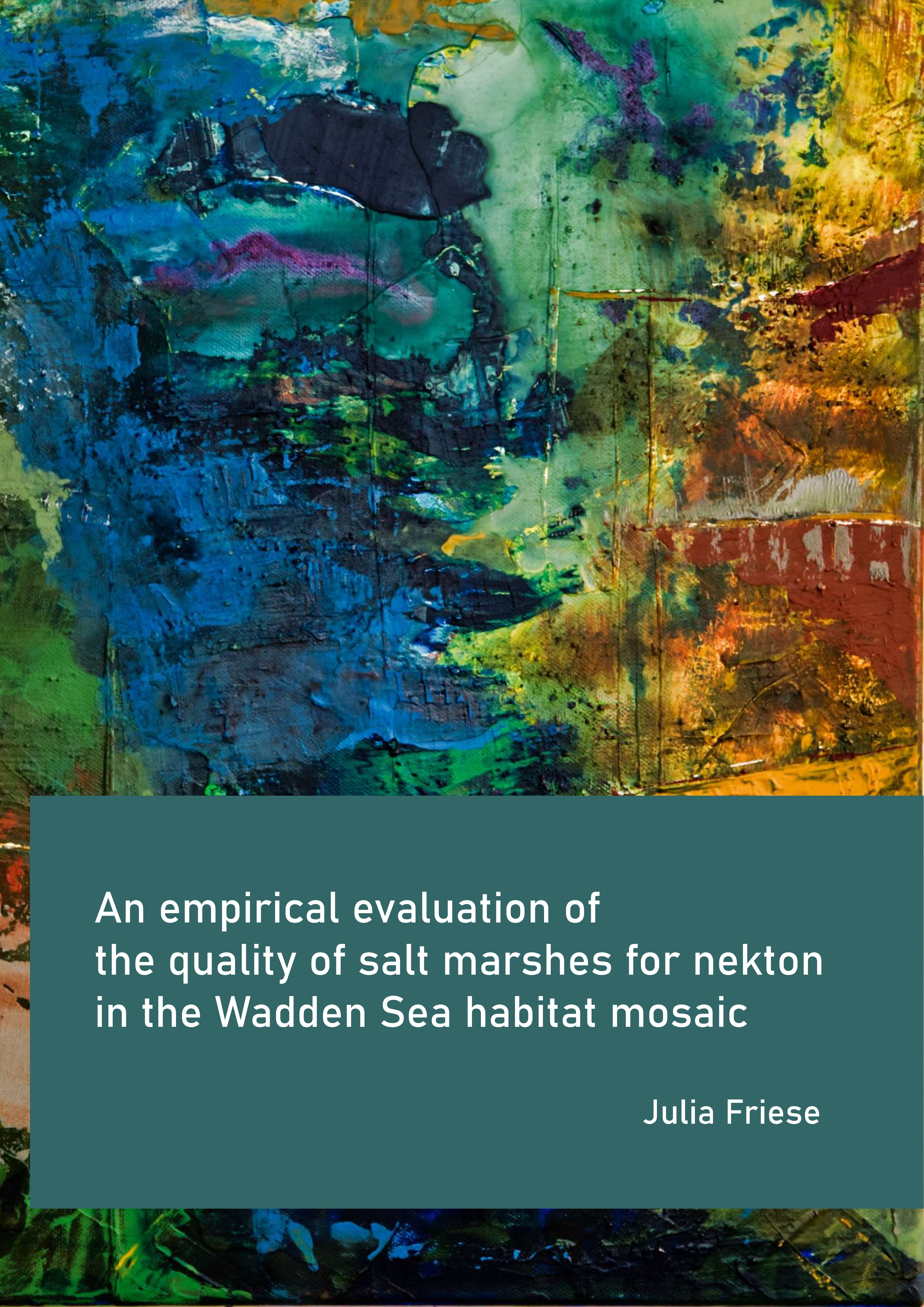

An empirical evaluation of the quality of salt marshes for nekton in the Wadden Sea habitat mosaic

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AN EMPIRICAL EVALUATION OF THE QUALITY OF SALT MARSHES FOR NEKTON IN THE WADDEN SEA HABITAT MOSAIC

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“The marsh is like a nursery,

where little fish can hide.

They eat the food that´s brought their way

with each new rising tide.”

From the children´s book
“A day in the salt marsh”
by Kevin Kurtz

Contents

Summary

In the Wadden Sea, a shallow coastline and a large tidal amplitude result in an overlap of land and sea, creating a unique pulsing ecosystem. The landward edge of this intertidal area is framed by salt marshes, that evolve, where low flow velocities allow for sediment accretion and settlement of halophytic plants. Salt marshes are valued worldwide as high-quality habitats for fish and crustaceans, because they provide shelter from predators and profitable feeding conditions. In the Wadden Sea, however, land reclamation, coastal protection measures, and agriculture have changed shape and function of salt marshes over centuries. Naturally meandering salt-marsh creeks connecting i. a. intertidal pools were largely replaced with short and straight creeks to ensure optimal dike drainage. Whether these mostly artificially created salt marshes can still support marine fauna and which species enter the confined salt-marsh creeks, hazarding beaching and unfavourable temperatures, was mostly unknown and is now addressed by this thesis. For the Wadden Sea area, it is the first comprehensive study showing which nekton species are characteristic for marine Wadden Sea salt marshes, evaluating habitat quality based on abiotic conditions, predation pressure, food availability and the body condition of fish, and examining the human impact on this habitat type, particularly sheep grazing.

