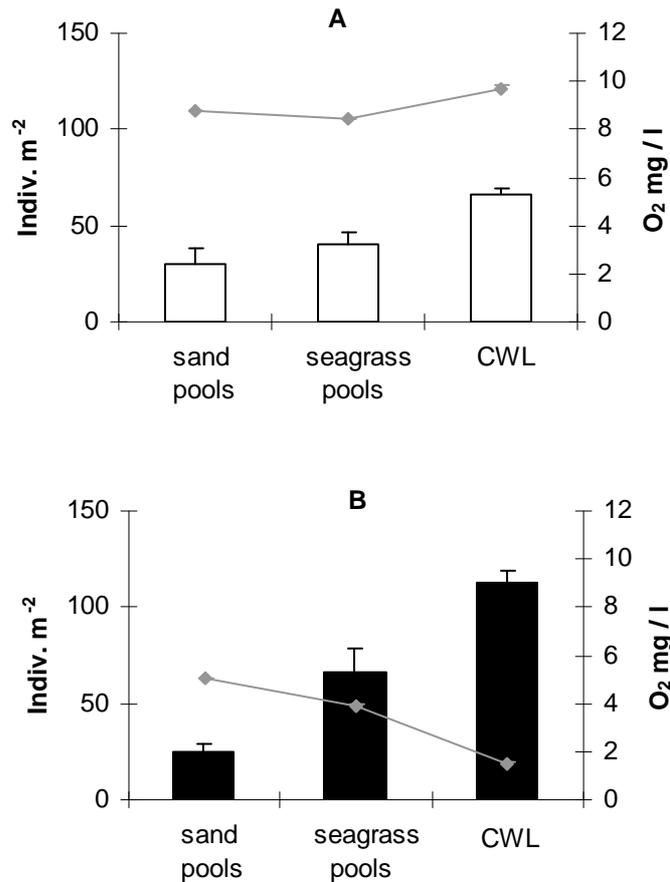


Fig. 9 Total density of mobile epifauna and level of dissolved oxygen ($n = 6$) within artificial tide pools on vegetated and unvegetated sites in comparison to the extended canopy water layer (CWL) at day (A) and night (B). At night oxygen level dropped drastically especially in the CWL, but faunal density remained highest there.

Discussion

Due to rapid changes of tidal water levels and subsequent fluxes in faunal abundance, in intertidal areas, the drop trap sampling (Pihl and Rosenberg 1982; Pihl Baden and Pihl 1984) is considered to represent the most effective method for quantitative, replicated captures of mobile epibenthos. As sampling periods during

high tide are relatively short in the upper intertidal zone, drop trap sampling allows a number of replicates to be taken in a defined time interval during the tidal cycle.

A number of studies dealing with distribution of mobile fauna dependent on certain habitats describe important diel variability of abundances and increased faunal activity during the night (Summerson and Peterson, 1984; Sogard and Able, 1994; Mattila et al., 1999).

Previous investigations at the sampling site, showed no significant diurnal variations of mobile epifaunal abundances (Polte et al. in press) at a certain tidal stage. Thus limitation of sampling during flood during the day is not considered to influence the general distribution patterns of dominant species in different intertidal habitat types.

Worldwide subtidal seagrass beds are considered to represent important nursery areas for fishes and epibenthos. These areas provide shelter from predation by increased habitat complexity (e.g. Virnstein et al. 1983; Orth et al. 1984; Hindell et al. 2000). As shallow water zones generally represent important refuges to avoid predation pressure by piscivorous fishes (Ruiz et al. 1993, Paterson and Whitfield 2000; Linehan et al. 2001), and additionally might promote faster growth due to higher temperatures (Gibson et al. 2002), the nursery function of vegetation might be superimposed by the distribution of juveniles along vertical depth gradients in shallow nearshore areas (Hyndes et al. 1996; Jenkins et al. 1997).

The intertidal areas of the Wadden Sea as a whole are generally known to act as nursery area for several species of crustaceans and fishes (Zijlstra 1972; Van der Veer et al. 2001). The role of single habitat types such as seagrass beds is difficult to define in this respect, especially if common North Sea generalists dominate species composition. Their occurrence is obviously not limited to certain habitats.

Except for isopods (*Idotea spp.*), 0-group individuals of dominant mobile epibenthos were common on tidal flats regardless of the presence of vegetation. Drop trap sampling of proximate seagrass and sand flats however indicates, that a preference for vegetated habitats is pronounced in all species, as the presence of juveniles in the intertidal zone is matched with the main vegetation period of *Z. noltii*. In June, before the seagrass beds reach their maximum density (Schanz and Asmus 2003) habitat preference of brown shrimps and gobiid fishes was not pronounced. This corresponds to previous studies where preference of mobile epifauna for seagrass beds depended on plant density, due to hydrodynamic exposure (Polte et al., in

press). In the main vegetation period of *Z. noltii* during July and August, abundances of dominant species were significantly higher within seagrass beds in two following years, although clear inter-annual differences in individual numbers existed. The reasons for a preference of vegetated tidal flats by 0-group epifauna may vary between species.

Settling of shore crabs occurs in several colonisation peaks from May to August depending on the severity of the preceding winter (Strasser and Guenther 2001). Thiel and Darnedde (1994) showed that *C. maenas* recruits accumulating in mussel clumps, diffusely spread in the upper intertidal zone, did not reveal higher densities than the surrounding seagrass bed. These findings underline the habitat attraction of seagrass structure for the first benthic stages of the shore crab. Caging experiments conducted by Moksnes (2002) at the Swedish west coast (Skagerrak) did not show a limiting effect of certain bottom structures on predation pressure on *C. maenas* post larvae but reveal a direct influence of seagrass plants and mussels on the settlement processes of megalopae stages actively avoiding unstructured bare sand areas during settling. Accordingly, abundances of shore crabs in the present study were significantly higher in the seagrass bed than on sand flats within the main settling period in the end of June. This distribution pattern, characterized by the dominance of individuals smaller than 5 mm, remained the same during the whole vegetation period until September. The percentage of larger specimens was higher on unvegetated sediments. In general, this size class distribution was maintained by all investigated species. As they all are important predators significantly influencing tidal flat benthic communities (Mattila et al. 1990; Beukema 1992; Strasser 2002; Baird et al. 2004), the shift of habitat preference is supposed to be due to predation success of older juveniles. Especially *Crangon crangon* is classified as a typical sand bottom inhabitant without strong linkage to bottom vegetation (Pihl 1986; Boström and Bonsdorff 1997). Also Isaksson and Pihl (1992) found a negative correlation between *Crangon* abundance and seagrass density. In contrast, the present results showed higher abundances of brown shrimp on vegetated tidal flats during the main vegetation period of *Z. noltii* in 2002 and 2003 (Fig. 5). Benthic post larvae of brown shrimps and common gobies invade the tidal flats from offshore areas. The presence of seagrass may contribute to the nursery function of tidal flats for 0-group brown shrimps described by various authors, while larger individuals are limited to subtidal

sand bottoms (Beukema 1992; Cattrijsse et al. 1997). Vertical size class distribution as well as non-significant *Crangon* abundances between vegetated and unvegetated areas in September indicates, that preference for bare sand habitats applies at later juvenile stages.

Albeit habitat preference shifts with increasing size class, production of all species were significantly higher within the seagrass bed compared to sand flats during the summer 2003. A higher secondary production in seagrass beds compared to sand flats was also detected for benthic macrofauna other than mobile epibenthos (Asmus and Asmus 2000) at the study site, although its contribution to the productivity of the total system was found to be low. In other mainly shallow subtidal systems seagrass beds show a major contribution to the secondary production (Pihl Baden and Pihl 1984; Fredette et al. 1990; Valentine and Heck 1993; Heck et al. 1995), in particular when the mobile epibenthic fauna is included (Edgar and Robertson 1992; Connolly 1994, 1997). As the amount of secondary production is a suitable criterion to identify nurseries (Heck et al. 2003), the results of this study indicate that including mobile epifauna, the contribution also of intertidal seagrass beds to the secondary production of the total ecosystem may be strengthened. A higher secondary production in the *Z. noltii* beds, mainly formed by 0-group individuals, underlines the particular importance of seagrass beds within the nursery area of the intertidal zone as habitats for juvenile epibenthos.

The role of *Z. noltii* beds as ebb tide refuge

Although the total abundance of mobile epibenthos within the seagrass bed was significantly higher at high tide (Fig. 8), a considerably number of individuals were found in the residual water layer retained by the seagrass canopy during ebb tide. As tidally migration to subtidal areas might expose juvenile epifauna to predation (Gibson 1973; Kneib 1987; Gibson et al. 2002; Amara and Paul 2003). Such water resources in addition to tide pools are alternatives allowing a permanent residence in the intertidal zone. However, van der Veer and Bergman (1986) showed increased nocturnal tidal migration of 0-group plaice towards tidal gullies due to physical stress caused by oxygen deficiency within remaining water films in the intertidal zone. In this context the results of quantitative comparisons of epifaunal abundance between the canopy water layer (CWL) and artificially installed tide pools on vegetated and

unvegetated tidal flats rather surprising showed a significantly higher faunal density within the CWL during low tide period at both, day - and night although oxygen level drops drastically in the CWL during ebb tide at night. In fact, at night epifaunal abundance within tide pools in different habitats and the CWL was reciprocally proportional to the oxygen content in the particular environment (Fig. 9). The decreasing oxygen content is probably attributed to plant respiration because during ebb tide at day no correlation between faunal abundance and oxygen content at the particular locations could be found. Oxygen level during the day showed no difference between bare sand pools and pools within the seagrass bed, probably due to photosynthetic activity of benthic diatoms on the bottom of the pools (Asmus et al. 1998). However oxygen content in sand pools did not drop as drastically at night as it did in seagrass pools or the CWL although water temperature was similar. Regarding the distribution of mobile epifauna it can be supposed that they are able to tolerate hypoxic conditions at least over the time period of tidal emersion as all species intensively used the CWL as ebb tide refuge albeit significant diurnal oxygen fluctuations.

As sampling success in tide pools might be promoted by accumulation of animals on a relatively small, submerged area the high faunal density found within the CWL is even more noticeable.

From field observations the ability of brown shrimps to outlast ebb tide by burying into the ground (Janssen and Kuipers 1980; Beukema 1992) is not considered to represent a preferred strategy compared to temporise in residual water resources.

Conclusions

Species composition of dominant, mobile epibenthos is not obligatory related to seagrass cover in the intertidal of the Wadden Sea. Solely *Idotea spp.* showed stronger linkage to vegetated habitats. However the presence of *Z. noltii* beds significantly increases abundances and production of 0-group epibenthos on the tidal flats during the main vegetation period of the plants. Additionally, the residual water layer within dense *Z. noltii* beds provides extended ebb tide refuges for dominant epifaunal species containing higher abundances than tide pools and puddles. This ecological function is not negatively influenced by hypoxic conditions occurring in tidally emerged seagrass beds at night. As a result intertidal seagrass beds clearly

contribute to the nursery function of the intertidal area in the northern Wadden Sea for key-species of the trophic network.

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Publication II

Structuring influence of seagrass beds (*Zostera noltii*) on fishes temporarily visiting the intertidal zone of the northern Wadden Sea

Abstract

A seagrass bed (*Zostera noltii*, Hornem) located within the intertidal zone of a shallow tidal basin in the northern Wadden Sea near the Island of Sylt (Germany) was compared to adjacent unvegetated tidal flats with respect to composition and abundance of tidal migrating fishes during the seagrass vegetation period in summer 2003. Referring to age classes found and to previous studies on this subject, fishes visiting tidal flats during flood could be briefly divided into the following functional groups: (i) “nursery visitors”: 0- group individuals inhabiting the tidal basin as nursery area, (ii) “spawning visitors”: Adult individuals producing demersal eggs, immigrating shallow waters for spawning and (iii) “tidal basin residents”: Species spending the major part of their life-cycle in the tidal basin. As the occurrences of these groups widely match the vegetation period of *Z. noltii*, the question arises, whether the presence of seagrass beds influences fish abundance and species distribution on inundated tidal flats.

Beach seine and drop trap samples monthly taken in the period from May to September generally resulted in varying distributions of 14 species according to the respective flood habitat.

Spawning visitors including garfish and three-spined stickleback were significantly more frequent in the *Z. noltii* bed. “Tidal basin residents” were only sporadically found composed of pipefishes (Syngnathidae), which were limited to sand flats. “Nursery visitors” in total showed no clear distribution patterns during the investigation period since the occurrence of fish species was subjected to strong seasonal variations within the course of the year. Dominant species represented by the common goby (*Pomatoschistus microps* Krøyer) and plaice (*Pleuronectes platessa* L.) were more abundant on vegetated tidal flats. Less abundant “nursery visitors” showed distinct preferences of certain habitats strictly varying on species level. Among the low-density juveniles three general groups were identified by cluster analyses of intertidal distribution patterns. Group 1 includes five species almost exclusively found in the *Z. noltii* bed; Group 2 is composed of two species primarily found in the seagrass bed but also in lower numbers on bare sand flats. Group 3 consists of three species almost exclusively limited to sand flats.

Exemplarily for 0-group whiting (*Merlangius merlangus* L.) the influence of seagrass cover on the intensity of tidal migration was investigated using light traps installed at

different tidal levels. In the seagrass site whiting immigrated far into the upper intertidal zone close to the mean high tide line whereas on bare sand flats fishes remained in the lower zone, within the reach of tidal gullies. It can be concluded that the occurrence of *Z. noltii* beds in the northern Wadden Sea increase diversity of fish fauna by (a) quantitatively influencing individual densities of dominant fishes and (b) qualitatively structuring species distribution of transient fishes temporary visiting tidal flats.

Introduction

In general seagrass beds are considered to represent important nursery habitats for fishes and invertebrates. They are known to reduce predation pressure by increasing habitat complexity (Heck and Thoman, 1981; Virnstein, 1984; Isaksson and Pihl, 1992; Hindell et al., 2001) and protect small individuals from being washed out by water flow (Fonseca et al., 1982; Gambi et al., 1990; Fonseca and Calahan, 1992). Additionally seagrass beds support accumulation of organic matter and thus increase food resources for benthic organisms (Asmus and Asmus, 2000).

Extended beds of subtidal *Zostera marina* disappeared from the Wadden Sea by the “wasting disease” in the 1930`s and did not recover ever since. As a consequence of the substantial loss, seagrass beds today are no longer involved by emphasising important nursery habitats for fishes in the Wadden Sea. Today habitat diversity is predominantly attributed to certain salinity gradients provided by estuaries and to the marine landscape itself with extended shallow water zones and intertidal areas (Dankers et al., 1978; Kerstan, 1991; Elliott and Dewailly, 1995; Jager, 1998; Breckling et al., 1998; Pihl et al., 2002). The remaining seagrass stocks of the Wadden Sea are largely constrained to the intertidal zone dominated by the dwarf seagrass (*Z. noltii*). For fishes, the availability of those seagrass habitats is a) restricted to high tide and b) restricted to the vegetation period of seagrasses during the summer month, because grazing of water fowl, ice-scouring and increased water dynamics reduces (above ground) canopies during winter (Nacken and Reise, 2000; Ganter, 2000; Schanz and Asmus, 2003). In general, species composition attributed to intertidal *Z. noltii* beds is not considered to differ from that commonly found on unvegetated tidal flats (den Hartog, 1983). However, previous studies suggested a significant, increasing impact of intertidal seagrasses on abundances of mobile

epibenthic macrofauna compared to adjacent tidal flats without bottom vegetation (Polte et. al., in press). Since a variety of fish species inhabit the tidal basin only temporarily during the year, it is hypothesised that seagrass cover might influence tidal migration and qualitatively structure species distribution patterns due to this habitat preferences.

Since information on the influences of Wadden Sea seagrass beds on shallow-water fish diversity is sparse, the aim of this study is to present an overview of fishes visiting tidal flats during the vegetation period of *Z. noltii*.

Based on the hypothesis that distribution patterns of fishes visiting tidal flats at high tide are influenced by the presence of *Z. noltii* beds, beach seine and drop trap samples were used for quantitative records of fish abundances on inundated tidal flats. Since juvenile whiting (*Merlangius merlangus*) is considered to represent one of the most important predators of benthic epifauna associated with tidal flats, it was exemplarily studied whether the intensity of tidal migration of whiting is linked to seagrass cover.

Materials and methods

Study sites

Investigations were carried out in the northern Wadden Sea (North Sea), Germany. A shallow tidal basin is composed by the islands Sylt (G) and Rømø (DK) (54°50' - 55°10' N, 8°20' - 8°40' E). It is almost enclosed by a artificial causeways connecting the islands with the mainland. One single inlet of 2.8 km width connects the tidal basin (Sylt-Rømø Bight) with the open sea. Tides are semi-diurnal with a tidal range of about 2 m. Salinity varies seasonally between 25 and 32. Mean water temperature during the sampling period was at 15 °C (May and June), and 18 °C (July to September) respectively. Tidal flats represent 1/3 of the 404 km² area of the tidal basin and about 12 % of intertidal area is covered by seagrass beds (Gätje and Reise, 1998) dominated by the dwarf seagrass *Z. noltii*.

Investigations were conducted in a *Z. noltii* bed of 0.5 km² area and adjacent tidal flats without vegetation. Both sampling sites were located at the same tidal level, near the mean high tide mark at the east coast of the island of Sylt. Mean shoot density of *Z. noltii* plants were 1088 m⁻² in May 2003 increasing to 12000 shoots m⁻²

in August (Schanz unpubl. data). Intertidal sampling sites located in the reach of the same tidal gullies were emerged for 4-6 hours during the tidal cycle. Water depth at high tide varied between 0.7 - and 1 m depending on wind speed and-direction.

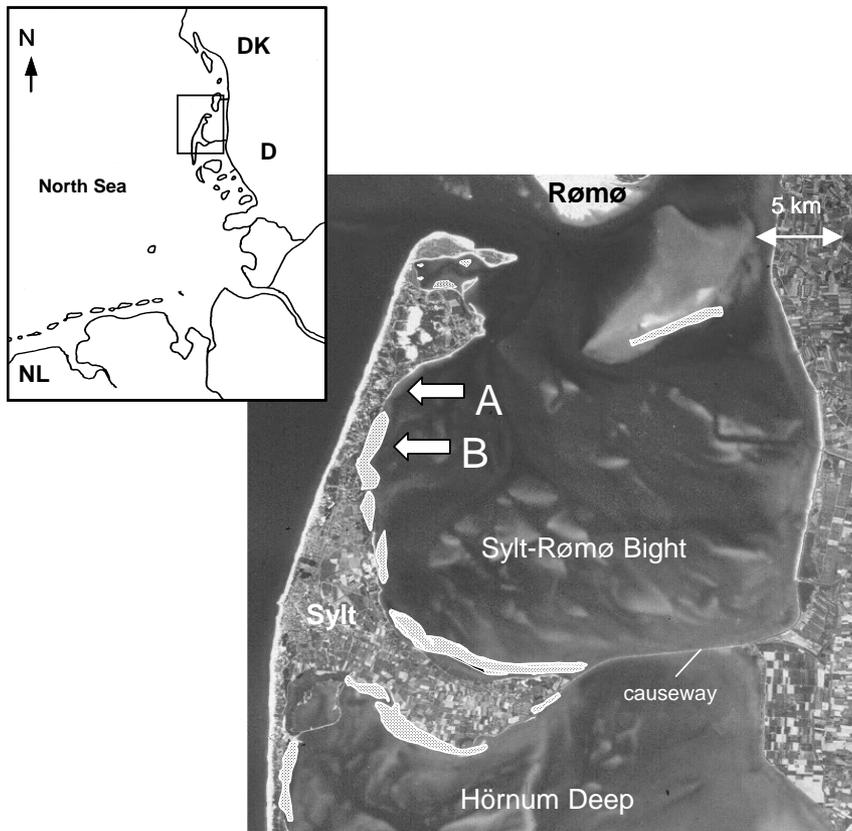


Fig.1 The Sylt-Rømø Bight located 54°50'-55°10'N, 8°20'-8°40'E in the northern Wadden Sea. Shaded areas show the distribution of intertidal seagrass beds. Sampling sites including a *Z. noltii* bed (B) and adjacent unvegetated tidal flats (A) were located at the east coast of the Island of Sylt.

Beach seine sampling

For quantitative captures of fish a 20 m wide and 1.5 m high beach seine (mesh size 10 mm) was used during daytime. In the centre of the seine a 2 m long bag (mesh size 4 mm) was located. The upper fringe of the net were kept at the water surface by buoys and the bottom line contained rounded weights for a better gliding on the ground. A small boat set the beach seine, while both wings of the seine were connected with the shore by towropes over a distance of 80 m. The seine was hauled to the beach by two people and shut at the last 20 m of the towropes by the

people walking in the direction of each other. Investigation area of 900 m² was composed of seine opening (15 m) and haul distance (60 m). In the Laboratory fishes were determined, counted, divided into size-classes and preserved by freezing at -18 °C.

Two hauls were taken monthly from Mai to September 2003, while the distance between hauls was a 100 m minimum to avoid disturbing sampling effects.

Sampling on different habitat types was carried out on following days during the same period within the rising tide (one hour before high tide to one our afterwards).

Drop trap sampling

We used a portable drop trap (modified after Pihl Baden and Pihl, 1984) for quantitative sampling of common gobies (*Pomatoschistus microps*) and juvenile plaice (*Pleuronectes platessa*), of the cohort <30 mm body length, on inundated tidal flats. Six replicate samples were taken monthly from May to September 2003 on vegetated and unvegetated tidal flats. The drop trap consisted of a 1.20 m high aluminium frame with a sampling area of 0.5 m² mounted at the bow of a small boat (4.16 m x 1.65 m) powered by an outboard motor. The trap was quickly lowered and stuck into the sediment by its own weight. The trap was emptied for animals using a hand net (1 mm mesh size) attached to a 1.5 m long handle. Animals were taken to the laboratory, counted and divided into age classes due to total body length.

Prove of habitat specific whiting migration by light traps

The intensity of tidal migration by whiting (*Merlangius merlangus*) was studied using light traps on vegetated and unvegetated tidal flats during the night. Traps consisted of round bow nets with a diameter of 60 cm and 1.2 m length (6 mm mesh size). Simultaneously in both sites one trap was installed in the lower intertidal part close to the mean low tide line (LTL) and one was set in the upper part close to the mean high tide line (HTL). A white, cold, chemical light (8 h OMNIGLOWTM) was placed within each trap at the beginning of flood tide. Traps were emptied for fishes in the following ebb tide period, before the tide was completely out. Traps on bare sand and in seagrass were set at the same time over a period of four days in August

2001. The numbers of whiting from each trap were pooled over the sampling period and demonstrated as mean number of individuals per trap / day.

Data analysis

Due to the functional role of intertidal habitats, fishes received by beach seine sampling were divided into (1) young of the year juvenile visitors (2) spawning visitors and (3) others.

Data of fish abundance were shown by arithmetic means \pm standard error (SE). Data were (1) pooled over entire sampling period to achieve a centralised mean abundance of species over the season and (2) pooled for each month to demonstrate main temporal distribution of species during summer 2003.

One-way ANOVA was used for statistical analyses. To reach homocedasticity of variances data were transformed using $\log + 1$ if necessary to fulfil the assumptions of ANOVA. Level of significance was set at $p < 0.05$.

Cluster analyses was conducted to demonstrate patterns of habitat preference by 0-group fishes visiting the intertidal zone.

Results

Species composition of fishes found on inundated tidal flats

A total amount of 14 fish species was observed occurring on inundated tidal flats during the sampling period. These species were primarily represented by young of the year (0-group) individuals. Most of them inhabiting the tidal basin temporarily during their first juvenile stages and were therefore classified as “nursery visitors” (Table.1). Adult fishes found in the intertidal zone frequenting their spawning grounds were classified as “spawning visitors” and were represented by the garfish (*Belone belone*) and the three spined stickleback (*Gasterosteus aculeatus*). Additionally, adult individuals of two Syngnathiid species were found visiting tidal flats. Nilsson’s pipefish (*Sygnathus rostellatus*) as well as the greater pipefish (*S. acus*) are considered to almost permanently inhabit the Sylt-Rømø Bight and were thus as classified as “tidal basin residents”.

Table 1 Composition of tidal migrants caught on vegetated and unvegetated tidal flats during flood. Fishes were classified to (1) "spawning visitors": Adult individuals occurring in respect of spawning, (2) "nursery visitors": 0-group fishes temporary occurring in the tidal basin and (3) "tidal basin residents": Species spending most of their life cycle in the tidal basin.

Fish composition on inundated tidal flats May-September 2003

"Spawning visitors"	Garfish	<i>B. belone</i>
	Three-spined stickleback	<i>Gasteosteus aculeatus</i>
"Nursery visitors"	Small sandeel	<i>Ammodytes lancea</i>
	European eel	<i>Anguilla anguilla</i>
	Sand-smelt	<i>Atherina presbyter</i>
	Garfish	<i>Belone belone</i>
	Herring	<i>Clupea harengus</i>
	European anchovy	<i>Engraulis encrasicolus</i>
	Thicklip mullet	<i>Mugil chelo</i>
	Flounder	<i>Platichthys flesus</i>
	Plaice	<i>Pleuronectes platessa</i>
	Common goby	<i>Pomatoschistus microps</i>
	Sand goby	<i>Pomatoschistus minutus</i>
"Tidal basin residents"	Greater pipefish	<i>Syngnathus acus</i>
	Nilsson`s pipefish	<i>Syngnathus rostellatus</i>

Distribution patterns of fish groups due to habitat type

1. "Spawning visitors"

The total amount of spawning visitors *B.belone* and *G. aculeatus* was significantly higher in *Z. noltii* beds than on bare sand flats ($p = 0.022$, $F = 5.991$, $df = 1$) during their residence on inundated tidal flats from late April to early August (Fig. 2). Mean abundance of *B. belone* received by pooled replicates taken in the period from April to August were 0.3 individuals $100\text{m}^{-2} \pm 0.03$, $n = 14$ in the seagrass bed, and 0.009 individuals $100\text{m}^{-2} (\pm 0.003, n = 11)$ on bare sand respectively. Mean abundance of *G. aculeatus* during that particular period was 1.4 individuals $100\text{m}^{-2} \pm 0.3$, $n = 14$ in the seagrass bed whereas no individuals could be found on bare sand.

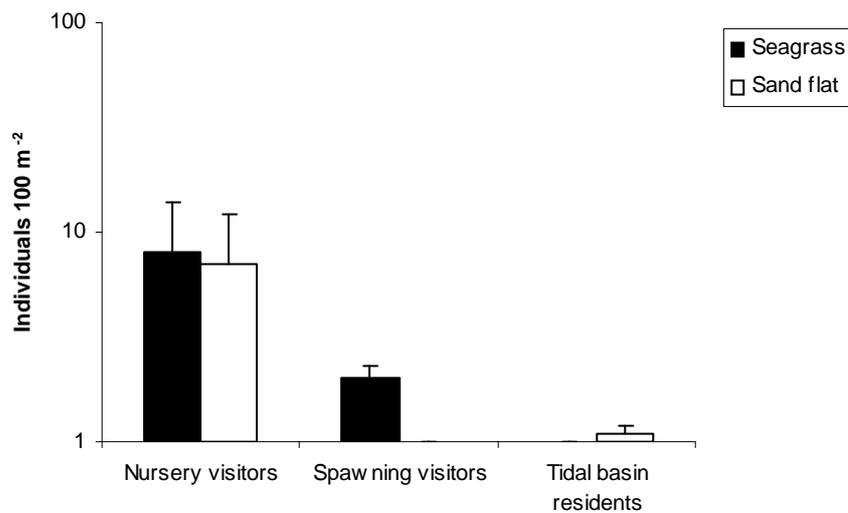


Fig.2 Total abundances 100 m⁻² of fishes classified to functional groups visiting tidal flats at flood. Data sets were composed of species abundances pooled over the sampling period (May to September) and set on a logarithmic scale. Whereas “spawning visitors” were significantly more frequent in the *Z. noltii* bed, the occurrence of “tidal basin residents” was limited to bare sand flats. “Nursery visitors” as a total showed no clear difference between vegetated and unvegetated tidal flats.

2. “Tidal basin residents”

Tidal basin residents solely represented by syngnathiid pipefishes were caught from early June until the end of the sampling period in late September. The occurrence of pipefishes was limited to unvegetated tidal flats (Fig. 2) and thus abundances were significantly higher than in *Z. noltii* beds ($p < 0.01$, $df = 1$, $F = 9.5$). Of the two species, *S. rostellatus* occurred more frequently (0.04 ± 0.02 individuals 100 m⁻²) than *S. acus* (0.02 ± 0.02 individuals 100 m⁻²). According to the low numbers of specimen caught during the sampling period standard errors are about 50 % (*S. rostellatus*) respectively 100 % (*S. acus*).

3. “Nursery visitors”

The total mean abundance of young of the year fishes visiting tidal flats in the period from late April to September 2003 (Fig. 2) did not differ significantly between vegetated and unvegetated tidal flats (ANOVA, $p > 0.05$, $df = 1$, $F = 1.94$). The total abundance of 0-group fishes pooled over the sampling period was dominated by the common goby (*Pomatoschistus microps*) and plaice (*Pleuronectes platessa*) of the

cohort <30mm to an amount of 99.6 %. Low-density species showed mean abundances of in 4.1 ± 2 individuals 100m^{-2} ($n = 18$) in the seagrass bed and 1.0 ± 0.3 individuals 100m^{-2} ($n = 15$) on bare sands. Hence a trend to increased individual numbers related to the presence of seagrass beds (Fig. 2).

The quantitative ranking of species differed between vegetated and unvegetated tidal flats (Table 2). Except the two 0-group fishes generally dominating on tidal flats, represented by *Pomatoschistus microps* (rank 1) and *Pleuronectes platessa* of the cohort <30 mm body length (rank 2). According to species abundances pooled over the sampling period *Atherina presbyter* ranked 3 in the seagrass habitat and 6 on bare sand flats. *Clupea harengus* is on rank 7 in the seagrass bed together with *Platichthys flesus*, *Mugil chelo* and *Anguilla anguilla*. *C. harengus* was the third abundant species on unvegetated tidal flats whereas the other species on rank 6 were absent on bare sands. Because of generally lower individual densities on bare sand flats, the difference of *Engraulis encrasicolus* abundance between vegetated and unvegetated tidal flats was limited to one rank (rank 4 in the seagrass bed and rank 5 on bare sands), although its abundance was as double as high in the *Z. noltii* bed. *Belone belone* and *Ammodytes lancea* were on rank 5 and rank 6 respectively in the seagrass bed and were found less abundant on sand flats (rank 9 respectively rank 8). The sand goby (*Pomatoschistus minutus*) held rank 4 on the sand flat but was less abundant in the seagrass bed (rank 7). 0-group plaice of the cohort <70 mm was generally less abundant than the cohort of <30 mm body length. This was classified to rank 7 on bare sands whereas it was absent in the *Z. noltii* bed.

Table 2. Species ranking of 0-group individuals 100 m⁻² found in the seagrass bed and adjacent sand flats. Ranks represent the seasonal mean of species abundance during the seagrass vegetation period based on pooled data of Beach Seine and drop trap (shaded lines) samples from May to September 2003.

Species	Seagrass		Sand	
	seasonal mean (\pm SE)			
	Rank		Rank	
<i>Ammodytes lancea</i>	0.22 (0.19)	6	0.05 (0.02)	8
<i>Anguilla anguilla</i>	0.01 (0.01)	7	0	
<i>Atherina presbyter</i>	3.2 (1.79)	3	0.17 (0.08)	6
<i>Belone belone</i>	0.25 (0.22)	5	0.01 (0.01)	9
<i>Clupea harengus</i>	0.01 (0.01)	7	0.27 (0.12)	3
<i>Engraulis engraulis</i>	0.41 (0.39)	4	0.18 (0.14)	5
<i>Mugil chelo</i>	0.01 (0.01)	7	0	
<i>Platichthys flesus</i>	0.01 (0.01)	7	0	
<i>Pleuronectes platessa</i>				
<30 mm	40 (5.8)	2	10 (3.2)	2
<70 mm	0		0.1 (0.06)	7
<i>Pomatoschistus microps</i>	827 (186)	1	453 (155)	1
<i>Pomatoschistus minutus</i>	0.01 (0.01)	7	0.2 (0.08)	4

Seasonal distribution of “nursery visitors” during the seagrass vegetation period

Strong seasonal restrictions affected the occurrence of fishes frequenting tidal flats. Among the nursery visitors abundances of most species were subjected to monthly fluctuations during summer 2003 (Fig. 3). The frequency of 0-group juveniles found in association with seagrass cover was limited to the main vegetation period of *Z. noltii* from July to September. However, dominant fishes assessed by drop trap samples (Fig. 3 shaded graphs) showed a wider seasonal distribution. *P. microps* entered tidal flats in June and abundances increased on *Z. noltii* flats during the main vegetation period from July to September (ANOVA, $p < 0.05$, $n = 6$). Juvenile plaice settled in the upper intertidal area in May reaching a higher abundance in the seagrass bed than on bare sands (ANOVA, $p < 0.05$, $n = 12$), although the shoot density of *Z. noltii* plants was relatively sparse (1088 ± 66 shoots m^{-2}). Larger individuals of plaice (<70 mm) reached their maximum abundance in late June and were limited to sand flats. Only within the particular period when some species (*A. presbyter*, *E. engraulis*, *A. lancea*, *C. harengus*, *P. minutus*) reached their highest abundance single individuals could also be found on the adjacent tidal flat regardless of bottom type. According to non-homogeneous variances, the limited quantity of monthly taken replicates did not allow reliable statistical analysis of low-density species when pooled over the whole sampling period (see above 3.3). The comparison of species abundances within single months showed clearer distribution patterns with respect to their occurrence on a certain habitat type (Fig.3).

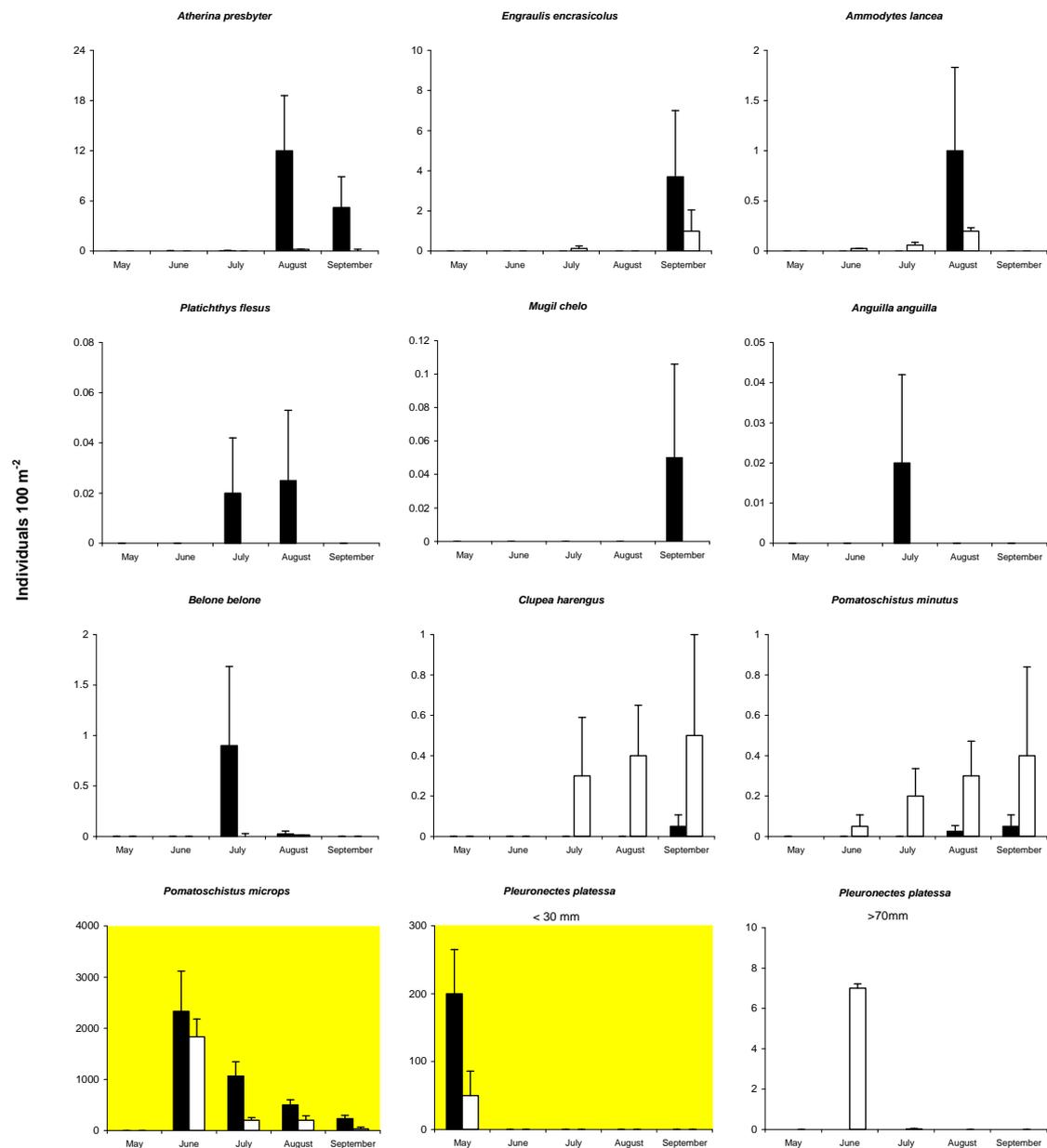


Fig. 3 Seasonal distribution of (0-group) "nursery visitors" on inundated seagrass bed (black bars) and bare sand flats (white bars) during the seagrass vegetation period. Species abundances are shown in mean individual numbers 100 m⁻². Most species were sampled using a beach seine, only dominant fishes (shaded graphs) were sampled by a drop trap. The occurrence of most fish species on tidal flats was highly variable during the sampling period and often limited to single months.

Structuring influence of seagrass cover on species distribution of “nursery visitors”

Juvenile fishes of lower individual densities assessed by beach seine sampling showed variable patterns of habitat preference during their temporary residence on inundated tidal flats. According to percentages of total individuals / species found on vegetated and unvegetated tidal flats during the seagrass vegetation period preferences could be identified on species level (Fig. 4). Whereas *Atherina presbyter*, *B. belone*, *Anguilla anguilla*, *M. chelo* and *P. flesus* were almost entirely (96 to 100 % total individuals/species) found in *Z. noltii* beds, occurrences of *Pleuronectes platessa* <70 mm, *Pomatoschistus minutus* and *C. harengus* were almost restricted to bare sand flats (94 to 100 % total individuals / species). *Ammodytes lancea* and *E. encrasicolus* were primarily found in the seagrass bed (>70 % total individuals / species) but did also occur on unvegetated tidal flats to a smaller percentage (<30 % total individuals / species).

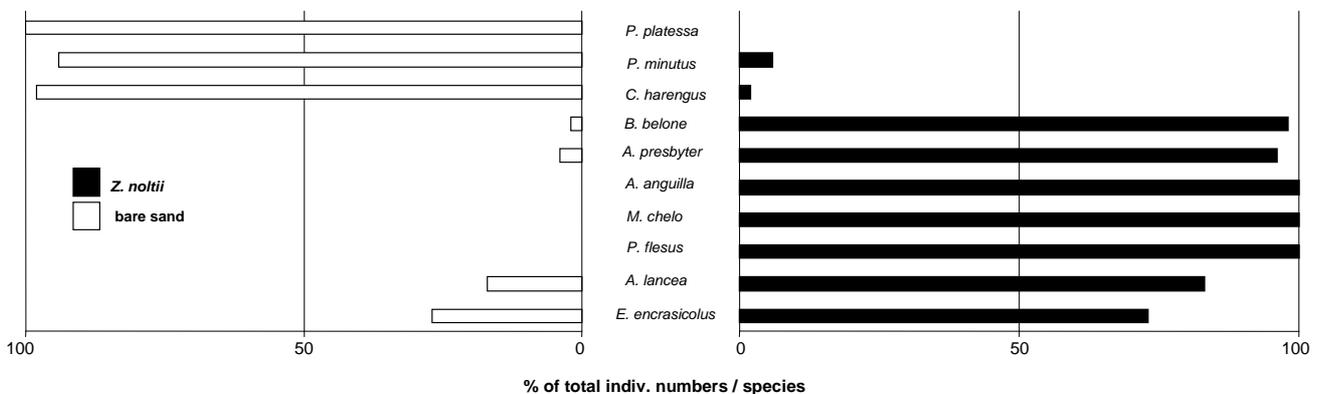


Fig. 4 Qualitative differences in species occurrence due to type of flood habitat, based on total amount of individuals caught per species during the entire sampling period. Distribution of (low-density) juveniles on vegetated and unvegetated tidal flats strictly varied on species level.

According to the demonstrated distribution patterns, cluster analysis basing on percentages of total individuals / species found on vegetated and unvegetated tidal flats resulted in the identification of three general groups of 0- group fishes structured by their occurrence within a certain intertidal habitat (Fig. 5). Group 1 includes five species almost limited to seagrass beds in the investigation areas; whereas group 2 were composed of two species primarily occurring on inundated

tidal flats covered by *Z. noltii* but could also be found on bare sand flats in lower numbers. Group 3 contained three species predominantly occurring on tidal flats without seagrass cover.