Chapter 1 introduces the subject of habitat quality evaluation and the value and theoretical concept of marine nurseries. Subsequently, salt marshes – the key habitat type of this study – are introduced concerning their typical characteristics and their value for fish and crustaceans. Afterwards, the regional specifics of Wadden Sea salt marshes are addressed describing their development and shape as well as their difference to other well-studied marshes. Finally, Chapter 1 identifies knowledge gaps and provides an outline of the thesis, including the research questions and hypotheses addressed in the single chapters.

Based on an inventory of the specific nekton community of German salt marshes, **Chapter 2** investigates habitat affinity as well as diurnal and seasonal abundance patterns. The salt marshes were inhabited by a specific, relatively species-poor and small-sized, nekton community, differing significantly from the adjacent subtidal. These findings reveal that some species found in the subtidal avoided the marsh creeks while others, e. g. common goby *Pomatoschistus microps* and brown shrimp *Crangon crangon*, preferred it. The composition of the salt-marsh-specific nekton community changed in the course of a year and included postlarvae, juveniles as well as adults of small-sized species. The preference for salt-marsh creeks by nekton can be related to smaller body sizes rather than to distinct life stages. One possible

explanation could be a low predator density in this habitat. Marshes with shorter access pathways to the subtidal tended to have higher nekton abundances. Obviously, the habitat quality for nekton depends not only on the specific habitat properties, but also on the accessibility and the quality of interconnected habitats in the seascape. The results demonstrate that Wadden Sea salt-marsh creeks are valuable habitats for small nekton, providing shelter from predators. Thus, small nekton using this habitat type will probably increase their chance of closing the life cycle.

Chapter 3 examines the abiotic habitat conditions of Wadden Sea salt marshes. Small-scale seasonal and tidal dynamics of hydrological (temperature, oxygen) and hydrodynamic (flow velocity, turbidity, sediment grain size) parameters were measured in four salt-marsh creeks and partly in the adjacent offshore area (tidal flat and subtidal) in the German Wadden Sea. The small water body in the marsh creeks adapted rapidly to the air temperature, resulting in seasonally more extreme temperatures than the subtidal. Despite temperature extremes in summer, oxygen concentrations were still sufficient for fishes and crustaceans, probably due to the primary production and tidal mixing. Compared to the subtidal, lower flow velocities, lower turbidity and finer sediments were found in the marsh creeks, providing good vision and ample food supply. Still, the salt-marsh creeks are extreme environments and species and life stages visiting this habitat regularly must be tolerant and robust towards the prevailing conditions. The very specific and highly variable physical conditions in the marsh creeks can explain why especially small nekton was found while large nekton avoided this habitat type: small fishes and crustaceans have a wider temperature tolerance, enabling them to cope especially with the temperature extremes found in the marsh creeks. Additionally, compared to larger nekton, small nekton can benefit more from reduced swimming effort in the low flow velocities potentially resulting in higher foraging success and a positive energy budget. The foraging success is also enhanced by the fine and detritus rich sediments that tempts the benthic infauna to feed on the surface and thus becomes available for the small nekton. Together, high temperatures, high food availability and low energy expenditure promote fast growth and, in the absence of predators, increase survival probability. When migrating back to the subtidal at receding tide, when marsh creeks are inaccessible, the well-fed nekton can stop foraging and fully concentrate on predator avoidance. Thus, by using two temporarily connected habitats, small nekton can reduce dietary competition and predation risk.

Chapter 4 evaluates the feeding habitat quality of salt-marsh creeks in comparison to the adjacent tidal flats and subtidal for four characteristic fish species occurring in both habitats: herring *Clupea harengus*, three-spined stickleback *Gasterosteus aculeatus*, common goby *Pomatoschistus microps* and sand goby *P. minutus*. Habitat-specific short- and long-term dietary condition (a. k. a. nutritional condition or body condition) were measured and the diet composition was compared to the food availability in each habitat type (salt-marsh creeks vs. subtidal / tidal flat). In addition,

potential diet competition was evaluated based on inter- and intra-specific diet overlap and predator and prey densities. Finally, potential limitation of selected prey resources was analysed by calculating the maximum fraction of prey resources that could hypothetically be exploited by each predator per tide. On the short-term the stomachs tended to be fuller in the salt-marsh creeks than in the subtidal, but the long-term condition was similar in both habitats. Except for the planktivore herring, diets varied between the salt-marsh creeks, where they were dominated by polychaetes, and the subtidal, where zooplankton and various other crustaceans contributed higher fractions of the diets. Planktonic prey was equally abundant in both habitats, while endobenthic prey, especially those species with a high surface activity, like the common ragworm *Hediste diversicolor*, occurred in significant higher densities in the salt-marsh creeks than in the offshore habitats. Although the diet overlap was comparably high in the salt-marsh creeks, the high endobenthos density, especially of *H. diversicolor*, together with the relatively low predator density relaxed the diet competition. The results indicate that the salt-marsh creeks are a profitable feeding habitat for small fish.

After Chapter 2 to 4 addressed the benefits and threats for nekton in the Wadden Sea salt marshes based on biotic and abiotic habitat conditions, in **Chapter 5** the effects of anthropogenic activities in the marshes are added. Chapter 5 investigates the seasonal availability of terrestrial prey for fish utilizing intertidal salt-marsh creeks and if and how it is affected by sheep grazing. Stomach contents of the dominant species (herring, three-spined stickleback, common goby and sand goby) caught in a grazed and an ungrazed marsh in Northern Germany from March 2015 to February 2016 were analysed. The importance of terrestrial prey differed significantly between predators, seasons and grazing treatment. Herring and sand goby did not feed on terrestrial prey, however, sticklebacks and common gobies exploited terrestrial prey in winter in the ungrazed salt marsh. Their preferred terrestrial prey was the detritus-feeding amphipod *Orchestia gammarellus*. Statistical modelling revealed that the flooding height and duration – and hence the accessibility – was most important for the consumption of *O. gammarellus* by sticklebacks. This key prey type occurred in significantly higher densities in the ungrazed than in the grazed marsh year round. The findings of this chapter provide important background for a holistic conservation of this endangered habitat type, addressing a species group usually underrepresented in conservation and management schemes. Attributes making salt-marsh creeks profitable habitats for fish are defined and recommendations for effective fish conservation in intertidal salt marshes are provided.

The thesis concludes in **Chapter 6** with a synthesis on the value of the Wadden Sea salt marshes for fishes and crustaceans, that summarizes and establishes the link between the results of Chapter 2 to 5. Together, the findings of the thesis indicate that the Wadden Sea salt marshes are valuable habitats for small nekton providing low predator and competitor densities, abundant and accessible prey, seasonally warm temperatures that promote fast growth, sufficient oxygen and low-energy hydrodynamics that reduce energy expenditure of the small nekton and foster successful foraging. Furthermore, Chapter 6 discusses the small-scale habitat value of specific marsh features and microhabitats within the salt marshes, and subsequently, turns the focus on the large-scale role of this habitat type within the seascape. In conclusion, salt-marsh creeks are worth protecting as they are a profitable habitat not only for juvenile commercially-used species but also for some mesopredators, such as the three-spined stickleback and the common goby that hold a central position in the coastal food web. Finally, Chapter 6 hints at further research needs and translates the findings of the thesis into applicable management measures that could improve the habitat quality of Wadden Sea salt marshes for nekton.

Zusammenfassung

Im Wattenmeer überlappen – aufgrund der flachen Küste und des großen Tidenhubs – Land und Meer, wodurch ein einzigartiges pulsierendes Ökosystem entsteht. Landwärts wird der Gezeitenbereich von Salzmarschen gesäumt, die dort entstehen, wo geringe Strömungsgeschwindigkeiten die Sedimentablagerungen und die Ansiedlung halophytischer Pflanzen begünstigen. Salzmarschen gelten weltweit als wertvolle Lebensräume für Fische und Crustaceen, da sie Schutz vor Prädatoren sowie günstige Nahrungsbedingungen bieten. Im Wattenmeer haben jedoch Landgewinnung, Küstenschutzmaßnahmen und Landwirtschaft im Laufe der Jahrhunderte Form und Funktion der Salzmarschen verändert. Natürlich mäandrierende Salzmarschenpriele, die u. a. Gezeitentümpel miteinander verbinden, wurden weitgehend durch kurze und gerade Priele ersetzt, um eine optimale Deichentwässerung zu gewährleisten. Ob diese überwiegend künstlich entstandenen Salzmarschen für die Meeresfauna dennoch von Bedeutung sind und welche Arten in die engen Salzmarschenpriele wandern und dabei das Risiko, zu stranden und ungünstigen Temperaturen ausgesetzt zu sein in Kauf nehmen, war bislang weitgehend unbekannt und wird nun in dieser Dissertation untersucht. Es handelt sich um die erste umfassende Studie, die aufzeigt, welche Nektonarten für die marinen Salzmarschen des Wattenmeeres charakteristisch sind und welche die Habitatqualität auf der Grundlage der abiotischen Bedingungen, des Prädationsdrucks, und der Nahrungsbedingungen, mittels Nahrungsverfügbarkeit und der Körperkondition der Fische, bewertet sowie den menschlichen Einfluss auf diesen Habitattyp hinsichtlich der Schafsbeweidung untersucht.

Die Dissertation beginnt in **Kapitel 1** mit einer allgemeinen Einführung in die Bewertung der Habitatqualität und den Wert und das theoretische Konzept mariner Kinderstuben. Anschließend werden Salzmarschen, der Habitattyp, auf den sich diese Studie konzentriert, in Bezug auf ihre typischen Merkmale und ihren Wert für Fische und Crustaceen vorgestellt. Im Folgenden werden die regionalen Besonderheiten der Salzmarschen des Wattenmeeres thematisiert und ihre Entwicklung und Form sowie ihr Unterschied zu anderen gut untersuchten Salzmarschen beschrieben. Schließlich werden Wissenslücken charakterisiert und die Gliederung der Dissertation, inklusive der Forschungsfragen und Hypothesen, die in den einzelnen Kapiteln behandelt werden, vorgestellt.