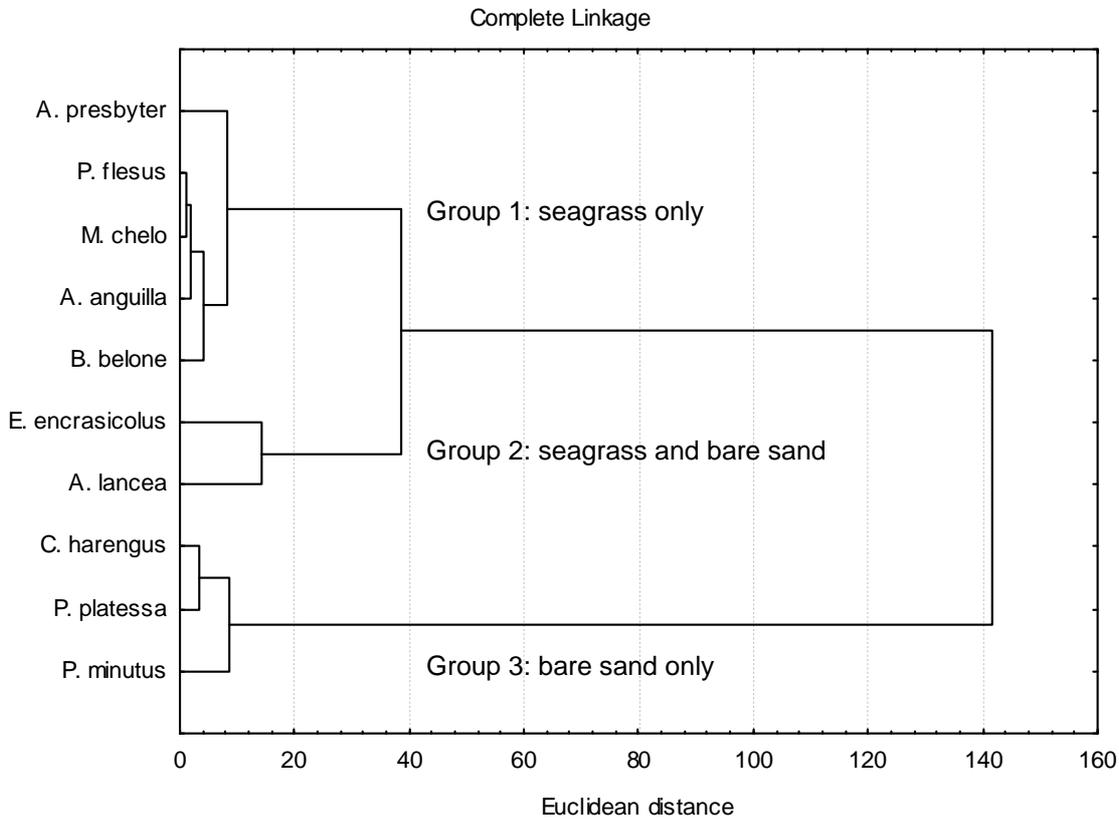


Fig. 5 Based on total amount of individuals caught per species during the entire sampling period, cluster analysis identified three major groups of “nursery visitors” which occurred in low densities. 5 species were almost exclusively found on seagrass flats (group 1). Two species primarily occurred on inundated tidal flats covered by *Z. noltii* but could also be found on bare sand flats in lower numbers (group 2). The occurrence of three species was almost limited to bare sands (group 3).

Intensity of whiting migration on vegetated and unvegetated tidal flats

During the investigation period, individuals of juvenile whiting (*Merlangus merlangius*) were not found in beach seine samples at daytime. However, light traps installed during the night on different tidal levels passively caught numerous individuals immigrating on inundated tidal flats at high tide. Numbers of whiting found varied clearly according to type of intertidal habitat (Fig.6). Individual numbers/trap/day close to the mean high tide mark (HTM) were significantly higher in the presence of seagrass ($p < 0.05$, $df = 1$, $F = 9.5$, $n = 4$) than on the adjacent sand flats.

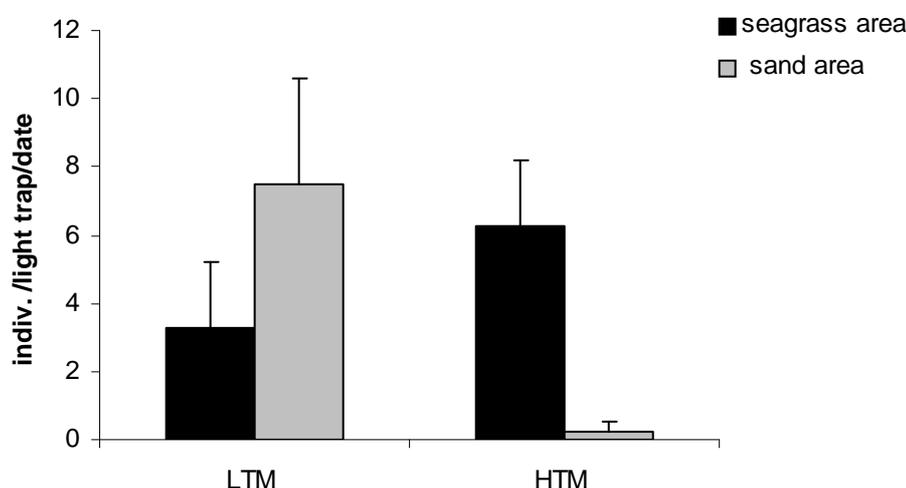


Fig. 6 Individuals of 0-group whiting caught by light traps placed in different tidal levels during flood on four consecutive nights ($n = 4$). Within the upper intertidal zone close to the mean high tide mark (HTM) significantly more individuals of whiting could be found in the presence of seagrass, whereas on unvegetated tidal flats fishes primarily remained in the lower part (LTM) close to the tidal gullies.

In the lower intertidal zone, near the mean low tide mark (LTM) numbers of whiting caught by light traps did not significantly differ between vegetated and unvegetated tidal flats ($p = 0.3$, $df = 1$, $F = 1.3$, $n = 4$). A trend showed increased numbers of caught specimens in the lower part (LTM) of the unvegetated tidal flat.

Discussion

For fishes the availability of seagrass habitats in the intertidal zone of the Wadden Sea is temporary within the course of the year as well as in the tidal cycle.

To receive a first overview of impacts seagrass cover has on tidal flat fish assemblages the classification of tidal migrating fishes into functional groups is considered as a suitable tool beyond merely description of species abundances. As a consequence of little background data available in respect of e.g. inter-annual variations of fish densities in the intertidal zone, classifications made are in some aspect superficial. The functional groups formed are likely not complete. They are based on species compositions observed during the present study. The group of fishes recorded as “Spawning visitors” was composed of species (garfish, three-spined stickleback) that obviously take advantage of *Z. noltii* beds as spawning grounds by attaching demersal eggs to the plants. The herring is at least one additional species that attaches spawn directly to seagrass leaves. Although huge amounts of herring eggs could be observed in the investigation area, spawning individuals could not be observed. Catches of adult garfishes and three-spined sticklebacks were almost limited to tidal flats covered by seagrass beds. This clear distribution pattern is supposed to be due to the particular function of *Z. noltii* plants as spawning substrate for these species, a significant feature of the Sylt-Rømø Bight (Polte and Asmus, unpublished).

Adults of pipefishes (Syngnathidae) were sporadically caught on tidal flats. Since they are considered to inhabit the tidal basin during the major part of their life cycle, they were classified as “tidal basin residents” although they might migrate to deeper waters during winter (Zijlstra, 1978). More species are known to inhabit the tidal basin permanently as residents but only pipefishes were found migrating to the intertidal zone during this study. Syngnathiids are considered to be underrepresented, since according to their thin habit they are not supposed to be efficiently caught by the used beach seine. Hiddink and Jager (2002) found up to 300 individuals 1000 m⁻² of *S. rostellatus* on tidal flats in the Dutch Wadden Sea using beam trawls (mesh size 0.5 cm) during September.

In general pipefishes are often described as typical seagrass residents (Steffe et al., 1989; Edgar and Shaw, 1995; Vincent et al., 1995; Jenkins and Wheatley, 1998).

Their distribution patterns on tidal flats showed a clear preference for unvegetated areas although abundances may have been underestimated.

According to species numbers juvenile fishes classified as “nursery visitors” represented the dominant group caught on submerged intertidal areas. 0-group individuals of migratory species, inhabiting the tidal basin as a nursery refuge often return to shallow Wadden Sea waters as adults for spawning or feeding (Dankers et al., 1978). The temporary occurrence indicated by the term “visitors” was primarily chosen with respect to tidal migration. Two species dominated the total abundance of “nursery visitors”. Newly settled plaice (<30 mm body length) and the common goby represented 99.6 % of 0-group fishes found on tidal flats during the investigation period.

After recruitment on tidal flats in June, when abundances of *P. microps* were similarly high on vegetated and unvegetated areas, individual densities of common gobies were constantly higher in *Z. noltii* beds during the seagrass vegetation period. The migration of post larval plaice from off shore spawning grounds into shallow coastal nurseries is described for several North Atlantic coasts (Van der Veer, 1986; Hjörleifsson and Pálsson, 2001; Pihl and Wennhage, 2002; Wennhage, 2002; Gibson et al., 2002). When juvenile plaice entered the tidal flats in May with a mean body length below 30mm they were significantly more abundant in the seagrass area. As (above ground) seagrass density is low during plaice recruitment, their abundance in seagrass areas might be indirectly promoted by accumulation of soft sediment by seagrass plants (Gacia et al., 1999; Van Keulen and Borowitzka, 2003) containing a higher content of organic matter (Asmus and Asmus, 2000) and thus a higher availability of infaunal food items.

With increasing body length the nursery habitat shifts from the intertidal the shallow subtidal zone and is finally concentrated to tidal gullies (Van der Veer and Bergman, 1986). During the present study larger cohorts of 0-group plaice (<70 mm body length) kept visiting tidal flats bare of seagrass cover at high tide. In addition to the vertical distribution described for different cohorts of plaice (Berghahn, 1984; Pihl et al., 2000; Van der Veer et al., 2001; Wennhage, 2002; Gibson et al., 2002), a horizontal distribution pattern was found among the particular cohort of intertidal settlers which is probably due to influences of *Z. noltii* meadows on the sediment type.

However, as *Pomatoschistus microps* (rank 1) and *Pleuronectes platessa* (rank 2) were dominating on both, vegetated and unvegetated tidal flats, the influence of seagrass cover is considered to be quantitative by increasing abundances compared to bare sand flats.

Among species occurring in lower densities *Z. noltii* beds were found affecting quantities of European anchovy (*E. encrasicolus*) and small sand eel (*A. lancea*). Both showed increased abundances in the seagrass bed but also occurred in lower numbers on unvegetated tidal flats.

In contrast, the distribution of the remaining eight species occurring on inundated tidal flats was qualitatively structured due to the presence of seagrass. Three species (*C. harengus*, *Pleuronectes platessa* <70 mm and *Pomatoschistus minutus*) were almost exclusively found on bare sand flats, whereas catches of five species (*A. presbyter*, *P. flesus*, *M. chelo*, *A. anguilla* and *B. belone*) were limited to the seagrass site. In addition to the individual distribution patterns due to the preferred type of flood tide habitat, occurrences of fishes during the seagrass vegetation period varied on species level. Herrmann et al. (1998) conducted otter-trawl fishery in the tidal gullies of the Sylt-Rømø Bight. They found similar seasonal distributions of herring (June to September) and the sand goby (July to September) but much higher individual densities. This is probably caused by factors such as accumulation of individuals in tidal gullies, higher catch efficiency of the sampling gear used in deeper waters or by inter-annual differences of fish density which are widely documented for common Wadden Sea species (Fonds, 1978; Van Leeuwen et al., 1994; Philippart et al., 1996; Van der Veer et al., 2000). Except the plaice, which reached the highest abundances from early May to late June most species showed highest individual densities in late summer (From the end of July to September) regardless of their distribution due to temporary habitats. During that period temperatures showed a comparably high mean of 18°C during daytime, which might be a crucial factor, influencing seasonal distributions. However, species belonging to (Cluster) group 1 (0-group fishes limited to *Z. noltii* beds) showed distinct peaks of abundance in single months primarily during the main vegetation period of seagrass when shoot densities reached a maximum of about 12000 shoots m⁻² (Schanz, unpublished). In contrast herring and sand goby predominantly found on bare sands (group 3) occurred rather constantly from July to September.

Both, the seasonal distribution and the preference of a certain habitat type in the intertidal zone strongly varied on species level and are therefore suggested to cause non-significant differences of total species abundances between vegetated and unvegetated tidal flats when pooled over the entire investigation period.

Ecological functions that intertidal seagrass beds provide for many flood tide visitors are considered to differ according to species biology. Therefore their particular investigation must be left to future studies. Guidetti and Bussotti (2000) already demonstrated associations of the sand smelt *Atherina presbyter* to subtidal *Z. noltii* beds in the Mediterranean Sea. They assumed planktivorous Atherinidae trophically independent from the presence of seagrass and attributed high abundances found in mixed meadows of *Cymodocea nodosa* and *Z. noltii* to spawning linked with plant coverage. The higher individual density of herring, also planktivorous, on unvegetated tidal flats corresponds to the assumption of trophical independence on habitat type. In the Wadden Sea spawning of *B. belone* is definitely related to *Z. noltii* cover and spawning of *A. presbyter* can also be assumed for studied seagrass sites but the consistent return of juveniles to the intertidal seagrass bed with the rising flood cannot be explained satisfyingly other than by involving factors such as enriched food supply or shelter from predation by habitat complexity.

The results received on the nocturnal distribution of whiting due to tidal level indicated that tidal migration of juvenile whiting (*Merlangius merlangus*) was influenced by the presence of seagrass beds. The increased number of specimens found in the upper intertidal zone suggests a certain attraction of the seagrass area which is assumed to be due to increased food availability.

Fishes feeding on epibenthic macro fauna such as the whiting are considered to profit from the quantitative influence seagrass has on juvenile epifauna. The protection habitat complexity offers for mobile epibenthos (Virstein et al., 1983; Orth et al., 1984; Summerson and Peterson, 1984; Hindell et al., 2002), might on the one hand lower predation success of predatory fishes but on the other hand lead to increased abundances of prey organisms (Polte and Asmus, in press) which eventually compensates higher predation effort.

Conclusions

Although the availability of intertidal *Z. noltii* beds for fishes is limited within the tidal cycle and within the year, their presence was found to quantitatively influencing dominant species abundances and qualitatively structure the occurrence of juvenile fishes during their residence in the intertidal area at flood. Additionally the occurrence of fishes entering Wadden Sea waters for spawning was found increased in intertidal seagrass beds and also tidal migration of predatory species was influenced. Thus it can be concluded that the existence of *Z. noltii* beds promotes fish diversity of the Wadden Sea, although ecological functions must be studied explicitly on species level. It is assumed that seagrass beds intensify the nursery function of the Sylt-Rømø tidal basin by contributing to habitat diversity.

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Publication III

Intertidal seagrass beds (*Zostera noltii*) as spawning ground for transient fishes in the Wadden Sea

Abstract

Since the major seagrass loss in the 1930s the occurrence of extended seagrass beds in the Wadden Sea (North Sea) is exclusively limited to intertidal areas. *In situ* spawning experiments combined with comparisons of fish activity and abundance in *Zostera noltii* beds and adjacent unvegetated areas indicate the importance of this community as spawning ground for garfishes (*Belone belone*), herrings (*Clupea harengus*) and the three spined stickleback (*Gasterosteus aculeatus*). The migration of *B. belone* is specifically directed to intertidal *Z. noltii* beds for mating and spawning. For *C. harengus*, recent observations show a facultative role of intertidal seagrass for reproduction. Macroalgae (*Fucus vesiculosus*) associated with bed groynes are used as alternative spawning substrate by the herring. *G. aculeatus* was found abundantly among intertidal seagrasses during early summer. As more than half of the captured females carried ripe ovaries, intertidal seagrasses are supposed to represent suitable spawning grounds for this species known as it builds disguised nests in vegetated areas and practises intensive parental care. Because of the tidal emersion of *Z. noltii* beds, they are only temporarily available habitats for fishes. Although visiting these biotopes requires an intensive tidal migration, this study demonstrates that intertidal seagrass beds are relevant for reproduction of common fish species. This study shows that one fundamental function documented for subtidal *Zostera marina* beds, lost in the 1930s during the “wasting disease”, has been partially preserved by the availability of the still surviving intertidal vegetation as spawning structure for transient fishes.

Introduction

Worldwide losses of coastal seagrass biotopes are often followed by a depletion of species diversity and abundances of invertebrate and fish communities, attributed to loss of habitat complexity (Thrush et al. 2001, Hughes et al. 2002, Wyda et al. 2002, Vanderkliff & Jacoby 2003). In the Wadden Sea, Wohlenberg (1935) documented that common transient fish species, such as the herring (*Clupea harengus*), lost important spawning grounds. This led to a long-lasting decrease of local herring stocks after the loss of subtidal seagrass beds following the “wasting disease” in the 1930s. Similar observations from subsequent “wasting disease” events in the White Sea around the 1960s (Gemp & Bryzova 1968, Goscheva 1970, Wechov 1987,

Rachor pers. communication) emphasise the adverse effects of seagrass losses on herring populations. A decline of fish diversity is rarely interpreted as a consequence of habitat loss in the North Sea area compared to other anthropogenic factors as e.g. overfishing and pollution (Lakke 1985, Jennings & Kaiser 1998, Philippart 1998, Groehsler & Zimmermann 2001, Christensen et al. 2003, Elliott 2003). One reason might be that consequences of habitat loss are mostly detected after the destruction of a system when its former ecological functions are difficult to evaluate. Further on, stocks of most commercially important fish species are not considered to depend obligatorily on the existence of seagrass systems.

Many studies documented the nursery function of subtidal seagrass beds for fish fauna (e.g. Orth et al. 1984, Connolly 1994, Edgar & Shaw 1995, Scott et al. 2000, Beck et al. 2001, Minello et al. 2003), whereas intertidal seagrass systems, especially in northern latitudes, have attracted less attention in this respect. Generally, the high structural complexity of seagrass beds provides shelter from predation (Nelson & Bonsdorff 1990, Mattila 1992, Hindell et al. 2001), supports larval settlement (Short & Short, 1984, Grizzle et al., 1997, Boström & Bonsdorff 2000, Moksnes 2002) and reduces currents and wave dynamics (Fonseca et al. 1982, Gambi et al. 1990, Fonseca & Calahan 1992, Koch & Gust 1999).

Nowadays the occurrence of seagrass beds in the Wadden Sea is exclusively limited to the intertidal area where they cover about 51 km² in total (Reise 2003). *Zostera noltii* forms extended meadows close to the high tide line whereas intertidal morphotypes of *Zostera marina* plants occur in small patches. Despite a general decline of *Z. noltii* stocks during the past three decades (den Hartog & Polderman 1975, Michaelis 1987) they remained almost stable in the northern part of the Wadden Sea (Reise 2003).

In the Wadden Sea seagrass beds are regularly exposed to long emersion periods during a semi-diurnal tidal cycle. They are therefore only temporarily available habitats during the day and display large fluctuations of physical environmental conditions. The question arises whether intertidal seagrass beds may have a similar function as nurseries and spawning habitats compared to subtidal beds or whether their function is totally different.

By means of *in situ* spawning experiments combined with experimental measurements of fish activity and quantitative sampling methods, this study is

dealing with functions of the remaining intertidal seagrass stocks in the Wadden Sea in terms of fish reproduction. As there is no information available about this subject it is hypothesized that (1) intertidal *Z. noltii* beds provide spawning structures for common, transient fish species and (2) the relevancy of *Zostera noltii* beds as spawning ground for selected fish species is triggered by the absence of alternative bottom structures. This study focuses on different reproduction strategies of three dominant fish species and their utilization of intertidal seagrasses as spawning substrate: (1) The garfish (*Belone belone*) as a k-strategist releases single, comparably large eggs (□ 3 mm) covered by numerous filaments (Fig. 1) facilitating passive attachment to bottom structures (Duncker et al. 1929, Rosenthal & Fonds 1973, Dorman 1991). (2) The herring (*Clupea harengus*) glues aggregations of up to several thousand eggs (r-strategist) on bottom structures (Messieh 1985, Hoshikawa et al. 2001).

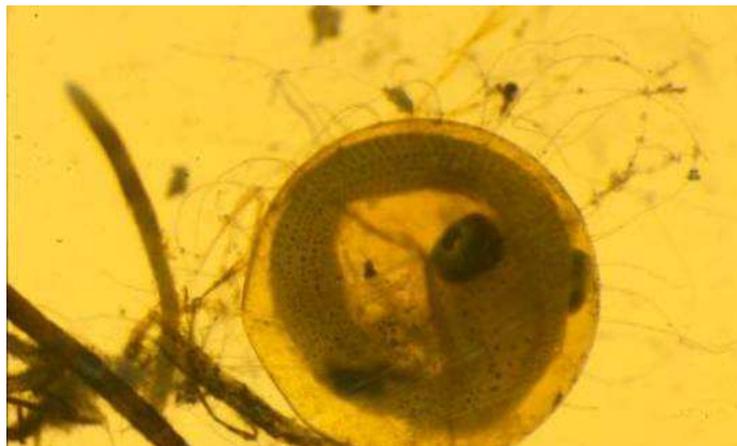


Fig. 1 Single egg (□ 3 mm) of the garfish (*Belone belone*) attached to seagrass leaves by numerous filaments.