Ausgehend von einer Bestandsaufnahme der spezifischen Nektongemeinschaft der deutschen Salzmarschen untersucht **Kapitel 2** die Habitataffinität, sowie die tageszeitlichen und saisonalen Abundanzmuster. Die Salzmarschen wurden von einer spezifischen und artenarmen Nektongemeinschaft mit verhältnismäßig kleiner

Körpergröße besiedelt, die sich signifikant vom angrenzenden Sublitoral unterscheidet. Die Ergebnisse zeigen, dass einige Arten, die im Sublitoral gefunden wurden, die Marschenpriele mieden, während andere, z. B. die Strandgrundel *Pomatoschistus microps* und die Nordseegarnele *Crangon crangon*, diese vorzogen. Die Zusammensetzung der Salzmarschen-spezifischen Nektongemeinschaft änderte sich im Laufe eines Jahres und umfasste Postlarven und Jungtiere sowie adulte Tiere kleiner Arten. Die Bevorzugung von Salzmarschenprielen durch Nekton kann eher auf kleinere Körpergrößen als auf unterschiedliche Lebensstadien zurückgeführt werden. Eine mögliche Erklärung könnte die geringe Räuberdichte in diesem Habitat sein. Salzmarschen mit kürzeren Zugangswegen zum Sublitoral wiesen tendenziell höhere Nektonvorkommen auf. Offensichtlich hängt die Habitatqualität für Nekton nicht nur von den spezifischen Habitateigenschaften, sondern auch von den Wanderrouten und der Qualität der vernetzten Habitate in der Küstenlandschaft ab. Die Ergebnisse zeigen, dass die Salzmarschenpriele des Wattenmeeres wertvolle Lebensräume für kleines Nekton sind und Schutz vor Räubern bieten. Kleines Nekton, das diesen Habitattyp nutzt, hat somit wahrscheinlich eine erhöhte Chance den Lebenszyklus zu schließen.

Kapitel 3 untersucht die abiotischen Habitatbedingungen der Salzmarschen des Wattenmeeres. In vier Salzmarschenprielen und teilweise im angrenzenden offshore-Bereich (Platen und Sublitoral) im deutschen Wattenmeer wurden kleinräumige saisonale und tidebedingte Dynamiken hydrologischer (Temperatur, Sauerstoff) und hydrodynamischer (Strömungsgeschwindigkeit, Trübung, Sedimentkorngröße) Parameter gemessen. Der kleine Wasserkörper in den Salzmarschenprielen passte sich schnell an die Lufttemperatur an, was im Verhältnis zum Sublitoral zu saisonal extremeren Temperaturen führte. Trotz der Temperaturextreme im Sommer waren die Sauerstoffkonzentrationen für Fische und Crustaceen ausreichend, vermutlich aufgrund der Primärproduktion und der tidenbedingten Durchmischung. Im Vergleich zum Sublitoral wurden in den Marschenprielen niedrigere Strömungsgeschwindigkeiten, eine geringere Wassertrübung und feinere Sedimente gemessen, wodurch eine gute Sicht und ein umfangreiches Nahrungsangebot zur Verfügung stehen. Dennoch handelt es sich bei den Salzmarschenprielen um extreme Umgebungen, und Arten und Lebensstadien, die dieses Habitat regelmäßig aufsuchen, müssen tolerant und robust gegenüber den vorherrschenden Bedingungen sein. Die sehr spezifischen und sehr variablen physikalischen Bedingungen in den Salzmarschenprielen können erklären, warum insbesondere kleines Nekton gefunden wurde, während großes Nekton diesen Habitattyp mied. Kleine Fische und Crustaceen haben eine größere Temperaturtoleranz, sodass sie besser mit den Temperaturextremen in den Marschenprielen zurechtkommen. Darüber hinaus kann kleines Nekton im Vergleich zu größerem mehr von dem reduzierten Schwimmaufwand bei den niedrigen Strömungsgeschwindigkeiten profitieren, was zu einem höheren Jagderfolg und einem positiven Energiehaushalt führen kann. Eine erfolgreiche Nahrungssuche wird auch durch die feinen und detritusreichen Sedimente verstärkt, die die benthische Infauna dazu verleitet, an der Oberfläche nach Nahrung zu suchen und so für kleine Nekton-Organismen verfügbar zu werden. Zusammen fördern hohe Temperaturen, eine hohe Nahrungsverfügbarkeit und ein geringer Energieaufwand ein schnelles Wachstum und erhöhen in Abwesenheit von Prädatoren die Überlebenswahrscheinlichkeit. Wenn das gut genährte Nekton bei Ebbe, während die Marschenpriele unzugänglich sind, in das Sublitoral zurückwandert, kann es die Nahrungssuche einstellen und sich vollkommen auf die Vermeidung von Räubern konzentrieren. Durch die Nutzung von zwei vorübergehend miteinander verbundenen Lebensräumen kann das kleine Nekton also die Nahrungskonkurrenz und das Prädationsrisiko verringern.

In **Kapitel 4** wird die Qualität von Salzmarschenprielen als Nahrungshabitat im Vergleich zu den angrenzenden Platen und Sublitoral für vier charakteristische Fischarten bewertet: Hering *Clupea harengus*, Dreistacheliger Stichling *Gasterosteus aculeatus*, Strandgrundel *Pomatoschistus microps* und Sandgrundel *P. minutus*. Die lebensraumspezifische kurz- und langfristige Ernährungskondition wurde gemessen und die Nahrungszusammensetzung mit der Nahrungsverfügbarkeit in jedem Lebensraumtyp (Salzmarschenpriele vs. Platen / Sublitoral) verglichen. Zusätzlich wurde die mögliche Nahrungskonkurrenz auf der Grundlage von inter- und intraspezifischen Nahrungsüberlappungen sowie Räuber- und Beutedichten untersucht. Schließlich wurde die potenzielle Limitierung ausgewählter Beuteressourcen analysiert, indem der maximale Anteil der Beuteressourcen, der von jedem Räuber hypothetisch je Tide erbeutet werden könnte, berechnet wurde. Die Mägen in den Salzmarschenprielen waren kurzfristig tendenziell voller als im Sublitoral, aber die langfristige Kondition glich sich in beiden Habitaten. Mit Ausnahme des planktivoren Herings unterschied sich die Nahrung zwischen den Salzmarschenprielen, wo sie von Polychaeten dominiert wurde, und dem Sublitoral, wo Zooplankton und verschiedene Crustaceen höhere Anteile der Nahrung lieferten. Während planktonische Beute in beiden Habitaten gleich häufig war, kamen endobenthische Beutetiere, insbesondere Arten mit einer hohen Oberflächenaktivität, wie der Schillernde Seeringelwurm *Hediste diversicolor*, in den Salzmarschenprielen in signifikant höherer Dichte vor als in den Offshore-Habitaten. Obwohl die Nahrungsüberlappung in den Salzmarschenprielen vergleichsweise hoch war, entspannte die hohe Endobenthosdichte, insbesondere *H. diversicolor*, zusammen mit der relativ niedrigen Räuberdichte die Nahrungskonkurrenz. Die Ergebnisse deuten darauf hin, dass die Salzmarschenpriele ein profitables Nahrungshabitat für kleine Fische sind.

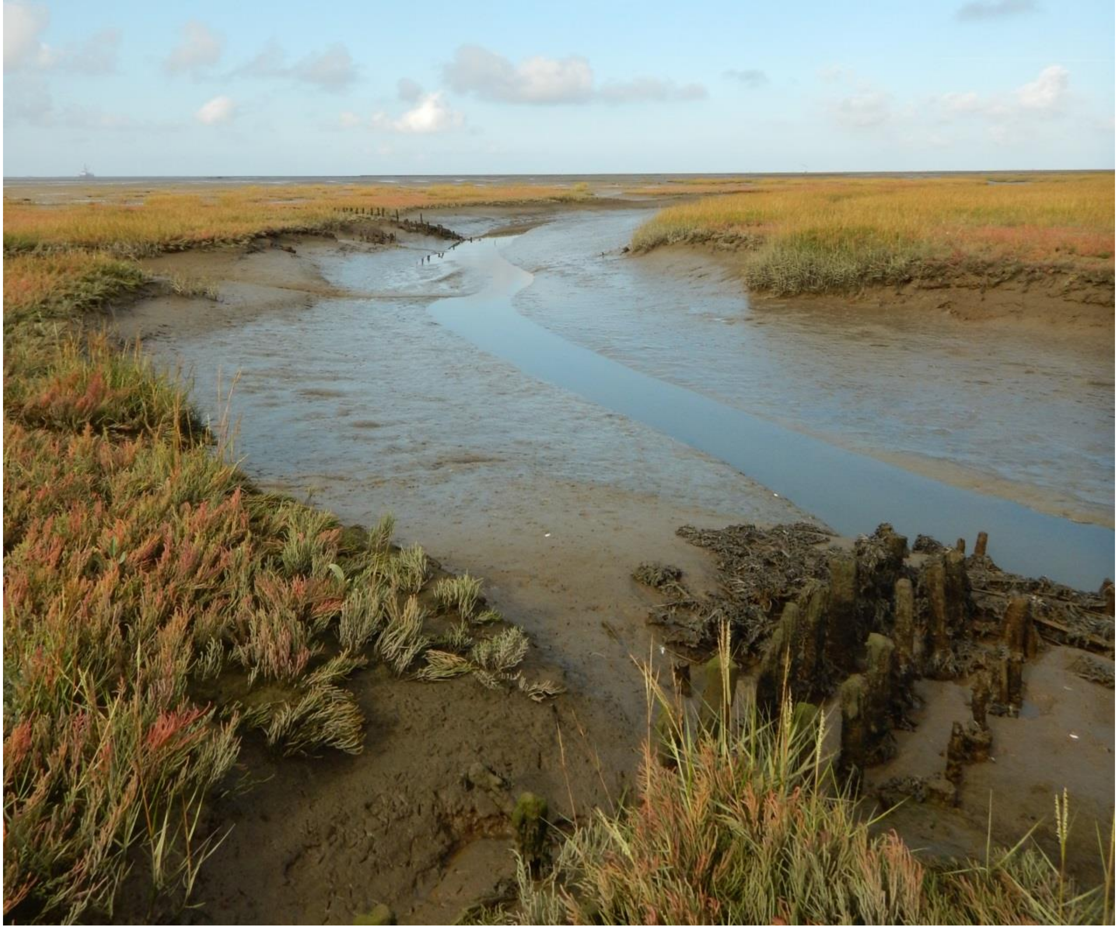
Nachdem in den Kapiteln 2 bis 4 die Vorteile und Gefahren für Nekton in den Salzmarschen des Wattenmeeres auf der Grundlage biotischer und abiotischer Habitatbedingungen behandelt wurden, kommen in **Kapitel 5** die Auswirkungen anthropogener Aktivitäten in den Salzmarschen hinzu. Kapitel 5 untersucht die saisonale Verfügbarkeit von terrestrischer Beute für Fische, die die Gezeitenpriele der Salzmarschen nutzen, und ob und wie diese durch die Beweidung mit Schafen