3). The three spined stickleback (*Gasterosteus aculeatus*) is usually known to migrate into freshwater environments for spawning (Zijlstra 1978). *G. aculeatus* builds nests from plant material containing aggregations of eggs provided by intensive parental care (Duncker et al., 1929, Reeb et al. 1984, Lachance & FitzGerald 1992, Rowland et al. 2002). As all of these species are described to behave opportunistic by choosing suitable spawning structures (Duncker et al. 1929) the occurrence of seagrass is not expected to be an obligatory requirement to maintain the survival of North Sea populations of these fishes. It is discussed whether

a lack of alternative spawning substrate might increase the importance of intertidal seagrasses significantly.

Materials and methods

Study sites

Studies were carried out in intertidal areas at the east coast of the island of Sylt in the German part of the Wadden Sea (North Sea) (Fig. 2). The investigated tidal flats are situated within a shallow tidal basin formed by the mainland and the islands Sylt and Rømø (Sylt-Rømø Bight). Along the tidal watersheds the bight is nearly closed by causeways connecting the islands with the mainland. One single inlet opens the basin to the North Sea. The tidal rhythm is semi-diurnal with an average amplitude of about 2 m. Salinity ranges seasonally from 28 to 32 psu. Mean annual water temperature is 9 °C. During the vegetation period of *Z. noltii* from May to September mean water temperature was about 18 °C with an extreme of 25 °C in the upper intertidal during late July 2003. Water depth in investigated intertidal locations ranges from 0.7 to 1 m at high tide.

In the Sylt-Rømø Bight 0.3 % of the intertidal area is covered by mussel beds (*Mytilus edulis*), half of which is covered by the macroalgae *Fucus vesiculosus* (Gätje & Reise 1998). Mussel beds are located close to the mean low tide mark, periodically emerged for 1-3 hrs during ebb tide (Asmus 1987, Buschbaum & Saier 2001). 12 % of the tidal flats are covered by seagrass beds, dominated by *Z. noltii*. Depending on their exposure to tidal currents shoot density varies from 2000 to 5000 shoots m⁻² during August and September (Schanz & Asmus 2003). Seagrass beds are located close to the mean high tide mark, exposed to emersion periods from 4-6 hrs (Schanz et al. 2002). Spawning experiments and quantitative sampling of fishes were carried out in a semi-exposed seagrass bed (Fig. 2 B) and nearby sand flats located 1.5 km northward. Mean velocities of tidal currents were 0.10 m s⁻¹ (Schanz et al. 2002). In order to map the activity of *Belone belone* within the Sylt-Rømø Bight, five different seagrass sites were sampled during June 2003 (Fig. 2 A, B, C, D, E). A reference site was located outside the Sylt-Rømø Bight on the southern side of the causeway separating the intertidal system (Fig. 2 F).

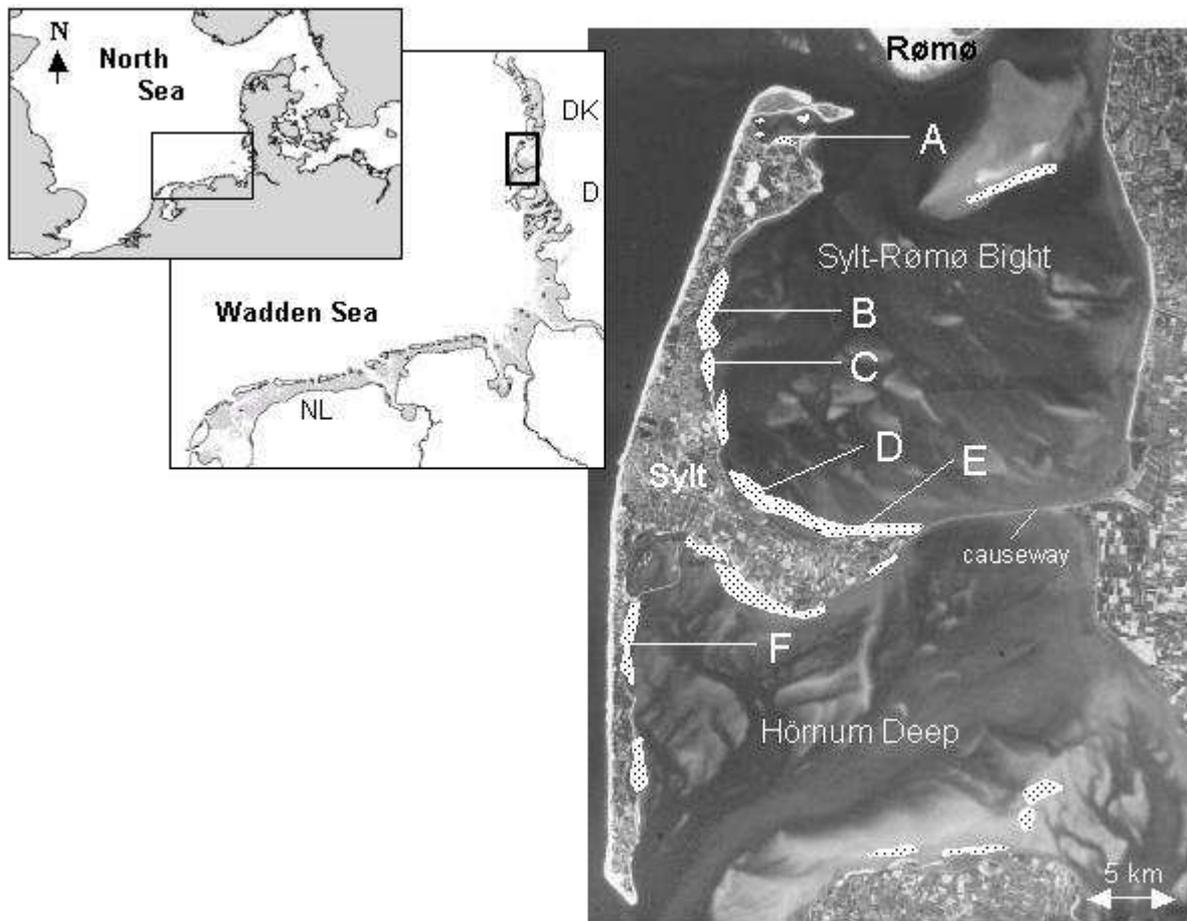


Fig. 2 Location of the study area in the northern Wadden Sea, North Sea. Distribution of intertidal seagrass beds (*shading*) along the east coast of the island Sylt, Germany. Sampling sites in the northern tidal basin “Sylt-Rømø Bight” (A, B, C, D, E) and reference site located in the southern “Hörnum Deep” tidal basin (F). Both basins are separated by a causeway connecting the island with the mainland.

***Belone belone*: Comparison of activity in different habitats**

The epipelagic fish species *B. belone* is highly mobile and thus extremely difficult to capture quantitatively by most current techniques. Former observations by fishermen describe garfishes jumping over flotsam drifting on the water surface. To prove the presence of *B. belone* they used to throw a piece of wood into the water and waited for the fish starting to jump. Due to that specific behaviour a method was derived comparing garfish activity in different habitats during the spawning season from early May to late July 2002. During the rising tide, about one hour before high tide, a rope 20 m long (\varnothing 0.8 cm synthetic fibre) was fixed on the water surface within a *Zostera*

noltii bed and an adjacent sand flat located on the same tidal level (Fig. 3). Over an investigation period of nineteen days the number of adult garfishes jumping over the rope was counted during a 30 minutes time period. For a direct comparison of fish activity each site was sampled at the same time during the tidal cycle, subsequently data were pooled. This method is termed jumping activity comparison (JUMP). Using this method a mapping was conducted in June 2003 to estimate the occurrence of garfishes in different seagrass sites. Five sites were sampled in the northern tidal basin, the Sylt-Rømø Bight, and one reference seagrass site in the intertidal of the southern basin, the Hörnum Deep basin (Fig. 2). During the main spawning period of the garfish in June, 16 potential tidal cycles allowed sampling at almost the same time of the day. As sampling success depends on weather conditions (strong easterly winds cause high water turbidity) most of the sites were sampled once. Site B was the first sampling location and was sampled again at the end of the study period to prove seasonal effects.



Fig. 3 Recording of *B. belone* activity in different seagrass meadows and adjacent sand flats. A rope (20 m) was fixed at the water surface. Number of fishes jumping over the rope were counted within 30 min. time intervals over the inundation period.

***Belone belone*: In situ spawning experiment**

To prove how essential intertidal seagrass plants are as spawning substrate for *B. belone*, different types of structures were offered to the fishes during the main spawning season in 2002. PVC mats of 0.5 m² area were provided with *Fucus vesiculosus* as the dominant macroalgal species (250 g fresh weight / 0.5 m²), and a potential alternative as spawning substrate for *B. belone*. Other mats were covered with bast fibres (50 g / 0.5 m²) presenting an artificial, standardized substrate to

show whether the type of structure is affecting the habitat choice. Six replicates of each structure were placed in a *Zostera noltii* bed and on the adjacent sand flat without vegetation. The surrounding area was sampled using a metal frame of 0.5 m² area with 6 replicates serving as control. In respect of seasonal spawning peaks, mats and controls were examined for *B. belone* eggs on 4 dates from the beginning of June to the middle of July. The eggs found on the experimental units were removed to prevent accumulation from different spawning events.

During this study *B. belone* eggs could be found on green algae (*Enteromorpha* spp., *Chaetomorpha* spp.) in a considerably amount when algae were present within seagrass beds. To prove the passive impact of seagrass cover on the hatching success of garfish larvae, clumps of *Enteromorpha* spp. with attached eggs were collected from the field. Eggs on each clump were counted and clumps were fixed at the ground. Ten replicate algal clumps were installed each on seagrass and adjacent sand flats. After five days algal clumps were controlled for egg numbers and condition. Due to the loss of one experimental unit data were pooled to 9 replicates on seagrass substrate and 10 replicates on bare sand.

Quantification of herring (*Clupea harengus*) spawn on different substrate types

During a spawning event in April 2002, extended *F. vesiculosus* beds associated with blue mussels (*Mytilus edulis*), single algae aggregations and different seagrass beds were controlled for presence of herring spawn in the intertidal zone along the east coast of the island. Presence of spawn on algae and on seagrass was quantitatively compared (egg numbers per unit plant biomass and size of spawning zones). Seagrass sites containing herring spawn were compared with sites without spawn in respect of aboveground plant biomass and shoot density. Shoot density was measured using a metal frame (25 x25 cm) randomly placed on the seagrass canopy ($n = 3$). Mean number of leaves per plant, mean length and width of leaves were measured of 139 randomly chosen plants. Box corer samples (100 cm²) were taken from brown algae ($n = 6$) and *Z. noltii* ($n = 12$). Plant material was dried at 80 °C (48 h) and combusted at 500 °C for 14 hrs to estimate ash weight and ash-free dry weight (AFDW). Egg numbers were quantified by the average weight per single

egg (g AFDW, $n = 15$). Size of spawning grounds was taken by a tape measure and plant biomass was calculated for the whole spawning area.

Fish abundance in different intertidal habitats using seine fishing

Sampling was carried out twice a month from April to September 2003. Two samples were taken each in the *Z. noltii* bed and in the sand flat on following days during the same period within the rising tide (one hour before high tide to one hour afterwards). For quantitative captures of fish a 20 m long beach seine was used. The walls of the seine consisted of 10mm netting and were 1.5 m high. In the middle section of the seine a 2 m long bag of 4 mm netting was fastened. The upper fringe of the net was kept at the water surface by buoys and the bottom line/rope contained rounded weights for a better gliding on the ground. The beach seine was set from a small boat and afterwards hauled to the shore by two people. To allow the disturbed system to settle, there was a 10 minutes pause between setting and hauling the seine. The net was pulled over a distance of 80 m while the 15 m wide mouth was shut at the last 20 m leading to a sampling area of 900 m². The bag of the seine was emptied into a bowl and plant material was removed carefully. In the laboratory fishes were determined, counted, divided into size-classes and preserved by freezing. Data for each species were pooled, and effects between abundances on vegetated and unvegetated tidal flats were analysed. For *Gasterosteus aculeatus* a random sample of 99 females was tested concerning the percentage of egg carrying individuals.

Data analyses

Results are presented as arithmetic means in addition with standard errors (SE). Effects were tested for significance using a one-way Analyses of Variance (ANOVA). Data were tested for homocedasticity by Cochran's test and transformed using $\log(x + 1)$ if necessary to fulfil the assumptions for ANOVA. Effects between single treatments of the spawning experiment were analysed using Post hoc Tukey's honest significant-differences (HSD) test. Statistical significance was assumed if p-level was < 0.05 .

Results

Belone belone: Comparison of activity in different habitats

With two exceptions all investigated *Z. noltii* beds located within the Sylt-Rømø Bight were visited by adult garfishes during the spawning season from May to July 2003. Activity of fishes was observed on sites B, C and D (Fig. 2) whereas sites A and E showed no garfish activity. In the reference seagrass site located in the separated southern Hörnum Deep tidal basin (Fig. 2, F), garfishes were also active. During the sampling period no seasonal fluctuation of garfish activity could be observed. On sampling site B (Fig. 2) where investigations started with 219 “jumps” / 30 min, the control showed almost the same number at the end of the study period (206 “jumps” / 30 min). During the spawning season, garfishes showed a significant higher activity on tidal flats covered by *Z. noltii* (Fig. 4) than on adjacent sand flats bare of vegetation (ANOVA $p = 0.001$, $df = 1$, $F = 12.81$, $n = 19$). With a mean of 105.11 (SE ± 14.08) the number of counted “jumps” over a period of 30 minutes were consistently four times higher in seagrass beds compared to those counted on sand flats (mean 24.42, SE ± 6.09).



Fig. 4 Comparison of garfish activity in vegetated and unvegetated intertidal habitats during the spawning season. Constantly more fish movements were measured in the seagrass bed ($p = 0.001$) over the investigation period of 19 days ($n = 19$).

The mean abundance of adult *B. belone* assessed by a beach seine from May to July 2003 was about 0.42 individuals per 100 m⁻² (SE ± 0.15) in the *Zostera* bed whereas 0.01 per 100 m⁻² (SE ± 0.01) individuals were caught on adjacent sand flats (Fig. 5 A). Fishes had a mean length of 56.37 cm (SE ± 0.91, *n* = 15) and a mean fresh weight of 223 g (SE ± 9.0, *n* = 15). The mean abundance of adult garfishes was significantly higher in the seagrass habitat (ANOVA, *p* < 0.05, *df* = 1, *F* = 5.61).

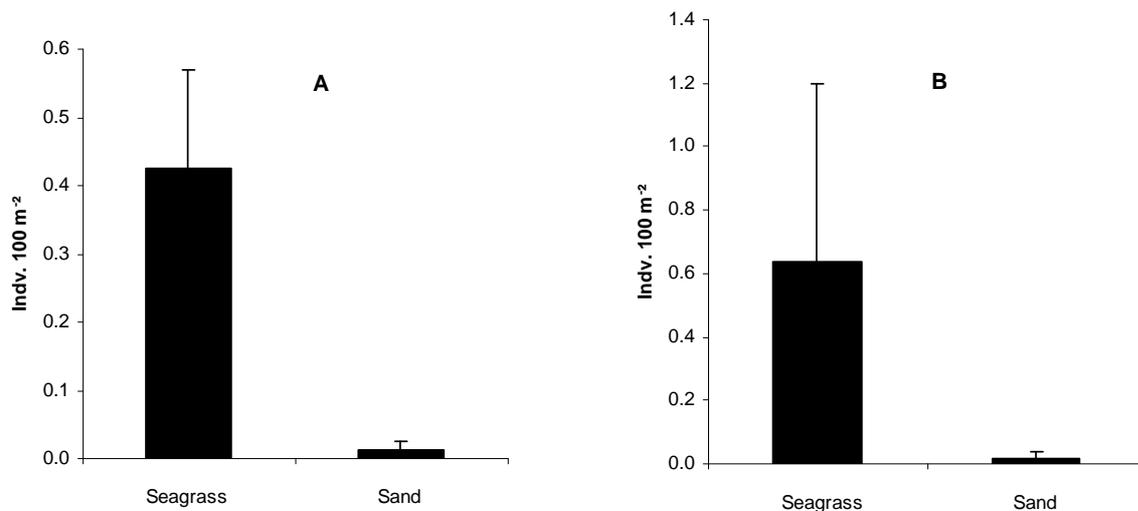


Fig. 5 (A) Abundance of adult *B. belone* due to habitat type. Mean individual numbers per 100 m⁻² were significantly higher (*p* < 0.5) in the seagrass bed (*n* = 11) than on bare sand (*n* = 8). **(B)** Mean abundance per 100 m² of juvenile (0-group) garfishes in the same sampling sites. In this case ANOVA showed no significant effect.

In July, the mean abundance of 0-group individuals was about 0.64 individuals per 100 m⁻² (SE ± 0.54) within the *Zostera* bed and 0.02 individuals per 100 m⁻² (SE ± 0.02) upon bare sand (Fig.5 B). No significant differences on mean abundance of juvenile garfish in vegetated and unvegetated tidal flats could be shown (ANOVA, *p* = 0.35, *df* = 1, *F* = 0.34). 0-group individuals had a mean length of 6.6 cm (SE ± 0.15, *n* = 40), mean fresh weight was 0.4 g (SE ± 0.04, *n* = 40).

***In situ* spawning experiment**

Generally the amount of *B. belone* eggs found on the experimental units was significantly higher in the *Z. noltii* bed than on adjacent bare sand flats (ANOVA *p* <

0.001, $df = 5$, $F = 33.35$) (Fig. 6). Within the seagrass bed the number of eggs on the mats covered with an artificial bast structure showed no relevant difference to seagrass controls (Tukey's test, $p = 0.46$). Seagrass and bast units were both significantly more covered with eggs than PVC mats covered with *F. vesiculosus* (Tukey's test seagrass, $p < 0.05$; Tukey's test bast, $p < 0.001$). Experimental units covered with *F. vesiculosus* showed in turn significantly higher egg numbers when they were placed in the *Z. noltii* bed compared to those placed upon bare sand (Tukey's test, $p < 0.01$). On bare sand macroalgae (mean 0.08 ± 0.08) and bast structures (mean 0.5 ± 0.3) did not contain significantly more eggs than the control areas where no eggs could be found during the investigation period.

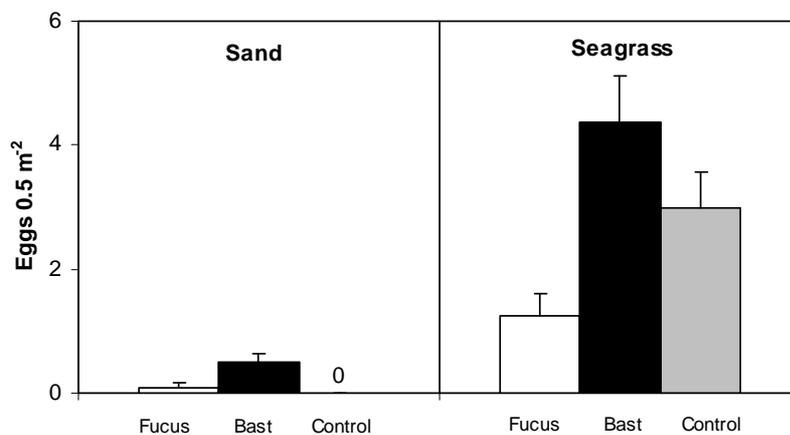


Fig. 6 Experimentally offered spawning substrate in vegetated and unvegetated tidal flats (0.5 m²). Control areas are untreated substrate surrounding the experimental set up. The amount of eggs on experimental units was significantly higher in the *Z. noltii* bed ($p < 0.001$, $n = 6$). *F. vesiculosus* mats were significantly less occupied with eggs than the seagrass control and the artificial bast structure ($p < 0.05$, $n = 6$).

The mean numbers of *B. belone* eggs on each experimental green algal unit at the start of the experiment were 6.44 (SE \pm 0.97) in the seagrass bed and 5.1 (SE \pm 0.53) on the sand flat. After five days a mean of 5.44 (SE \pm 0.67) eggs could be recovered on seagrass ($n = 9$) and 3.3 (SE \pm 0.47) eggs were found on sand ($n = 10$). The percentage of recovered eggs (Fig. 7) was significantly higher within the *Z. noltii* bed (ANOVA, $p < 0.01$, $df = 1$, $F = 9.19$). Of the eggs recovered a mean amount of 1.44 SE (\pm 0.41) was damaged on seagrass substrate whereas on sand bottom 3.1 (SE \pm 0.53) eggs were broken. The percentage of damaged eggs was significantly higher when seagrass was absent (ANOVA, $p < 0.05$, $df = 1$, $F = 7.39$).

As a result *B. belone* eggs were found attached to all experimental treatments as far as they were located in the seagrass bed.