beeinträchtigt wird. Die Mageninhalte dominanter Arten (Hering, Dreistacheliger Stichling, Strand- und Sandgrundel), die in einer beweideten und einer unbeweideten Salzmarsch in Norddeutschland von März 2015 bis Februar 2016 gefangen wurden, wurden analysiert. Die Bedeutung der terrestrischen Beute unterschied sich je nach Räuber, Jahreszeit und Beweidungstyp. Während sich Hering und Sandgrundel nicht von terrestrischer Beute ernährten, nutzten Stichlinge und Grundeln terrestrischer Beute im Winter in der unbeweideten Salzmarsch. Ihre bevorzugte terrestrischer Beute war der detritusfressende Amphipode *Orchestia gammarellus*. Statistische Modellierungen zeigten, dass die Überflutungshöhe und -dauer – und damit die Zugänglichkeit – am wichtigsten für die Konsumption von *O. gammarellus* durch Stichlinge war. Dieser wichtige Beutetyp kam in den unbeweideten Salzmarschen das ganze Jahr über in signifikant höheren Dichten vor als in den beweideten Salzmarschen. Die Ergebnisse dieses Kapitels bieten wichtige Grundlagen für einen ganzheitlichen Schutz dieses gefährdeten Habitattyps, wobei eine Artengruppe thematisiert wird, die normalerweise nicht ausreichend berücksichtigt wird. Es werden Eigenschaften definiert, die Salzmarschenpriele zu profitablen Habitaten für Fische machen, und Empfehlungen für einen wirksamen Fischschutz in intertidalen Salzmarschen abgegeben.

Die Dissertation schließt in **Kapitel 6** mit einer Synthese über den Wert der Wattenmeersalzmarschen für Fische und Crustaceen, die die Ergebnisse der Kapitel 2 bis 5 zusammenfasst und miteinander verknüpft. Zusammengenommen deuten die Ergebnisse der Arbeit darauf hin, dass die Salzmarschen des Wattenmeeres wertvolle Lebensräume für kleine Nekton-Organismen sind. Sie bieten eine geringe Dichte an Räubern und Konkurrenten, eine abundante und zugängliche Beute, saisonal warme Temperaturen, die ein schnelles Wachstum fördern, ausreichend Sauerstoff und eine niedrige hydrodynamische Energie, die den Energieverbrauch des kleinen Nektons reduzieren und eine erfolgreiche Nahrungssuche begünstigen kann. Darüber hinaus wird in Kapitel 6 der kleinskalige Habitatwert spezifischer Salzmarschenmerkmale und Mikrohabitate innerhalb der Salzmarschen diskutiert. Anschließend wird der Fokus auf die großskalige Rolle dieses Habitattyps innerhalb der Küstenlandschaft gelegt. Schlussfolgernd sind Salzmarschenpriele also schützenswert, da sie nicht nur für juvenile, kommerziell genutzte Arten, sondern auch für einige Mesopredatoren, wie z.B. den Dreistacheligen Stichling und die Strandgrundel, die eine zentrale Position im Nahrungsnetz der Küste einnehmen, einen profitablen Lebensraum darstellen. Abschließend weist Kapitel 6 auf weiteren Forschungsbedarf hin und übersetzt die Ergebnisse der Dissertation in anwendbare Managementmaßnahmen, die die Habitatqualität der Salzmarschen des Wattenmeeres für Nekton verbessern könnten.

1

Introduction



General Introduction

Habitat quality evaluation

Fishes and crustaceans migrate between different habitats within seascapes (Nagelkerken et al., 2015) for reasons of spawning, growing, feeding or overwintering (Harden Jones, 1968). Habitats, i. e. the resources and biotic and abiotic conditions in areas occupied by an organism, species or population (Hall et al., 1997), affect growth, survival and reproduction of their inhabitants (Johnson, 2007; Rountree and Able, 2007). Habitats of high quality will maximize the lifetime reproductive success of its inhabitants by providing favourable physicochemical conditions, a high quality and quantity of food and shelter from predators or other mortality sources (Hall et al., 1997; Johnson, 2007). Individuals with the ability to select high quality over low quality habitats are favoured by natural selection (Clark and Shutler, 1999). In the past, the linkage between habitat quality and habitat selection led to the assumption that high population densities would be a valid indicator of a high quality habitat (e. g. Bond et al., 1999). However, density can be a misleading indicator of habitat quality, especially in years of high population densities, because of e. g. territorial behaviour and density-dependent competition (van Horne, 1983; Hobbs and Hanley, 1990). Low quality habitats would also need a higher population size to ensure persistence despite low survival and production rates (van Horne, 1983). Likewise, when considering for example spawning habitats, high densities may indeed increase reproductive success in some cases, e. g. for fish with external fertilization releasing eggs and sperm into the water. Thus, contrasting processes affect the habitat quality: from an individual´s perspective a habitat providing low mortality and a positive energy budget are attractive, but when too many individuals select that habitat and exceed its carrying capacity, the quality of the same habitat decreases. On a population level it can therefore be beneficial when also less profitable habitats, e. g. with abundant but lower quality resources, are selected (Johnson, 2007).

Although habitat selection has consequences on a population level and, in turn, can be affected by population dynamics, migration towards and thus selection of habitats is a processes operating on the individual level (Lawlor and Smith, 1976; Rosenzweig and Abramsky, 1985; McMahon and Matter, 2006). Harden Jones (1968) defined three strategies fish use for migratory movements, (1) drift, including e. g. selective tidal transport via vertical movements, (2) random locomotory movements, and (3) orientated locomotory movements. Exploratory behaviour of fish is regulated via a negative feedback loop comparing internal drivers for needed resources and conditions with those provided by the environment (Sale, 1969; McMahon and Matter, 2006). If the stimulus perception of cues indicates a match between internal needs and external conditions, exploratory behaviour is either (1) reduced, possibly leading to residency or otherwise to a continuing search for a better habitat (Sale, 1969; McMahon and Matter, 2006) or (2) movements are directed towards the stimulus (Harden Jones, 1968). However, animals cannot measure, how their habitat selection will affect their lifetime reproductive success (Kristan, 2003). Therefore, individuals rely on environmental cues to evaluate habitat quality (Kristan, 2003). These cues can be incomplete or misleading with the result that animals erroneously select a poor-quality habitat (Kristan, 2003). Especially, when habitats change suddenly due to human activity, the evolutionary developed cues can become unreliable, luring animals into ecological traps, i. e. habitats that are more attractive for organism than they should be according to their habitat quality (Schlaepfer et al., 2002; Kristan, 2003). Thus, an evaluation of habitat quality should be primarily based on how well the habitat conditions meet the requirements of their inhabitants than on the abundance of the inhabitants alone. Craig and Crowder (2002) classified five factors determining habitat quality: abiotic factors, food resources, bioenergetics, competition and risk of predation. The individual´s needs and the environmental supplies of these factors can vary during the fish´s ontogeny and on tidal, diel, seasonal, and interannual time scales (Craig and Crowder, 2002). For an evaluation of habitat quality it is therefore required to measure multiple biotic and abiotic environmental factors and their effects on species inhabiting the habitats to the most encompassing spatiotemporal scales possible (Johnson, 2007).

Nursery habitats

Coastal ecosystems are characterized by highly variable environmental conditions and consist of a high diversity of structurally complex and interconnected habitat types. These habitat types can differ in depth and thus tidal inundation, flow velocities, sediment types, temperature dynamics and whether they are vegetated (e. g. sea grass meadows and salt marshes) or not (e. g. mud flats) or contain hard structures (e. g. rocky shores and oyster reefs). Fishes and crustaceans in coastal ecosystems connect these different habitat types with each other during their migrations. They either use the different habitats (1) for feeding, and thus link local food webs over larger areas, (2) for spawning, where some species depend on specific substrates, or (3) as nurseries, where larval and juvenile fish find good growth conditions and refuge from predators (Beck et al., 2003; Wouters and Cabral, 2009; Ryer et al., 2010). Habitat diversity and species diversity are positively correlated (Asherin et al., 1979). Thus, habitat diversity and connectivity are essential for ecosystem functioning and resilience. For a successful conservation of ecosystem services, the quality, function, and connectivity of each habitat type within a seascape should be evaluated. Shallow coasts with large intertidal zones often consist of a mosaic of different habitat types, such as e. g. channels, mudflats, tidal pools, oyster reefs, coral reefs, rocky, sandy, and muddy tidal flats, sea grass meadows, and salt marshes in temperate or mangroves in equatorial latitudes. Shallow water habitats are unstable, harsh environments, favouring r-strategists, with short generation times, high fecundity and relatively small body size (Pianka, 1970; Southwood, 1977). Body size of at least demersal fish tends to increase with depth (*Heincke´s Law*, Heincke, 1913; Macpherson and Duarte, 1991). Thus, small fish could find shelter from larger predators in shallow water habitats (*shallow-water-refuge hypothesis*; Boesch and Turner, 1984; Paterson and Whitfield, 2000; Baker and Sheaves, 2007). Therefore, these nearshore habitats are also valued as nurseries and juvenile habitats (e. g. Rauck and Zijlstra, 1978; Kuipers and Dapper, 1984; Beck et al., 2003; Polte et al., 2005; Seitz et al., 2014).

Beck et al. (2001) defined nurseries as areas, where juvenile fish or invertebrates are more abundant, find more successfully shelter from predators, and have higher growth rates than in other areas. The growth rate is an important indicator of the quality of nursery grounds. Fast growth can reduce lifetime mortality, because the number of potential predators decreases with increasing body size due to gape size limitations of the predators (Pauly, 1980; Bailey and Houde, 1989; Gislason et al., 2010). In marine ecosystems trophic levels are closely linked to body size (*bigger-is-better hypothesis*, Anderson, 1988; Miller et al., 1988) . Early life stage have the highest mortality rates, mainly caused by predation (Bailey and Houde, 1989). Thus, survival rates of the early life stages are most often decisive for the cohort size and thus for the adult stock size (Houde, 1987; Nash and Dickey-Collas, 2005). High growth rates can be achieved in areas of high food availability in combination with sufficient oxygen levels and relatively high water temperatures within the thermal tolerance window of the organism (Pedersen and Jobling, 1989; Cushing, 1990; Munk, 1993; Pörtner and Knust, 2007; Hufnagl and Temming, 2011a). Enzyme activity increases with increasing temperature (*van't Hoff's rule*) resulting in an elevated metabolic rate (Schulte, 2015). At sufficient nutrient and oxygen supply the increased metabolism can thus increase the growth rate. Fish or crustaceans that are able to reduce the time span being comparably small-sized, can reduce their vulnerability to predation and increase their chance to recruit to the adult stock and finally reproduce and close the life cycle (Houde, 1987). Beck et al. (2001) related the value of such a nursery to the average contribution it has to the recruitment to the adult stock in terms of numbers per unit area. Dahlgren et al. (2006) argued that large nurseries with a small per-unit-area contribution may be more important than small habitats with a high per-unit-area contribution to the adult stock. Therefore, they specified the nursery concept of Beck et al. (2001) by introducing the term "*Effective Juvenile Habitat*", which describes a habitat that contributes a larger proportion to the total recruits compared to other juvenile habitats and is therefore important for maintaining stock size while being independent of the area of the juvenile habitat. Sheaves et al. (2006) criticised both nursery concepts for oversimplification. Habitats are not discrete units but continuous gradients (Kristan, 2003) and the categorization of an area as a habitat depends on the species and life stage and on temporal scales, e. g. seasons (Sheaves et al., 2006). Species use various habitats during their ontogeny (Gillanders et al., 2003) and thus attempts to quantify the importance of a particular habitat are unpromising (Sheaves et al., 2006). Habitats, such as e. g. salt marshes, consist of multiple microhabitats, e. g. tidal creek segments, pools and ponds, or the flooded vegetated marsh surface, and are embedded in macrohabitats, e. g. the seascape (Nagelkerken et al., 2015) consisting of e. g. different salt marshes, the subtidal, or tidal flats. Thus, when evaluating habitat quality the scale must be defined beforehand (Sheaves et al., 2006). Furthermore, habitats are connected within the seascape with other habitats. Animals need to migrate between different habitats or their prey species might depend on a neighbouring habitat (Gillanders et al., 2003; Sheaves et al., 2006). Finally, Sheaves et al. (2006) argue that the value of a nursery depends on the reproductive contribution to future generations and not only on the numerical contribution to the adult population. A nursery producing large numbers of recruits in a low nutritional condition and with low reproductive success, is less important for a sustainable population size, than a nursery releasing few recruits, that produce abundant offspring (Sheaves et al., 2006).