Algal structures played a minor role as spawning substrate compared to artificial

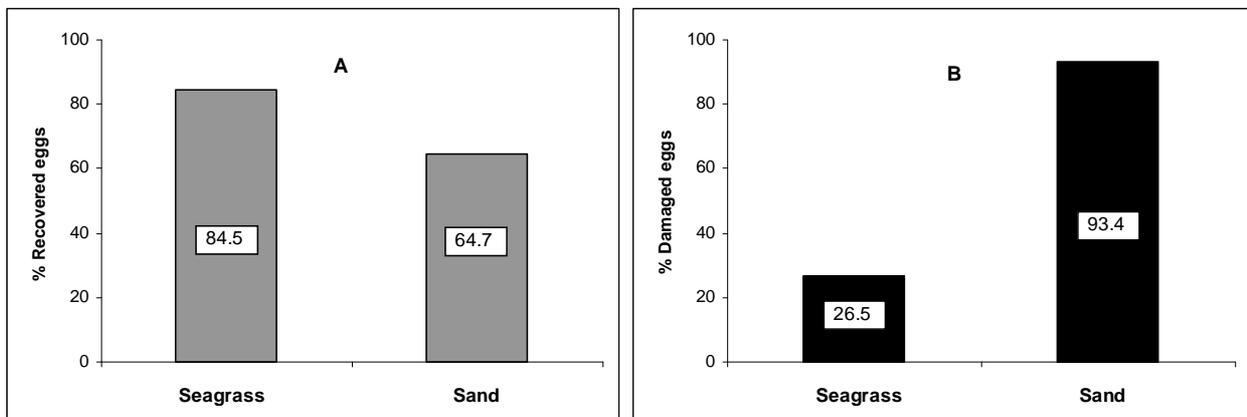


Fig. 7 (A) Percentage of *B. belone* eggs recovered on experimental green algae units after a period of five days. (B) Percentage of eggs found damaged basing on the amount of recovered eggs.

structures whereas the seagrass bed showed no significant differences compared to the artificial substrates. From the beginning of June to the middle of July the mean density of eggs in the seagrass habitat was 6 m^{-2} ($\text{SE} \pm 1.1$). For a total seagrass area of 0.5 km^2 in the study site (Schanz & Asmus, 2003) a value of 3,000,000 *B. belone* eggs could be estimated.

Clupea harengus

In the intertidal area, *Fucus vesiculosus* thalli as well as *Zostera noltii* plants were used as substrate by spawning herrings (*C. harengus*) in April 2002. Herring spawn was not homogeneously distributed but accumulated in certain zones or “nests”. On the intertidal area of the southern tidal basin, Hörnum Deep (Fig. 1, F) a belt within the *Z. noltii* bed was identified as spawning zone. The belt was 190 m along the coast and had a width of about 9 m. In this belt the mean number of seagrass plants was 3088 m^{-2} with a mean biomass of 55 g AFDW m^{-2} . The *Z. noltii* plants had a mean leaf length of 8.38 cm, 0.95 mm width ($n = 139$) and a mean number of 2.49 leaves per plant ($n = 139$). Herring spawn was attached to the leaves forming aggregations. The mean number of eggs was 26.72 per seagrass plant ($n = 139$).

In the northern basin, Sylt-Rømø Bight, (Fig. 1) the density of *Z. noltii* cover in April was much lower. Plant biomass was only about 9 g AFDW m⁻². In this area spawn could not be detected on seagrass leaves but it was found attached to two *F. vesiculosus* patches associated to groynes located in the upper intertidal region.

Table 1 *Clupea harengus*. Quantitative description of a spawning event in April 2002. Egg numbers in relation to plant biomass (pb) projected to the dimensions of spawning zones (sz) found in the intertidal area.

Intertidal spawning areas	area 1	area 2	area 3
Substrate	<i>F. vesiculosus</i>	<i>F. vesiculosus</i>	<i>Z. noltii</i>
Dimension of spawning zone (m ²)	2.10	19.25	1653
Plant Biomass (g AFDW) / area sz	1049.73	9622.5	90915
Number of eggs / g AFDW pb	66.55	66.55	1500.3
Number of eggs / area sz	69859	640377	136402320

Within the macroalgal patches, spawning zones were limited to nests with a length of 3.5 m and 0.6 respectively 5.5 m width. Algal biomass was 500 g AFDW m⁻². The amount of herring spawn in relation to plant biomass and spawning zone is given in Table 1. The number of herring eggs in the seagrass spawning zone was almost 200 to 2000 times higher than those calculated for the two *F. vesiculosus* nests. Other nests of herring spawn could not be found in *F. vesiculosus* patches along the east coast of the island.

Gasterosteus aculeatus

In the period from late April to June the three spined stickleback (*Gasterosteus aculeatus*) occurred on tidal flats covered by seagrass with a mean abundance of 3 individuals per 100 m⁻² (SE ± 0.9, *n* = 7) on tidal flats covered by seagrass, whereas on unvegetated areas no sticklebacks could be found. The mean total length of captured individuals was 6.2 cm (SE ± 0.09, *n* = 20), mean weight was 2,3 g (SE ± 0.10, *n* = 20). Females with ripe ovaries had a mean length of 7.1 cm (SE ± 0.12, *n* = 20) and a mean weight of 3.5 g (SE ± 0.16, *n* = 20). A random sample of 99 female

fishes showed an amount of 54.6 % spawn carrying individuals (Fig. 8). Additionally in another sample of 99 fishes containing both sexes, 52 males in breeding colours were identified.

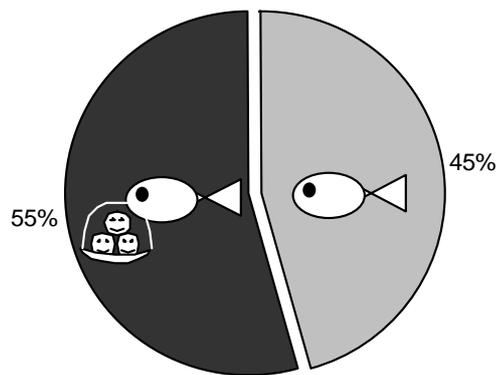


Fig. 8 Percentage of female *G. aculeatus* with and without eggs found within their ovaries. Taken of a random sample including 99 female sticklebacks caught in the *Z. noltii* bed during early summer 2003.

Discussion

The results of this study demonstrated the function of intertidal seagrass beds as spawning ground for migratory fishes. The present investigations directly and indirectly identified spawning activity of three common fish species in relation to the presence of intertidal seagrass cover. The sand smelt *Atherina presbyter* is assumed to represent one more species utilising *Z. noltii* beds for spawning. Although higher abundances of *A. presbyter* were found within the seagrass habitat compared to bare sand flats during summer 2003 (Polte in prep.) no explicit evidence of spawning activity could be demonstrated yet. In view of extreme conditions, such as long emersion periods and strong variations of temperatures and salinities, predominating in the intertidal area, together with the low faunal diversity generally described for northern latitudes (Virnstein et al. 1984, Virnstein 1995, Macpherson & Duarte 1994, Mattila et al. 1999), a considerable amount of common migratory fishes frequented *Z. noltii* habitats for spawning. This is even more noticeable as spawning of the named species is not obligatory linked with seagrass occurrence. Immigrating to the intertidal zone in terms of spawning might be due to the absence of alternative bottom structures in the subtidal area but direct supporting influences of the intertidal environment on embryonic development are also conceivable.

The comparison of garfish activity in vegetated and unvegetated intertidal habitats indicate that tidal migration of adult fishes is especially directed to intertidal *Z. noltii* beds. The significantly lower garfish activity on bare sand flats adjacent to seagrass beds is due to passing these areas during tidal migration. Although the used JUMP-method is not an adequate mean to estimate abundances, it is a very suitable method to prove dispersal and habitat preference whilst avoiding major disturbances capturing this mobile epipelagic species. The observation of fish movements in different seagrass sites at the east coast of the island of Sylt suggests that garfishes enter the intertidal with the rising tide and migrate to those *Z. noltii* meadows which are located within the reach of the main tidal gullies (Fig. 2, B, C, D, F). The reference seagrass site located in the southern tidal basin of the island showed *B. belone* activity as well. The fact that the two basins are separated by a causeway reveals that the preference for intertidal seagrass beds as spawning substrate is transferable to other areas within the Wadden Sea.

In contrast to the high numbers of counted fish movements at the sampling sites abundance of adult garfish measured by beach seine catches seemed to be under represented. The speed of hauling over a distance of 80 m by two people might be too slow to capture this mobile fish species quantitatively. Although the efficiency of the beach seine is limited, numbers of individuals caught on vegetated and unvegetated tidal flats demonstrate a significant preference for the seagrass bed which underlines the hypothesis of a directed migration of these fishes into the intertidal *Z. noltii* habitats.

The results from the *in situ* spawning experiment strongly supports the hypothesis of a migration distinctly directed to the seagrass habitat for spawning, because eggs were attached to any suitable structure as long as it was located inside the *Z. noltii* bed. Macroalgal structures are no alternative spawning substrates since less eggs were found attached to *Fucus vesiculosus* compared to artificial structures and the surrounding seagrass bed. The mean density of eggs found in the seagrass habitat was 6 m⁻² whereas a mapping of garfish eggs on *F. vesiculosus* stocks associated with mussel beds (*Mytilus edulis*), carried out in summer 2002 showed no single positive report on three locations in the Sylt-Rømø Bight (Polte unpublished). As other types of complex bottom structures are rare in the tidal basin the seagrass

beds might be almost obligatory spawning places for garfish reproduction in this region. As *Z. noltii* beds are exposed to long emersion periods within the tidal cycle, this habitat seems at first to be disadvantageous for the development of fish spawn. However, dense *Z. noltii* meadows (2000 – 5000 shoots m⁻²) located in the sheltered parts of the Sylt-Rømø Bight (Schanz & Asmus 2003) prevent tidal flats from complete emersion by retaining a water layer of several centimetres between the leaves over the low tide period. Probably this permanent water layer is responsible for the survival of eggs in the intertidal. Additionally embryonic stages of *Belone belone* can tolerate huge fluctuations in temperature and salinity (Rosenthal & Fonds 1973, von Westernhagen, 1974, von Westernhagen et al. 1975). The relatively quick warming of the thin water layer during the day might even shorten incubation time of larvae as von Westernhagen (1974) found out that at a temperature of 24 °C eggs developed much faster than at 18 °C. This temperature difference in fact represents approximately that between shallow subtidal and intertidal water layers in the Wadden Sea during the investigation period. Thus it can be assumed that intertidal conditions promote development of larvae and therefore underlines the function of the seagrass beds. The results from the field experiment dealing with the hatching success of garfish eggs attached to green algae could also be explained by the existence of the residual water layer remaining in intertidal seagrass beds at ebb tide. During the high tide period, clumps of green algae are often erected within the water column above the seagrass canopy. Thus algal structures potentially collect a quantity of eggs before they reach the sea floor. When the water level drops, the bottom dispersed algal clumps are unfurled in direction of the tidal currents. Eggs attached to algae located on bare sediments are considered to be damaged by drying whereas the percentage of damaged eggs remains low if the moisture of the seagrass bed keeps the algal substrate wet.

The quantitative results for the 0+-group *B. belone* recruiting from the spawning event in early summer 2003 are potentially not reflecting real abundances. While increase of body length is very fast in the first life stages of juvenile garfish (Dorman 1991), the diameter of the body (without fins) increases rather slowly. The mean body length of 6.6 cm measured in August represents a diameter of 5 mm and the juvenile garfish would pass through the meshes of the used netting at this stage. Accumulation of plant material inside the net may accidentally lead to a higher value

of captured individuals in the seagrass habitat, which however did not significantly differ from abundance measured on unvegetated tidal flats because of the high standard deviation. As there is a lack of information on 0+-group garfish in the intertidal area of the Wadden Sea, this study is the first report demonstrating that juvenile garfishes return to the upper intertidal zone with the rising flood pointing at its role as nursery area for juvenile fishes.

In contrast to garfishes, intertidal *Z. noltii* beds are classified as facultative spawning grounds for herrings in the northern Wadden Sea. From the studied spawning event in April 2002 it can be concluded that macroalgae generally act as spawning substrate additionally to seagrasses. However, herring spawn found was limited to the upper intertidal zone, where the occurrence of extended *F. vesiculosus* mats is rare.

Whereas Rasmussen (1973) stated that seagrass loss in the North Atlantic during the 1930s had no catastrophic effects on the fisheries, it is documented from the White Sea (Gemp & Bryzova 1968, Goscheva 1970, Wechov 1987, Rachor, pers. com.) and the Wadden Sea (Wohlenberg 1935) that herring stocks drastically decreased after the collapse of *Zostera marina* beds during an “wasting disease” event. The survival of *Z. noltii* stocks in the intertidal areas was obviously not able to lessen the consequences of the major habitat loss for the local herring population. The findings of spawn found in association with *Z. noltii* is considered as not important for total North Sea herring stocks. But the (“adopted-migrant”) hypothesis assuming that juvenile fishes learn to find suitable spawning grounds by following the adults (McQuinn 1997, Corten 1993, Corten 2001) might increase the meaning of these local spots for genetic biodiversity and might point to a proceeding recovery of eastern North Sea populations (Zimmermann pers. com.). From the Baltic Sea it is documented that herring began to spawn on bare sediments because of missing bottom vegetation leading to increased embryonic mortality (Raid 1990). From these reports it could be derived that reproduction success of herring is benefited by the presence of certain bottom structures.

As spawning of herring is concentrated to winter and early spring in the Wadden Sea region (Dankers et al. 1978) probably a mismatch between spawning season and seagrass availability exists. Although *Z. noltii* is a perennial plant, the aboveground parts of most Wadden Sea meadows are lacking in winter because of harsh weather

conditions, ice drift (de Jonge & de Jong 1992, Schanz & Asmus 2003;) and grazing by brent geese (*Branta bernicla*) (Ganter 2000, Nacken & Reise 2000). Thus they might not provide reliable spawning grounds for winter and spring spawners. The low plant density of the intertidal seagrass site in the northern tidal basin in April 2002 (Fig. 1, B) is representing the consequences of grazing by waterfowl and leaf loss caused by abiotic factors during winter. In conclusion, an indirect influence of various factors leading to seagrass loss during winter and the function of the seagrass system as spawning ground for the herring can be assumed.

The stickleback (*Gasterosteus aculeatus*) is known to leave the marine environment in spring migrating into brackish- and freshwater for spawning (Zijlstra 1978). During this study a considerable amount of sticklebacks were found in the *Zostera* beds whereas no individuals could be captured on unvegetated tidal flats. A surprisingly high percentage of females caught in seagrass beds had eggs in their ovaries. Additionally single nests of sticklebacks were found but due to the fact that nests were effectively hidden, quantitative data were not available. The investigated seagrass habitat is isolated from freshwater inflow (except for ground water), and the salinity during spawning season is characterized as polyhaline (29 psu). This Wadden Sea study demonstrates that *Gasterosteus aculeatus* spawns in marine intertidal systems. As this species is a very popular example of intensive parental care and territorial behaviour (Duncker et al. 1929, Reebbs et al. 1984, Lachance & FitzGerald 1992) it is still questionable how males cope with exposed nests at low tide. A subspecies or close relative of *Gasterosteus aculeatus* is the white stickleback (*Gasterosteus sp.*) (Jamieson et al. 1992, Horn et al. 1999, Blouw 1996). From white sticklebacks of Nova Scotia Mac Donald (1995) describes abandonment of parental care in connexion with intertidal spawning. Embryonal development of sticklebacks in the intertidal zone is described as being faster than on adjacent subtidal areas (Mac Donald et al. 1995a, Mac Donald et al. 1995b). It is left to further studies if *G. aculeatus* in the Wadden Sea use similar strategies. On population level the intertidal seagrass beds are not considered to be very important for the reproduction of the stickleback but in terms of dispersal and ecological corridors the existence of these marine spawning grounds must be taken into account.

A direct nursery function of intertidal meadows in terms of supporting abundance and production of juveniles is supposed to be limited to few taxa of demersal fishes and crustaceans which are able to outlast emersion periods without tidal migration (Reise 1985, Polte in preparation). However the existence of seagrass beds in a sedimentary environment poor in three dimensional bottom structures enriches habitat diversity and might indirectly contribute to the nursery role of the whole tidal basin.

Conclusions

The results of this study show that intertidal *Zostera noltii* systems are of significant relevance for the reproduction of transient North Sea fishes although seagrass beds are only temporarily available during the tidal cycle. Dominant fish species embarking on different spawning strategies use seagrass plants as substrate for spawn in the intertidal area. In the geologically young Wadden Sea ecosystem (Streif 2002) most fish species are profoundly opportunistic in respect of feeding and reproduction behaviour (Duncker et al. 1929). Recent seagrass stocks in the Wadden Sea must be generally classified as facultative spawning grounds for fishes. However, a lack of alternative spawning structures may intensify their importance. Since intertidal seagrass stocks are considered to be an important but not an essential habitat for transient fishes in the northern Wadden Sea continuous seagrass losses might not endanger the survival of fish populations. However, a further decline of seagrasses might remarkably effect trophic structure, biodiversity and population density on a regional scale. On species level, the present study indicates that vegetated intertidal areas promote larval development providing beneficial environmental conditions over the whole tidal cycle. For species as the garfish intertidal seagrass beds must be classified as essential spawning grounds as alternative spawning structures are rare in the Wadden Sea.

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Publication IV

Changes of shallow water fish assemblages 7 decades after the major seagrass loss (*Zostera marina* L.) in the subtidal zone of the northern Wadden Sea

Abstract

A substantial loss of seagrass beds (*Zostera marina*, L.) occurred in the whole North Atlantic area due to the “wasting disease” about 70 years ago in the 1930`s. In the North Sea extended subtidal seagrass beds failed to recover and thus subtidal seagrass beds remained absent also in the entire Wadden Sea until today. As a consequence severe changes in the composition of faunal communities were observed and have been attributed to this habitat loss. Diversity of shallow water fish assemblages was considered to have declined.

This study reconstructs changes of fish composition due to the loss of seagrass habitats by comparing historical documents and present observations assuming a certain degree of habitat linkage of fish species. The investigations are restricted to qualitative comparisons on species level, since historical pre-impact data do not include species abundances

In this study a particular area of a former seagrass bed was investigated as well as habitats present in the northern Wadden Sea such as mussel beds (*Mytilus edulis*, L.) and intertidal seagrass beds (*Zostera noltii*, Hornem).

Only three species of fishes formerly occurring in association with subtidal *Z. marina* are presently found absent in the investigated, shallow Wadden Sea waters. Those species are assumed to represent resident fishes with closer links to a certain habitat.

Numerous species were found in addition to those recorded in the historical list. Thus the Sørensen similarity index of fish assemblages in former subtidal seagrass beds compared to those presently found on mussel beds was 60 %. Fish species, which were described to enter former seagrass beds for spawning, were found to utilise predominantly intertidal *Z. noltii* beds as spawning grounds.

As a result, diversity of shallow water fish assemblages and important habitat functions are considered to be widely maintained by residual habitats as mussel beds and intertidal seagrass meadows. Since their existence is continuously endangered, consequences of seagrass loss might become visible in the future, decades after the “wasting disease” occurred.

Introduction

Coastal biotopes provided by seagrasses throughout the world are generally considered to represent examples for positive impacts of complex habitat architecture on faunal composition. One of the most mentioned ecological functions attributed to seagrasses in coastal waters is providing important nurseries for fishes and invertebrates by lowering predation pressure due to habitat complexity (e.g. Orth et al., 1984; Mattila, 1992; Hindell et al., 2001; Beck et al., 2001). Seagrass beds are often quoted as spawning grounds for fish species reproducing by demersal eggs attached to bottom structures. However, it is rarely proven how essential seagrass habitats are for reproduction of fishes especially in temperate waters where inshore spawners are relatively uncommon (Jackson et al., 2001). Numbers of fish species permanently inhabiting seagrass beds for their entire life cycle are less than those temporary visiting seagrasses for a particular phase (Kikuchi, 1974). The distribution of these often small and “cryptic” residents is mostly not exclusively limited to seagrass habitats (Edgar & Shaw 1995a).

Substantial seagrass losses that consistently occur throughout the world (Short & Wyllie-Echeverria, 1996), might have different effects on groups of fishes with a certain type of habitat linkage, but these effects might be additionally triggered by the availability of other complex types of bottom structures such as e.g. beds of epibenthic bivalves, corals and mangroves coexisting in a particular system.

However, the reconstruction of effects of seagrass loss in the past on fish assemblages is often difficult as quantitative pre-impact data are scarce. To evaluate consequences of seagrass loss on fish composition and species abundance several studies used to compare present seagrass stocks with unvegetated areas especially those where seagrass beds have been disappeared (Edgar & Shaw, 1995; Jenkins et al., 1997; Hughes et al. 2002). These studies imply that seagrasses partly survived within a certain system or that beds meanwhile are re-established.

Extended *Zostera marina* beds remained absent in the subtidal zone of the entire Wadden Sea area about 70 years after the severe seagrass loss, whereas stocks recovered along various European coasts. It is still discussed controversially which processes led to the collapse of seagrass stocks and which reasons are mainly responsible for the failure of their re-establishment in the Wadden Sea until today

(De Jonge and Ruiter, 1996; van Katwijk et al., 2000; De Jonge et al., 2000). However, there is a consensus about general changes of faunal composition due to the drastic habitat loss (Reise et al., 1989; Reise, 1994; Ducrotoy et al., 2000; Wolff, 2000; Asmus and Asmus, 2000). However, consequences of seagrass loss on shallow water fish assemblages are difficult to evaluate as reconstruction of habitat functions are complicated by various factors: a) Historical investigations do rarely contain quantitative pre-impact data. b) Seagrass beds are not the only biogenic habitats lost in the Wadden Sea during the past 70 years c) Ecological functions of habitats formerly coexisting with *Z. marina* beds and still being present today, are widely unknown.

The extent of former biocoenoses as well as the composition of associated fauna is well documented in the northern Wadden Sea by Hagmaier & Kaendler (1927). They described the presence of oyster – and *Sabellaria* reefs located in the subtidal zones which meanwhile became entirely extinct due to over-exploitation or wilful destruction respectively to prevent fishing gear from being damaged (Riesen and Reise, 1982; Reise and Schubert, 1987). Nienburg (1924) documented a map showing dense seagrass beds extending from tidal flats to the shallow subtidal zone partially intermitted by mussel beds (*Mytilus edulis*) located at the low tide mark. Intertidal seagrass beds were not affected by the “wasting disease” in this extent (Vergeer and Den Hartog, 1991; Philippart and Dijkema, 1995). Although their stocks were declining in the south (NL) and central (D) Wadden Sea during the past four decades (Den Hartog & Polderman, 1975; Michaelis, 1987; Kastler and Michaelis, 1999), they extensively recovered in the northern parts (D, DK) of the Wadden Sea (Reise, 2003). Less information is available on habitat functions of intertidal *Z. noltii* meadows and mussel beds nowadays and in former times when they coexisted with subtidal *Z. marina* beds.

Species composition of fishes associated with subtidal *Zostera marina* beds was described by Wohlenberg (1935) who documented direct consequences of the wasting disease on the species composition. Unfortunately these historical data sets do not include species abundances but useful descriptions of species linkage to the seagrass community. Beside the disappearance of resident fishes, he described that stocks of seasonal visitors as the herring (*Clupea harengus*) dropped drastically due to the loss of spawning grounds.

Based on the fish community attributed to subtidal *Z. marina* beds by Wohlenberg (1935) this study tries to characterise the changes of species composition of fish in the Wadden Sea. Considering different types of habitat linkage the present species composition of fishes was investigated within the particular part of the Wadden Sea where historical data were once received. A former *Z. marina* bed, bare of vegetation today was included in the investigations as well as beds of dwarf seagrass (*Z. noltii*) and blue mussels (*M. edulis*) present in the intertidal zone.

Due to the lack of quantitative pre-impact data this study focus on species numbers. The presence of residual habitats was hypothesised to mitigate the effects of seagrass loss on fish diversity in the northern Wadden Sea.

Materials & Methods

Study sites

Investigations of shallow water fish assemblages were carried out at the east coast of the island of Sylt located in the northern Wadden Sea (North Sea), Germany. A shallow tidal basin (404 km²) is formed by the islands of Sylt and Rømø (Denmark) and almost closed by artificial causeways connecting the island with the mainland. One single inlet of 2.8 km width connects the basin (Sylt-Rømø Bight) with the open sea. Tides are semi-diurnal with a tidal range of about 2 m. Salinity varies seasonally between 25 and 32. Stocks of subtidal seagrasses (*Zostera marina*) are entirely absent since the “wasting disease” in the 1930`s. Nowadays the occurrence of seagrass beds is limited to the upper intertidal zone of the Sylt-Rømø Bight covering 12% of tidal flats dominated by the dwarf seagrass *Z. noltii*. Mussel beds (*Mytilus edulis*) cover about 0.3 % of the intertidal area exposed to emersion periods from 1-3 h during low tide (Gätje & Reise, 1998, Asmus, 1987; Buschbaum & Saier, 2001). Mussel beds are located at the mean low tide line and expand into the shallow subtidal zone up to a maximum water depth of 0.5 to 1m (mean low tide) (Saier, 2002).

The mean water temperature during the sampling period was 18 °C.

Sampling sites included shallow subtidal areas located between 0 -and 3 m below mean low tide level in a 6 km² wide subsystem of the tidal basin (“Königshafen”). Subtidal sites, characterised by sandy sediments, were identified as former locations

of *Z. marina* beds by historical documents of Nienburg (1924) (Fig.1, C). Mussel beds, *Z. noltii* meadows and sand flats were located about 8 km southward within the regime of the same tidal gully (Fig.1, B). Seagrass sites and adjacent sand flats were sampled on the same tidal level close to the mean high tide line at a distance of about 1.5 km of each other, whereas the sampled mussel bed was located below the low tide mark on the seaward side of a tidal gully.

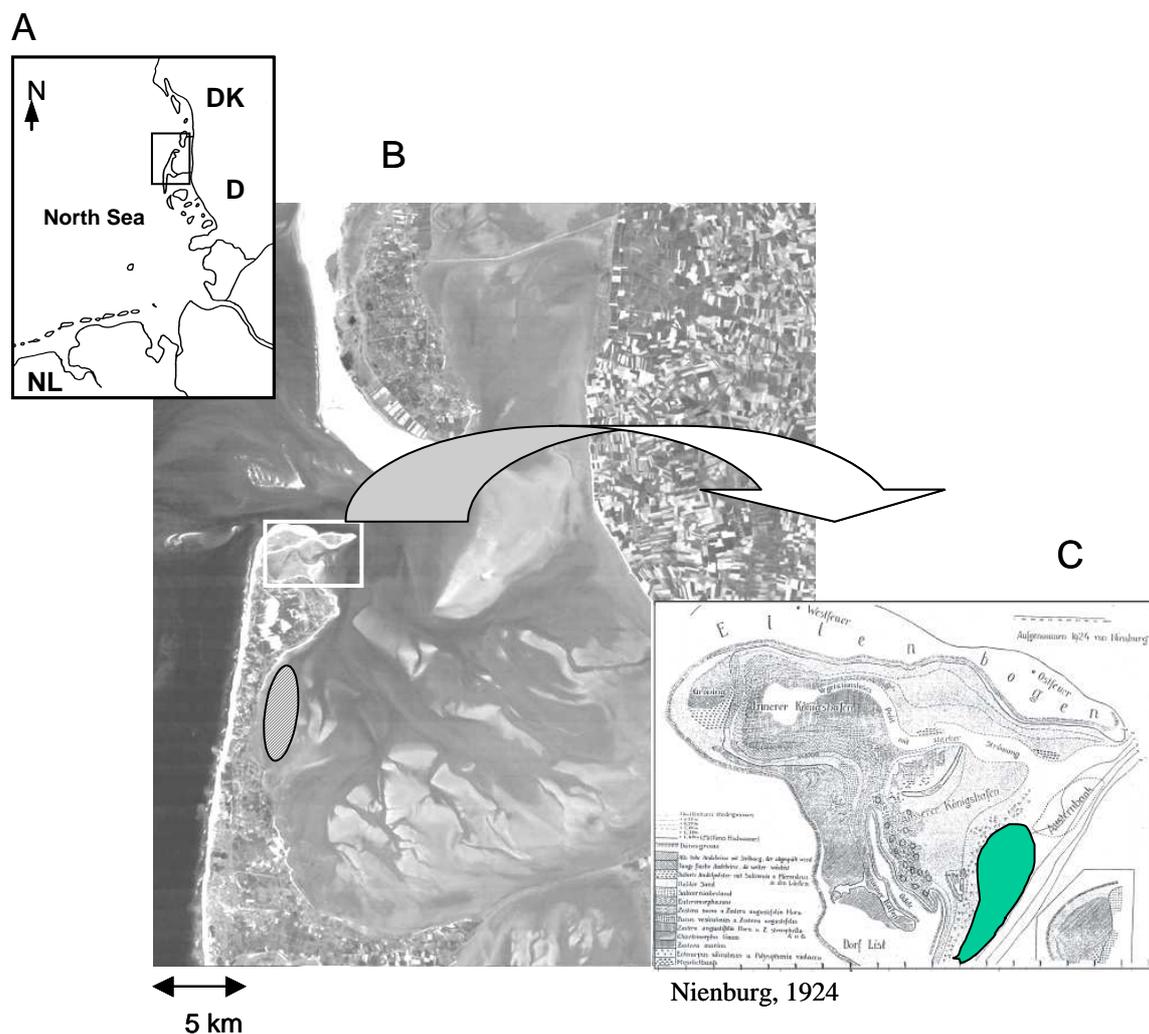


Fig. 1 Location of the Sylt-Rømø Bight within the Wadden Sea area (A). The position of the investigated intertidal area (shaded), including mussel beds, *Z. noltii* beds and bare sand flats at the east coast of the Island of Sylt (B). Map (C) was modified after Nienburg (1924) showing the "Königshafen" area with former beds of subtidal *Z. marina* (green area).

Fish composition

Sampling of fish fauna on seagrass- and sand flats as well as on the former *Z. marina* area was conducted using a beach seine (20 m wide, 1.5 m high, mesh size:

10 mm). The seine was set by a small boat and hauled to the beach by two people over a distance of 80 m, while the opening of the seine was 15 m wide. After trawling a distance of 60 m, the mouth of the seine was closed to minimize sampling artefacts according to depth gradients. The investigation area was 900 m². Seine fishing on intertidal sites was carried out at high tide at a water depth of 0.7 to 1 m, monthly from April to September 2003. The former *Z. marina* area was sampled monthly from May to September 2003 at low tide, at a similar water depth than the intertidal sites.

The mussel bed was sampled monthly from June to November at high tide. Four replicate transects of 250 m length were fished using a dredge (1 m wide, mesh size 10 mm). The trawl velocity was about 1.5 knots at a water depth of 1.5 to 2 m. Fishes were separated from mussel and algal by catch on board of the research vessel FS "MYA" and stored in sea water.

Fishes caught by both sampling techniques were determined to species level, counted and divided into "young of the year"- and 0+ groups due to total body length.

Changes of fish assemblages due to seagrass loss

To evaluate changes in shallow water fish assemblages, results were compared to historical data on the species composition of fish associated with subtidal *Z. marina* beds.

Faunal similarity to the *Z. marina* community was calculated for the species number of each investigated habitat according to Sørensen (1948) including species not listed by Wohlenberg (1935).

$$QS (\%) = \frac{2G}{SA + SB} \times 100$$

G = number of species found in area A and B, corresponding to the former *Z. marina* community

SA,SB= number of species recorded either in area A or B respectively

Additionally numbers of fish species found in present habitats as well as in the historical species inventory of *Z. marina* beds (G-species), were recorded explicitly to estimate quantitative consequences of seagrass loss on species richness.

Fish species were roughly classified according to the degree of habitat utilisation based on former observations of particular species biology (Fig. 2) (Wohlenberg, 1935; Dankers et al., 1978), age classes and own previous studies (Polte & Asmus, unpublished) The following groups have been distinguished a) Species spending the major part of their life-cycle in shallow Wadden Sea waters were classified as “residents” regardless of minor tidal and seasonal migration patterns b) Species temporary immigrating Wadden Sea habitats as adults for spawning were characterised as “spawner” and c) Species present predominantly as “young of the year” juveniles during the first period of their life-cycle were classified as “nursery residents”.



Fig: 2 *Z. marina* leaf (A) covered by herring spawn, photograph by Wohlenberg (1935). (B) Leaves of *Z. noltii* covered by herring spawn (2002).

Species that could be attributed to a certain habitat in more than one category (e.g. as adult “spawner” and juvenile “nursery residents”) are listed only once, if possible, due to the habitat linkage corresponding to former descriptions.

Results

Interpretation of documented species compositions attributed to subtidal *Z. marina* habitats

Wohlenberg, 1935 attributed 17 species to the fish community of subtidal *Zostera marina* beds in the shallow subtidal zone of the “Königshafen” (Table 1). This assemblage was mainly composed of small-sized species as e.g. pipefishes (Syngnathidae, *Entelurus aequoreus*), sea-sticklebacks (*Spinachia spinachia*) and eelpouts (*Zoarces viviparus*).

Table 1 Fish species attributed to subtidal *Z. marina* habitats by Wohlenberg (1935) and those found in present habitats. Species were classified to functional groups according to their habitat linkage.

	<i>Z. marina</i> , Wohlenberg 1935	* former <i>Z. marina</i> location	mussel bed	sand flat	<i>Z. noltii</i> bed
<i>Agonus cataphractus</i>	R	—	R	—	—
<i>Syngnathus rostellatus</i>	R	R	R	R ^a	—
<i>Syngnathus acus</i>	R	—	R	R ^a	—
<i>Syngnathus typhle</i>	R	—	—	—	—
<i>Entelurus aequoreus</i>	R	—	—	—	—
<i>Myxocephalus scorpius</i>	R	—	R	—	—
<i>Pholis gunellus</i>	R	—	R	—	—
<i>Pomatoschistus minutus</i>	R	R	R	NR	NR
<i>Zoarces viviparus</i>	R	—	R	—	—
<i>Spinachia spinachia</i>	R	—	—	—	—
<i>Psetta maxima</i>	NR	—	NR	—	—
<i>Anguilla anguilla</i>	NR	—	NR	—	NR
<i>Platichthys flesus</i>	NR	—	—	—	NR
<i>Belone belone</i>	SP	—	—	—	SP
<i>Clupea harengus</i>	SP	NR	—	NR	SP
<i>Gasterosteus aculeatus</i>	SP	—	—	—	SP
<i>Cyclopterrus lumpus</i>	SP	—	SP	—	—
<i>Ciliata mustela</i>	—	—	R	—	—
<i>Liparis liparis</i>	—	—	R	—	—
<i>Merlangius merlangus</i>	—	NR	NR	NR	NR
<i>Gadus morhua</i>	—	—	NR	—	—
<i>Ammodytes tobianus</i>	—	NR	—	NR	NR
<i>Hyperoplus lanceolatus</i>	—	NR	—	NR	—
<i>Atherina presbyter</i>	—	—	—	—	NR
<i>Mugil chelo</i>	—	—	—	—	R ^a
<i>Trisopterus luscus</i>	—	—	—	—	NR
<i>Osmerus eperlanus</i>	—	—	—	—	NR
<i>Engraulis encrassicolus</i>	—	—	—	—	NR
<i>Pleuronectes platessa</i>	—	NR	NR	NR	NR
<i>Pomatoschistus micops</i>	—	R	R	R	R

R= resident species; NR=nursery residents; SP= Spawner

* presently unvegetated,
shallow subtidal

a = resident but tidal migrator

Despite possible seasonal fluctuations (e.g. migration to deeper water layers during winter) these species are considered to spend most of their life in a particular area. Therefore, they were classified as “residents”. Some larger, pelagic species as garfish (*Belone belone*) and herring (*Clupea harengus*) were described as regular, seasonal immigrant utilising seagrass beds as spawning ground. Additionally nest building species with distinct parental care behaviour as the stickleback (*Gasterosteus aculeatus*) and the lumpfish (*Cyclopterus lumpus*) were considered to be associated to complex seagrass canopies providing suitable spawning substratum. In this study both groups were summarised and classified as “spawner”. Flatfishes as turbot (*Psetta maxima*) and flounder (*Platichthys flesus*) are known to inhabit shallow, coastal waters as nursery areas during a relatively short period within their life cycle. Thus their occurrence in former *Zostera* beds is assumed to be temporally limited and therefore they were classified as “nursery residents”. The same is assumed for eels (*Anguilla anguilla*). This katadromous species has a limited habitation period in the tidal basin and individuals are predominantly subadults.

In this study, the classifications of fishes into certain functional groups partly differ on species level due to age classes. For example the individuals of herring were composed of 0-group specimens and therefore were regarded as “nursery visitors” instead of “spawner”. 0-group gobiid fishes (*Pomatoschistus minutus*) found in the intertidal areas were attributed to “nursery residents” whereas adult fishes found in the shallow subtidal zone were classified as “residents”. Herring (*Clupea harengus*) and Sticklebacks (*Gasterosteus aculeatus*) were classified as “spawner” in intertidal *Zostera noltii* beds because of extended amounts of eggs attached to seagrass leaves and huge amounts of females carrying ripe ovaries respectively (Polte & Asmus, unpublished).

According to high densities of juveniles, the sand smelt (*Atherina presbyter*), was classified as “nursery visitor”. Although adults specimens are assumed to spawn inside *Z. noltii* beds but evidence by is lacking so far.

Faunal similarity

The species similarity of present Wadden Sea habitats compared to the fish composition described for the former *Z. marina* community was predominantly

influenced by additional species found, which were not listed by Wohlenberg (1935) (Table 1). In the investigated present habitats a total of 13 species were found that were not listed for the *Z. marina* community. Mainly according to the number of additional species found, the maximum species similarity was $Q = 61\%$ on the investigated mussel bed (Fig. 3), whereas the presently unvegetated former *Z. marina* area contained the lowest Sørensen ratio ($Q = 26\%$).

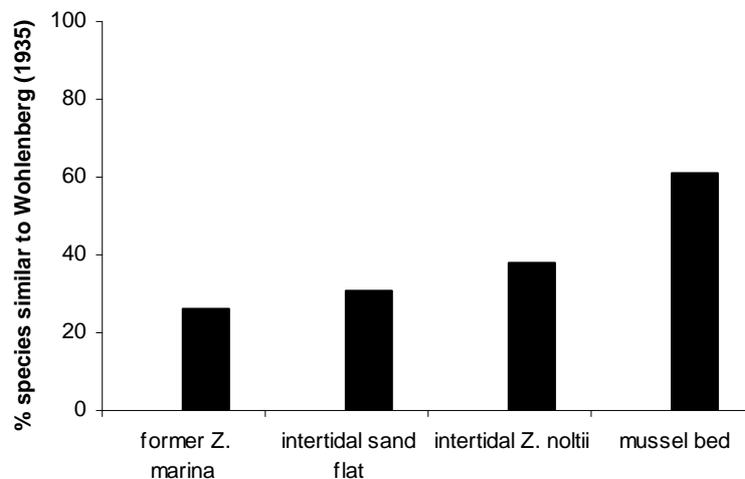


Fig. 3 Sørensen ratio of species found in presently existing habitats corresponding to the species composition of *Z. marina* beds described by Wohlenberg (1935). The highest similarity of species composition was found on mussel beds.

Numbers of species found in present habitats that explicitly corresponds with the former *Z. marina* community (G-species) is shown in Fig. 4. Within each of the investigated coastal habitats species of the former *Z. marina* community could be found. The mussel bed contained the majority of corresponding species ($G=10$). 6 G-species were recorded in *Z. noltii* beds and four species were found on bare sand flats while visiting the intertidal zone. In the sandy, shallow subtidal area of the former *Z. marina* bed, only three G-species were detected.

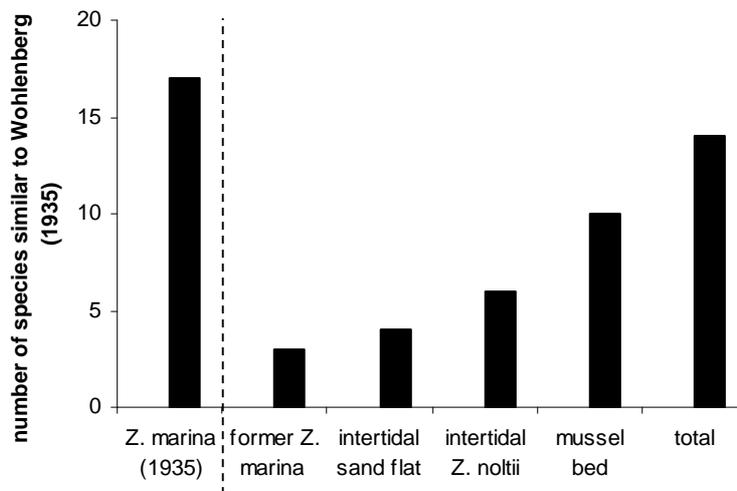


Fig. 4 Numbers of species found in different Wadden Sea habitats corresponding to former fish composition. The total amount of recovered species showed a difference of three species compared to the historical documentation.

Due to the different investigated habitats various species showed overlapping distribution patterns (Table 1). Thus a synopsis of corresponding species currently occurring in diverse Wadden Sea habitats resulted in a total amount of $G=14$, and displayed a difference of three species (Table 1), which were listed by Wohlenberg (1935), but were not found in present habitats.

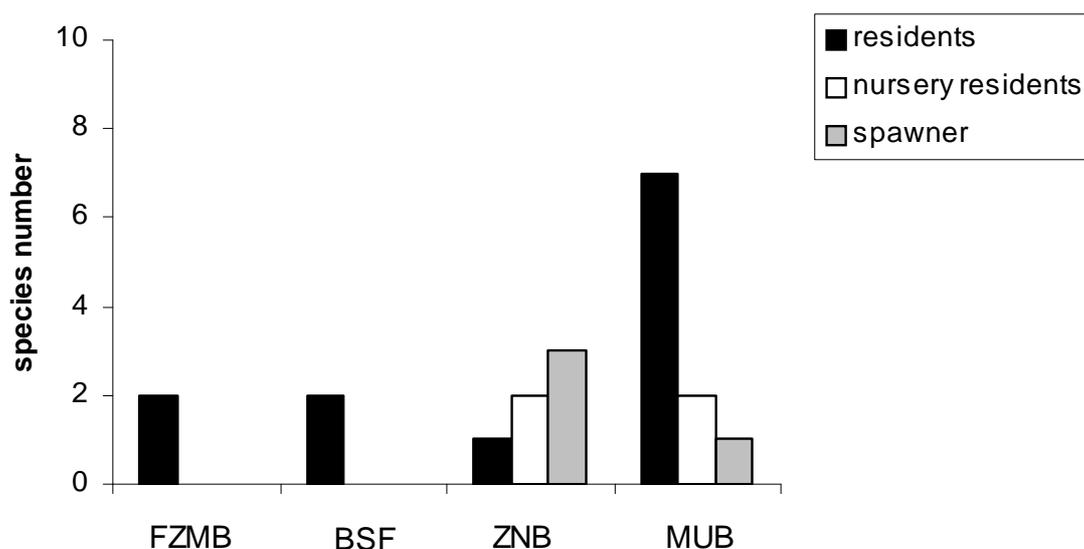


Fig. 5 Composition of (G-) species, corresponding with historical data, found in the former *Z. marina* area (FZMB), on bare sand flats (BSF), in an intertidal *Z. noltii* bed (ZNB) and on a intertidal mussel bed (MUB) separated due to habitat linkage. The occurrence of “spawner” and “nursery residents” were limited to *Z. noltii* beds and mussel beds. Tidal basin residents were additionally found migrating to sand flats and in the formerly vegetated subtidal area.

Changes of fish assemblages due to habitat linkage

The fish community formerly described for the lost *Z. marina* beds were predominantly composed of “residents” (R= 10) (Fig.5).

The investigated mussel bed contained the majority of corresponding resident species (G-R= 7). Classification of G-species to functional groups reduced the number of corresponding species in the shallow subtidal (former *Z. marina* area) and on bare sand flats because type of habitat linkage differed on species level (e.g. herring occurred as “nursery visitor” but not as “spawner”). As a result composition of G-species was exclusively limited to few residents (G-R= 2) in both habitats (Fig. 5) (see Table 1 for particular species). G-species of “nursery visitors” (NV) and “spawner” (SP) were confined to *Z. noltii* meadows (G-NR= 2, G-SP= 3) and mussel beds (G-NR= 2, G-SP= 1). G-species found in both habitats represented the whole amount of “nursery visitors” and “spawner” documented for the former *Z. marina* community (Fig. 6).

Three species were not recovered in the present study (Fig. 6). The sea stickleback (*Spinachia spinachia*), the broad-nosed pipefish (*Syngnathus typhle*) and the snake pipefish (*Entelurus aequoreus*) formerly described as tidal basin residents, could not be found during the investigation period

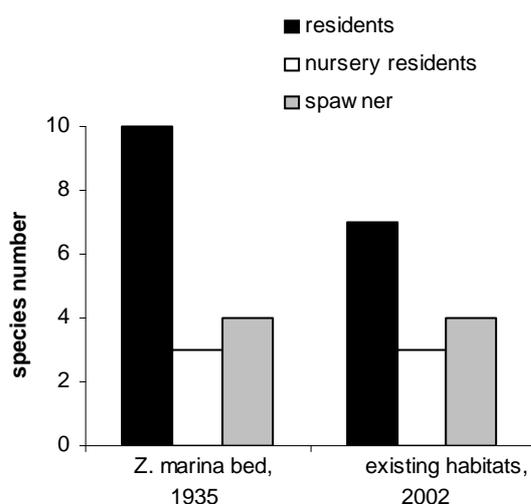


Fig. 6 Species numbers separated due to habitat linkage as it is documented for the *Z. marina* community (Wohlenberg, 1935) and as it was presently found in all existing habitats investigated. The difference in species composition finally observed included an amount of 3 “resident species”.

Discussion

The present study is based upon results received by varying sampling methods and field observations. Therefore it represents a qualitative overview of historical changes within shallow water fish assemblages of Wadden Sea habitats. Sampling artefacts are not considered to be of major relevance, as species abundances could not be involved in faunal reconstructions due to the lack of quantitative pre-impact data. Consequently no predictions can be made on individual densities or biomasses that may have changed during the last 70 years according to seagrass loss. In the present case comparisons of species numbers are assessed as a suitable tool to demonstrate capacities of present Wadden Sea habitats to maintain species richness of shallow water fish community.

The basis of this study was the species composition of fishes attributed to the former *Zostera marina* community and listed by Wohlenberg (1935). Dealing with this species list is not unproblematic in at least two respects: 1) sampling methods Wohlenberg (1935) used are not possible to reconstruct. It is assumed that most information documented is based on field observations and communication with local fishermen. 2) other complex bottom structures such as oyster beds and *Sabellaria* reefs existed simultaneous to seagrass beds in the deeper subtidal zone (Hagmaier & Kaendler, 1927). These habitats completely disappeared because of over-exploitation and wilful destruction respectively to prevent fishing gear from being damaged (Riesen and Reise, 1982; Reise and Schubert, 1987). As a result the degree for which the documented *Z. marina* community was additionally influenced by these types of biogenic substrata is hardly possible to reconstruct.

Nowadays, subtidal parts of the Sylt-Rømø Bight are considered to be dominated by bare sediments. Thus the observed changes of shallow water fish assemblages are likely to be interpreted as consequences of habitat loss. However, climatic changes and fishery impacts can not be excluded to interact with the observed changes.

The classification conducted due to the functional role of Wadden Sea waters was simplified after Zijlsta (1978). He differentiated between “resident” - and “near-resident” species and defined residents as species “staying in the area during their whole life-cycle and consequently in all seasons”. “Near residents” in contrast included species “staying in the area during the larger part of the year”, but leave the area for spawning in the ocean or in fresh water respectively, or migrate into deeper

waters during winter. A summation of both groups was considered as beneficial in this study to point on functional roles of habitats. The same is true for the group of “nursery visitors”. Here Zijlstra (1978) differentiated between species “for which the Wadden Sea functions as the main nursery of their North Sea population” as well as species of which juveniles occasionally immigrates to the Wadden Sea but “to which the area does not represent an indispensable nursery”.

Classification of fish species to the group of “spawner” based primarily on own previous studies (Polte & Asmus, unpublished) and former descriptions of particular species biology (e.g. Dunker et al., 1929).

Even if they are considered to belong to more than one group, species were listed once to clarify changes of species numbers according to habitat relation. To meet correspondence to historical data usually the group was chosen which fitted to habitat linkages formerly described. As a result garfish (*Belone belone*) and lumpfish (*Cyclopterus lumpus*) were classified as “spawner” although additionally juvenile individuals were observed temporary inhabiting the particular spawning grounds for nursery (Polte & Asmus, unpublished; Buschbaum pers. Comm.).

Results showed that three species (*Spinachia spinachia*, *Syngnathus typhle* and *Entelurus aequoreus*) attributed to the former *Z. marina* community were absent in investigated biotopes present in the northern Wadden Sea. These findings are consistent with previous descriptions of consequences that the disappearance of subtidal seagrass beds had on the fish composition after the “wasting disease” (Wolff, 2000). The snake pipefish *Entelurus aequoreus* often mentioned in context with Wadden Sea seagrass loss (Asmus & Asmus, 2000) was absent in the present study but was recently observed within the investigated Wadden Sea area in association with the invasive macro algae *Sargassum muticum* (Buschbaum pers. comm.). In the “Red list of threatened lampreys and marine fishes of the Wadden Sea”, Berg et al. (1996) evaluated the broad-nosed pipefish (*Syngnathus typhle*), the greater pipefish (*Syngnathus acus*) and the sea-stickleback (*Spinachia spinachia*) as endangered or vulnerable species respectively according to extensive habitat loss. *Syngnathus acus* appearing on the “Red List” as a vulnerable species was found in this study inhabiting the mussel bed as well as migrating to bare sand flats with the raising tide.

In the North Sea, two of the missing species in investigated habitats inhabit shallow water habitats outside the Wadden Sea. Thus *Spinachia spinachia* and *Entelurus aequoreus* were found associated to macro algae (*Laminaria spp.*) at the island of Heligoland (own observations). Consequently most of the fish species listed by Wohlenberg (1935) are considered as opportunists who potentially cope with inhabiting different types of complex substratum. Only the broad-nosed pipefish (*Syngnathus typhle*) might be as strictly specialised to subtidal seagrass environment as the geographical nearest evidence of its occurrence is located in the Limfjord, Denmark where extended *Z. marina* stocks are present about 300 km northward of the Sylt-Rømø Bight (Götz, 2004).

Referring to functional categories chosen, results indicated that missing species belong exclusively to the group of “residents”. Entirely all of the “nursery visitor” and “spawner” species described for the former *Z. marina* community in the Sylt-Rømø Bight were still occurring in existing mussel beds and intertidal *Z. noltii* meadows. While intertidal seagrass beds were predominantly used as spawning grounds by transient fishes, mussel beds provided suitable refuges for most of the “residents” of former seagrass beds. Tidal migrating „nursery visitors“ to an almost similar amount frequented both habitats.

In summary the results indicate minor consequences of substantial seagrass loss on fish assemblages of the Wadden Sea. However, changes of individual densities or reproductive success are impossible to evaluate, since quantitative pre-impact data are not available. The drastic decreases of herring stocks documented for the northern Wadden Sea (Wohlenberg, 1935) and for the White Sea (Gemp & Bryzova 1968, Goscheva 1970, Wechov 1987, Rachor, pers. com.) suggest quantitative consequences attributed to the loss of spawning grounds according to the disappearance of subtidal *Z. marina*. Additionally mussel- and *Z. noltii* beds presently cover a relatively low percentage of Wadden Sea area. They are therefore considered as residual habitats. Consequences of historical seagrass loss are assumed to become visible more drastically on species level if those residual refuges will further decrease. Mussel beds and *Z. noltii* beds were found to keep specific habitat functions for particular species. Losses of species and reproductive success of Wadden Sea fish fauna may have been buffered on ecosystem level by the diversity of those remaining biogenic habitats.

Conclusions

Mussel beds and *Z. noltii* meadows formerly coexisted in the “Königshafen” subsystem with subtidal seagrasses (Nienburg, 1924). Unfortunately no data are available about the ecological role of those intertidal bottom structures for fish diversity before the wasting disease took place in the 1930`s. Thus it can only be hypothesised that they provided similar functions as they presently do but were of minor importance as complex habitats due to the presence of extended *Z. marina* beds. Today however, they are considered to represent essential, residual habitats conserving species richness and providing important facilities for fish reproduction.

Implications

The results of the present study suggest that the survival of mussel beds and *Z. noltii* meadows lowered the consequences of subtidal seagrass loss qualitatively while consequences on fish abundances could not be taken into account. If those residual habitats decline, the consequences of seagrass losses would become more drastic decades ago. If on the other hand a re-establishment of subtidal seagrass beds will ever occur in the Wadden Sea, there is a chance for a recovery of the fish assemblage as long as residual resources preserves the species pool.

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General Discussion

4 General Discussion

4.1 Impact of intertidal *Z. noltii* beds on epibenthic macrofauna and fishes

Seagrass beds in the intertidal zone of the Wadden Sea were hardly noticed as ecologically significant for the composition of associated fauna, because this assemblage was assumed not to differ significantly from that generally common on tidal flats (den Hartog, 1983). Thus, after the loss of subtidal seagrass beds the nursery function described for the Wadden Sea is no longer attributed to single biogenic habitats, but is generally considered as a function of sheltered locations and a consequence of a rich food supply provided by the whole ecosystem (Zijlstra, 1972; Cattrijsse et al., 1997; del Norte-Campos and Temming, 1998; Hostens and Mees, 1999; van der Veer et al., 2001). The faunal uniformity of intertidal *Zostera noltii* beds is in contrast to other particularly subtidal seagrass systems in the world, harbouring a specific faunal community. In the Wadden Sea only two species of herbivorous isopods (*Idotea balthica*, *I. chelipes*) showed closer ties to the seagrass habitat and were absent on bare sand flats.

An increase of epifaunal diversity estimated for numerous seagrass habitats worldwide (Bell et al., 1992; Edgar and Shaw, 1995; Heck et al., 1995; Borg and Phil, 1997; Bostöm and Bonsdorf, 1997; Matilla et al., 1999) could not be assigned to the *Z. noltii* beds of the Wadden Sea as long as only species numbers are considered. The reason for this extensive similarity of species composition on vegetated and unvegetated tidal flats is probably that the appearance of above ground parts of the plants is restricted to the summer months. Due to this relatively short vegetation period (May to September) seagrass beds in the Wadden Sea are not representing permanently available habitats throughout the year and therefore prevent the settlement and development of sessile- and mobile fauna specialised on seagrass habitats. Since the vegetation period of intertidal seagrasses coincides with the main recruitment period of dominant macrofaunal species and with temporary appearance of several fishes in shallow water areas, various ecological functions were identified that *Z. noltii* beds fulfil for species in the Wadden Sea. Several functions provided by *Z. noltii*, such as offering spawning places or nursery areas, were proven to increase numbers of fish species visiting tidal flats and

significantly increase abundances and secondary production of juvenile mobile epibenthos compared to unvegetated intertidal areas. This way *Zostera noltii* beds even enhance the ecological function of inherently valuable intertidal areas. Considering the consistency of the species pool between intertidal seagrass beds and other intertidal areas, it is stated that the extent of ecological functions and the support of biodiversity is not necessarily linked to a habitat-specific faunal composition.

4.2 Basic differences between subtidal- and intertidal seagrass systems

Due to the fact that present seagrass beds in the Wadden Sea are restricted to the intertidal zone, ecological features beneficial for fishes and mobile epibenthos in the northern Wadden Sea, differ significantly from those generally attributed to subtidal seagrass beds.

Habitat functions for fish and invertebrate species most frequently attributed to seagrass beds are (a) providing a permanent habitat, that allows the fauna to accomplish a full life cycle (Jackson et al., 2001) (b) representing important feeding grounds due to increased food supply compared to unvegetated areas (Edgar and Shaw, 1995b) (c) providing important nurseries for juvenile stages (Orth et al., 1984; Heck et al., 1995) and (d) supporting of larval pre- and post settlement processes (Orth and van Montfrans, 1987; Boström and Bonsdorff, 2000; Moksnes, 2002). An explicit factor subordinated to (a) and (c) is providing shelter from predation caused by increased habitat complexity (Heck and Thoman, 1981; Virnstein, 1984; Isaksson and Pihl, 1992; Hindell et al., 2001). To demonstrate similarities and differences to those primary functions of subtidal and intertidal seagrass beds, an overview is given in Table 1 and particular ecological functions are discussed in the following:

Table 1: Primary habitat functions for fishes and invertebrates provided by subtidal seagrass beds (see review in Jackson et al., 2001) vs. those identified for *Z. noltii* beds in the northern Wadden Sea.

Function for fishes and decapod crustaceans	Subtidal seagrass bed	Intertidal seagrass bed
Habitat for resident species	+	-
Spawning ground	(+?)	+
Constant nursery	+	-
Shelter from predation	+	(+)
Increased food supply	+	+
Promotion of larval settlement	+	+
Ebb tide refuge (intertidal)	-	+

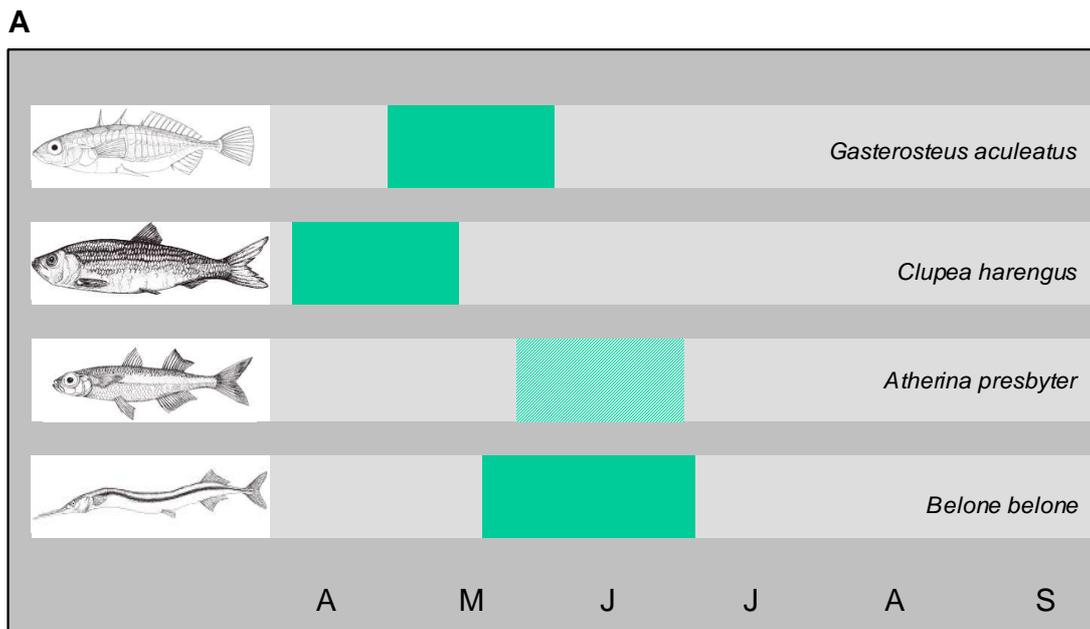
4.2.1 Permanent habitat for residents

A prominent difference to subtidal meadows is the absence of species permanently resident in *Z. noltii* beds. Seagrass residents are primarily dominated by small and stationary species (e.g. pipefishes) without major relevance for fishery (Kikuchi, 1974). In general the minority of fishes associated to seagrasses permanently inhabit these habitats during their entire life cycle. However, as intertidal seagrass beds in cold temperate zones are only temporarily available habitats on a) tidal scale: long emersion periods during ebb tide and b) seasonal scale: absence of (above ground) plants during winter, they provide no suitable niche for stationary species. The common goby (*P. microps*) was the only species found inhabiting the intertidal zone during the entire tidal cycle but regularly migrated to deeper waters in winter. As the occurrence of common gobies is not restricted to vegetated tidal flats they are to be classified rather as an intertidal (summer) resident than a seagrass resident. Despite the migration of most mobile species to deeper waters during winter, when harsh environmental conditions predominate in shallow Wadden Sea waters, they are considered to represent Wadden Sea residents (Zijlstra, 1978). According to that, seasonal migration patterns due to temperature might be generally superimposed to habitat linkage in the Wadden Sea.

4.2.2 Functional roles of intertidal seagrasses for temporary visitors

Seasonality

The investigation of influences of seagrass beds on the occurrence of transient fishes on tidal flats was complicated by strict seasonal distribution patterns of particular species. However, for the Sylt-Rømø Bight area, this study gives an overview on the variety of fish species periodically immigrating into upper tidal flats with the rising flood, and the study describes the extremely strong seasonality of species occurrence on intertidal areas. (see publ. II for detailed description). Separating between adult visitors and juvenile (0-group) fishes Fig. 1 summarises the appearance of fishes during the season from late April to the end of September 2003.



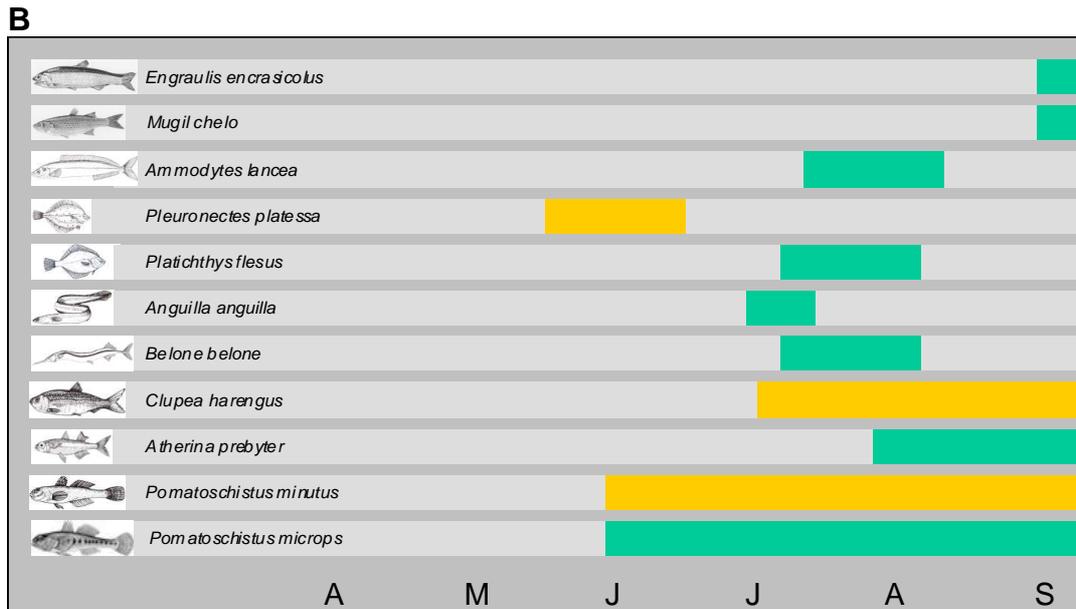


Fig. 1 Seasonal distribution of A) adult fishes immigrating into tidal flats in respect of spawning and B) 0-group juveniles mainly visiting the intertidal zone temporarily with the raising flood. Distribution patterns indicate preferences for seagrass beds (green bars) or sand flats (yellow bars). *A. presbyter* was included in spawning species (A, shaded bar) based on numerous indications (hatched juveniles, mature adults), but evidence by explicitly finding eggs is still lacking (see below 5.2)

4.2.3 Seagrass beds as spawning grounds

Although seagrass beds are often cited to represent important spawning grounds for fishes, explicit examples are scarce in the current literature.

Among those fish species found to enter tidal flats for inshore spawning, this was clearly linked to seagrass cover. They all produced demersal eggs but pursued different spawning strategies.

Garfish

The eggs of the garfish are widely described to be found attached to bottom structures such as plants and rocks. Although the information available about locations of garfish spawning grounds in Baltic- and North Sea is rather anecdotal, and it is assumed that spawning of *B. belone* is not exclusively restricted to the presence of seagrass beds. However the results of this study suggests that *Z. noltii* beds are an essential substratum for demersal garfish eggs in the Wadden Sea

because relevant alternatives, as e.g. the dominant macroalga (*Fucus vesiculosus*) was found to represent no suitable spawning structure (publ. III) and rocky hard substratum is scarce. Spawning of garfishes in the subtidal zone could not be completely excluded during this study, but according to investigations conducted by von Westernhagen (1974, 1975) it is suggested that higher temperatures measured in the intertidal zone (publ. III) significantly promotes the rate of embryonic development, and therefore spawning in this area is of advantage for the reproduction success of this species.

Herring

Because it was not documented that herring (*Clupea harengus*) presently frequents the Wadden Sea for spawning. Therefore the spawning activity of the herring in the upper intertidal zone was rather surprising. Additional to *Z. noltii* plants aggregations of *Fucus vesiculosus* attached to bed groynes were densely covered by spawn, whereas on *Fucus* associated with mussel beds located in the lower intertidal zone no spawning occurred. A spawning event similar to that observed in early April 2002 (quantitatively demonstrated in publ. III) has been noticed in May 2004 when high densities of herring spawn were found attached to *Z. noltii* leaves in a distance of about 30 m from the shore line close to the high tide mark. Although the seagrass-spawning grounds of the northern Wadden Sea are not considered to be of quantitative relevance for North Sea herring stocks, their existence however might be of particular importance: The “adopted-migrant” hypothesis (McQuinn, 1997; Corten, 1993; Corten, 2001) assumes that juvenile herring learn to find suitable spawning grounds by following the adults. This would significantly increase the meaning of local spots for genetic diversity also indicates to a proceeding recovery of eastern North Sea populations (Zimmermann pers. com.).

In addition it proves the existence of a local spring herring stock in the German Wadden Sea.

Stickleback

Camouflaged nests of the three-spined stickleback (*Gasterosteus aculeatus*) were only sporadically be found within dense seagrass canopies. The majority of female individuals caught within *Z. noltii* beds in late spring, however, carried ripe ovaries.

Due to the layer of residual water remaining on vegetated tidal flats at low tide, intertidal seagrass beds provide suitable spawning grounds for small species with distinct parental care behaviour.

4.2.4 The nursery role

Availability

Subsequent to the stickleback spawning season, investigations conducted in the Danish Limfjord showed enormous amounts of juvenile sticklebacks inhabiting shallow subtidal *Z. marina* meadows (Götz, 2004). At the same time almost none 0-group juveniles could be found in intertidal *Z. noltii* beds of the Wadden Sea located about 300 km southward. As a result it can be suggested that the role of *Z. noltii* as a spawning ground for a certain species does not necessarily include a function as a nursery for juveniles. Therefore, the stickleback is considered to be a suitable example to demonstrate the key difference between subtidal and intertidal seagrass habitats with respect to the function as a nursery area. In contrast to subtidal beds, intertidal canopies do not provide constantly available nursery habitats for juveniles until a certain juvenile stage has been completed.

Despite the lack of a continuous habitat availability, caused by tidal emergence, a surprisingly large amount of “young of the year” juvenile fishes were found preferring seagrass beds during their temporary visit on inundated tidal flats (publ. II). Those fishes were not limited to individuals hatched from eggs attached to seagrass but were to a considerable amount composed of off-shore spawning species such as the European anchovy (*E. encrasicolus*), the small sand eel (*A. lancea*) and the flounder (*P. flesus*) entering coastal waters during their post-larval stages. The reasons for a preference of vegetated tidal flats while immigrating to the intertidal zone might vary according to particular species' biology but seem to be mainly influenced by food supply provided by *Z. noltii* beds.

Refuge from predation

In general intertidal zones of rocky and sandy shores are equally evaluated as important nurseries for invertebrates and fishes (Raffaelli & Hawkins, 1996; Horn et

al., 1999; Amara and Paul, 2003). This could also be validated for the extended intertidal area of the Wadden Sea dominated by sand and mud flats (Zijlstra, 1972; Reise, 1985; Cattrijsse et al., 1997; del Norte-Campos and Temming, 1998; Hostens and Mees, 1999; van der Veer et al., 2001). Due to limited predation pressure abundances of common epifaunal species are generally enriched on tidal flats (Zijlstra, 1972; Beukema, 1992). As tidal flats inherently represent shelter from predation the role of intertidal seagrass cover in this context is difficult to distinguish from the overall effect of tidal flats. However, the presence of dominant predators was found to be increased on inundated *Z. noltii* canopies. Thus the intensity of tidal migration of juvenile whiting (*Merlangius merlangus*) at night differed between vegetated and unvegetated tidal flats (publ. II). When seagrass was present whiting entered the upper intertidal area close to the high tide mark whereas on bare sand flats these fishes remained in the lower intertidal zone within reach of the tidal gulleys. The differing patterns of tidal migration of this predatory fish are suggested to be due to increased densities of epibenthic prey (*Crangon crangon*, *Pomatoschistus microps*) within the preferred size classes (Pohle, 2004). On the other hand increased densities of epifaunal organisms significantly reduce infaunal species such as e.g. newly settled bivalves (Polte, 2000). This demonstrates the central role of epibenthic fauna in the food web of the tidal basin causing a bottom up effect on predatory fishes as well as a top down effect on benthic infauna. It is difficult to decide whether seagrass beds provide significant shelter from predation as it varies according to trophic guild of animals.

Settlement processes

Moksnes (2002) showed that biogenic structures such as epibenthic bivalves (*Mytilus edulis*) and seagrass beds (*Zostera marina*) promotes the larval settlement of shore crabs (*Carcinus maenas*) at the Swedish west coast, whereas due to the enrichment of predators (older juveniles) mortality of settlers was higher in these nursery habitats compared to bare sands. Thus habitat selection at settling was identified as a “proximate process responsible for habitat specific distribution of epibenthic juveniles”. During the present investigations in the intertidal zone of the Wadden Sea, newly settled shore crabs (*Carcinus maenas*) were significantly more frequent in seagrass beds than on bare sands. The maximum abundances of *C. maenas* recruits found in *Z. noltii* beds during June 2003 (711 individuals m⁻²) (publ.I)

was presumably a result of an increasing impact of *Z. noltii* leaves on abundances of *C. maenas* instars by extensively collecting megalopae stages from the water column (Polte, 2000). Major densities of first benthic stages of *C. maenas* found end of June correspond to densities of megalopae sampled during plankton surveys (Strasser, unpublished) and underline the strong influence of settling processes on shore crab abundance. One month after settling density of recruits within the seagrass canopy was reduced by 74 % from 711 individuals m⁻² to 184 individuals m⁻² whereas a decline in density on unvegetated tidal flats was 22 % (46 indiv. m⁻² to 36 indiv. m⁻²). According to Moksnes (2002) the decline of individual densities is attributed to predation pressure, probably caused by older shore crab juveniles, rather than by emigration. However, increased density of conspecific prey implies higher food supply on species level. Thus seagrass habitats contribute significantly to the secondary production of *C. maenas* on tidal flats.

Ebb tide refuge

During the summer season conditions at low tide become extreme for habitation of mobile epifauna in the intertidal zone. Small tide pools and puddles, which are exposed to strong fluctuations in temperature and salinity, represent sporadic resources of residual water where especially shrimps and gobiid fishes accumulate in the upper intertidal zone. The complex structure of dense seagrass beds usually retains a water layer of several centimetres trapped between the leaves during the entire ebb tide period. This canopy water layer (CWL) is used as a refuge by epifaunal species to survive ebb tides without migrating to subtidal zones (publ. I). Abundances of species was demonstrated to be constantly higher within the CWL than in artificially installed tide pools during August, when seagrass density in the investigation areas was highest (12000 shoots m⁻²). Although oxygen level in the CWL dropped drastically at night the epifaunal density remained significantly higher than that measured in tide pools ($p < 0.001$, $df = 2$, $F = 28$). Investigations carried out in the Swedish Skagerrak and the Baltic Sea, (Pihl, 1986; Isaakson and Pihl, 1992; Boström and Bonsdorff, 1997) showed that brown shrimps (*C. crangon*) abundant in the shallow subtidal zone preferred bare sand bottom to *Z. marina* beds. However, in the intertidal zone of the Sylt-Rømø Bight *C. crangon* reached its highest abundance inside the *Zostera noltii* bed. The discrepancy of habitat choice by shrimps between

the subtidal seagrass beds of the Skagerrak and Baltic Sea on the one hand and the intertidal zone of the Wadden Sea on the other hand is probably due to the refuge function of the thin water layer developed in dense seagrass canopies at low tide, causing a preference of juvenile shrimps for vegetated tidal flats.

The function as ebb tide refuge is restricted to intertidal systems, and explains differences between seagrass beds in the Wadden Sea and subtidal beds of other shallow coastal zones by an additional function that may outweigh the loss of ecological importance due to temporary availability.

4.3 Effects of biogenic habitats on shallow water fish diversity

Tidal emergence was identified to represent the predominant factor causing functional differences of subtidal and intertidal seagrass systems. However, evaluating the importance of single marine habitats, individual requirements of species must be taken into consideration. Most dominant fishes and crustaceans inhabiting the Wadden Sea area are opportunists showing less specialisation to a certain habitat. E.g. fishes permanently inhabiting macrophyte habitats often inhabit seagrass- as well as macro algal habitats. The herring (as mentioned above) uses aggregations of *F. vesiculosus* as spawning substratum alternatively to *Z. noltii* beds. The factor water depth might be superimposed to vegetation type, as herring spawn found attached to *Fucus* was limited to the upper intertidal zone, whereas in the lower intertidal zone where *Fucus* was associated with mussel beds, no spawn could be found. The opportunistic biology of many North Atlantic fishes might also have contributed to the low rate of species that disappeared as consequence of the substantial seagrass loss during the “Wasting Disease” in the 1930’s.

Although differences between subtidal and intertidal seagrass habitats are considered to be of major importance for ecosystem functioning, the reconstruction of fish diversity in the investigated areas before the historical seagrass loss showed only few changes compared to the present situation. However, effects on fish density are assumed to be more drastic but cannot be reconstructed, as former abundances of species has not been documented. Dealing with simple numbers of fish species and their linkage to biogenic habitats results showed that three species of small macrophyte residents are missing in the shallow waters of the Sylt-Rømø Bight (Publ. IV). Most recently (one year after the present investigations in summer 2004),

one of those species, the snake pipefish *Entelurus aequoreus* was frequently discovered in the investigation area in association with the introduced macroalgae *Sargassum muticum* (Buschbaum, Polte unpublished observations). Consequently, fish vanishing due to seagrass loss are the sea stickleback (*Spinachia spinachia*) and the broad-nosed pipefish (*Syngnathus typhle*). Although *S. spinachia* can be sporadically found associated to macroalgae in shallow North Sea waters other than the Wadden Sea (own observations at the island of Helgoland), both species are considered to be closely linked with seagrass habitats and are still abundant in subtidal *Z. marina* beds in the Limfjord, Denmark (Götz, 2004). The present results indicate that species diversity of Wadden Sea fish assemblages have been sustained by the coexistence of different habitats on a regional scale. Especially the coexistence of intertidal seagrass beds and mussel beds widely conserves important ecological functions for fishes in the Sylt-Rømø Bight (see publ. IV for details). However, the extent of both habitats is limited to a small percentage of the systems area (*Z. noltii* beds ~12 %; *M. edulis* beds ~ 1 %) (Gätje and Reise, 1998). The effects of historical habitat losses on fishes might be more significant concerning abundances of particular species than species composition. Significant effects on fish diversity may become subsequently visible when those residual habitats will further decrease.

4.4 Methodological considerations

The used beach seine in general is considered as suitable gear for quantitative sampling of fishes on upper tidal flats. Compared to stationary enclosure systems sampling locations and -area dimensions can be adjusted according to bottom type and fish density. Sampling efficiency however is probably linked with hauling speed, which was limited by the power of two people. Therefore abundances received for highly mobile species (garfishes) might have been underestimated. Another problem was the lack of extensive replicate sampling which is caused by a) disturbing interaction of hauls and b) the time needed for one haul did not allow taking more than two samples within (almost) the same tidal period. Unfortunately samples were less accessible to seasonal data pooling because occurrences of fish species were subjected to extreme seasonality (Fig. 1).

Drop trap sampling is considered to be highly effective for quantitative assessment of 0-group, mobile epifauna on inundated tidal flats. According to environmental conditions in intertidal areas with rapid changes of water levels and subsequently effects on faunal abundances, sampling periods with comparable water levels at flood are relatively short. The drop trap allows taking a quantity of replicate samples in a defined time interval during one tidal cycle. Thus individual densities of 0-group plaice (*Pleuronectes platessa* < 30 mm body length) (publ. II), shore crabs (*Carcinus maenas*), brown shrimps (*Crangon crangon*), common gobies (*Pomatoschistus microps*) and isopods (*Idotea spp.*) (publ. I) presented are considered to be highly accurate as standard errors were mostly below 30 % of abundance measured (Pihl & Rosenberg, 1982) when individual density was > 5 individuals m⁻².

4.5 Conclusions

Compared to subtidal seagrass meadows, the role of intertidal seagrass beds as habitat for fishes and crustaceans in the Wadden Sea is less obvious and has not been paid much attention so far. In fact ecological functions of *Z. noltii* beds significantly differ from those widely attributed to various seagrasses constantly submerged. Due to temporary availability induced by periodical tidal emergence and seasonal fluctuations *Z. noltii* beds do not provide suitable habitats for permanent residents and constant nursery areas for larger (pelagic) fishes. In contrast to that they fulfil certain functions for common Wadden Sea species. They provide extensive ebb tide refuges allowing epifaunal organisms to remain on sheltered tidal flats at low tide. In the Wadden Sea intertidal seagrass cover significantly increases individual densities and secondary production of shore crabs (*C. maenas*), brown shrimps (*C. crangon*) and common gobies (*P. microps*). The quantitative enrichment of epifauna is considered to be caused by higher food supply and representing favourable structures for larval settlement. In contrast to the dominant epifaunal species the composition of migratory fish on vegetated and unvegetated tidal flats differs in quality. Despite strong seasonal variability of species occurrence most fishes shows distinct preference of seagrass beds during their residence on inundated tidal flats. For juvenile fishes reasons for frequenting *Z. noltii* beds during flood are assumed to vary according to species (or trophic guild) and therefore must be left for future studies. Adult specimen of common North Sea fishes, however,

evidently utilises *Z. noltii* beds as spawning grounds. For the garfish (*B. belone*), the herring (*C. harengus*), the stickleback (*G. aculeatus*) and (most probable) the sand smelt (*A. presbyter*) can be concluded that intertidal *Z. noltii* beds provide relevant spawning structures in the Wadden Sea. In combination with other (biogenic) habitats seagrass beds sustain diversity of Wadden Sea fish assemblages and definitely contribute to the nursery function of the entire ecosystem.

Remaining questions and
future perspectives

5 Remaining questions and future prospects

5.1 Influences on habitat architecture by plant-morphology

Differences of functional roles between seagrass systems are to a certain degree caused by the morphology of plant species and could not be considered in the present study. However, differences of habitat functions between subtidal and intertidal seagrass beds are certainly not limited to the factor of inundation.

Due to species morphology and plant dimensions seagrasses can differ significantly in respect of habitat complexity (Duarte, 2000; MacArthur and Hyndes, 2001). Studies comparing e.g. *Z. marina* and *Z. noltii* habitats are as problematic where quantity and quality of associated fauna might be influenced by habitat architecture due to species morphology and meadow homogeneity ("patchiness"). *Z. marina* plants with leaf length up to 1.20 m (den Hartog, 1970) are considered to form more complex habitats than meadows composed by the dwarf seagrass (*Z. noltii*) with a maximum leaf length of 22 cm (den Hartog, 1970). Since *Z. marina* in the Wadden Sea does rarely form extended meadows in the intertidal zone and on the other hand *Z. noltii* plants does not penetrate into the subtidal zone, differences between seagrass species in respect of habitat functions are difficult to investigate without considering the impact of depth gradients. With the knowledge of some newly identified functions, future research results will allow comparisons between intertidal *Z. noltii* habitats of the Wadden Sea and subtidal *Z. noltii* beds located at other (European) coasts.

5.2 *Atherina presbyter* Cuvier

Although the distribution of the sand smelt (*A. presbyter*) covers the north-eastern Atlantic from Morocco to the Swedish Kattegat (Moreno and Morales-Nin, 2002) it is predominantly classified as a warm temperate species with its main distribution around the Canary Islands (Pajuelho and Lorenzo, 2000) and the Mediterranean Sea (Guidetti and Bussotti, 2000). Historically the sand smelt was described to sporadically enter the Wadden Sea but was classified as absent in the German parts by Witte & Zijlstra (1978). During this study it could be documented that *A. presbyter* reproduced in the Sylt-Rømø Bight during two successive summers of 2003 and

2004. Adult individuals as well as post larval stages and later, older juveniles have been observed on tidal flats, especially in association with seagrass beds. Additionally post-larval individuals suddenly appeared within seagrass transplants incubated *in vitro* during the summer month of 2004 (Zipperle pers. communication). Thus several indications point to a linkage of spawning of sand smelt with *Z. noltii* cover, as Guidetti and Bussotti (2000) already described for the Mediterranean Sea populations, but direct evidence in the Wadden Sea is still missing. As the spawning biology of *A. presbyter* is similar to that of the garfish by releasing eggs with hairy filaments it might be possible in the future to quantify eggs of the sand smelt within intertidal seagrass beds and to demonstrate adaptations of invasive fishes to Wadden Sea habitats.

Further studies might focus on a) analysis of multiple factors leading to migration of *A. presbyter* into the Wadden Sea for reproduction (e.g. increased water temperatures and presence of seagrass-spawning grounds) and b) the degree to which Wadden Sea food webs are influenced by the introduction of such planktivorous species (Asmus, unpublished).

5.3 Contribution of single habitats to ecosystem functions

The present study shows a significant quantitative enrichment of juvenile epifaunal organisms on tidal flats by the presence of intertidal seagrass beds. Because 0-group individuals are leaving tidal flats in autumn and migrate to deeper water the question arises to which extent epifauna is released from the comparably small seagrass area to total the system and contributes to 0+group stocks of epibenthic prey and thus intensifies the nursery function of the whole tidal basin for North Sea fishes. Predominantly shrimp and gobies of the 0-group age class represent the preferred prey of predatory fishes such as the whiting (Pohle, 2004) who temporary inhabits the Sylt-Rømø Bight as nursery resident.

Future studies dealing with the impact of habitat diversity on the nursery function of the Sylt-Rømø Bight should be extended to mussel beds and other biogenic habitats.

5.4 Effects of seagrass cover on plankton and nekton density

Among the fishes found preferring *Z. noltii* beds during their presence on tidal flats numerous were planktivorous (e.g. *Atherina presbyter*, *Engraulis engrassiculos*, *Clupea harengus*). Their occurrence in the upper intertidal zone is attributed to increased food supply rather than shelter from predation.

Own (unpublished) preliminary observations using a bongo net (meshsize: 500 μm) on vegetated and unvegetated tidal flats indicated higher densities of planktonic organisms and pelagic crustaceans (e.g. mysids) within the water column above the seagrass canopy than above bare sands. Investigations on this subject could not be consolidated during the present study but are suggested as important for an entire understanding of ecological functions provided by intertidal seagrass beds.

General References

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