Salt marshes

Development and Morphology

One habitat type described worldwide as nursery for fishes and crustaceans, is the salt marsh ecotone (Weinstein, 1979; Rogers et al., 1984; Minello et al., 2003; Whitfield, 2017). Salt marshes evolve in the temperate zone – similarly as mangrove forests, their counterparts in the tropics – along sheltered shallow coasts with considerable tidal amplitudes (Steers, 1977; Wiegert et al., 1981). They can either develop from autochthonous substrates caused by isostatic emergence of the seafloor, or by allochthonous substrate, i. e. by marine sediment deposition. Sediment surface elevation increases slowly, where flow velocities are low enough to allow more sediment to settle down with each tidal flooding, than gets resuspended by currents and waves. Due to the increased elevation, flooding frequency and duration decreases. Eventually, conditions become adequate for pioneering vascular halophytic plants, such as cordgrass (*Spartina spp.*) or glasswort (*Salicornia spp.*). These reduce the currents catching further sediments. Creeks are dragged into the marsh by the ebb flow resulting in a ramified salt-marsh creek system. These creeks can be intertidal, i. e. falling dry at low tide, or subtidal, i. e. inundated during the whole tidal cycle. The confined space in the creek beds might accelerate ebb and flood currents, but at the same time the tidal flow slows down around high water, allowing fine-grained sediment to precipitate (Bayliss-Smith et al., 1979; Healey et al., 1981; Reed et al., 1985; Wang et al., 1999; Fagherazzi et al., 2008). The vegetation and the unflooded marsh areas can also shelter the water body from wind and waves and reduce the currents (Healey et al., 1981; Reed et al., 1985). The increasing elevation fosters also successive settlement of other halophytic plants that foster further sediment accretion, reduce sediment resuspension and add organic detritus to the marsh surface.

For most vascular plants salt causes physiological stress. However, halophytic plants evolved several strategies of salt resistance. They either avoid to incorporate salt (excluders) or incorporate salt and deal with the consequences (includers) (Koyro et al., 2008). The adaptations to regulate the salt balance include for example (1) succulence, (2) a water uptake reduction combined with an increased water use efficiency, (3) excretion via glandular cells, or (4) storage e. g. in leaves or hairs, that can break off and be regrown, or in intracellular vacuoles (Koyro et al., 2008). Most halophytes can grow well at low salinities, but are superseded by other plants in the freshwater zone. The elevation of salt marshes – characterized by a tidal influence and halophytic plants – is mostly determined by the maximal high tide water level, that brings the sediment needed for vertical marsh accretion (Allen and Pye, 1992). The spatial extent of mud flats and salt marshes, on the other side, is predominantly influenced by wind and waves (Allen and Pye, 1992). Contrary to the salt water flooding, the importance of rainfall increases with increasing elevation resulting in a vertical salinity gradient. Thus, a decreasing flooding frequency and duration with increasing elevation leads to a vertical zonation of different plant communities depending on their tolerance to salt water flooding and desiccation. This zonation of salt marshes, based on flooding frequency and vegetation type, varies among geographical regions. North American marshes are for example usually classified in a low marsh dominated by a tall form of smooth cordgrass (*Spartina alterniflora*), which increases in height towards the marsh edge, and a high marsh with shorter grasses (e. g. short form of *Spartina alterniflora*, *Spartina patens*, *Juncus geradii*; Wiegert et al., 1981). The transition zone to the fresh water, classified as the upland border, is characterized by taller vegetation, e. g. by common reed (*Phragmites australis*). Salt marshes on the southern North Sea coast, i. e. in the Wadden Sea, on the other side, are classically sectioned into a pioneer zone (*Salicornia spp.*, *Spartina anglica*), the low marsh (i. a. *Puccinellia maritima*, *Atriplex portulacoides*, *Aster tripolium*), and the high marsh (i. a. *Elytrigia atherica, Festuca rubra*; Adam, 1993). Occasionally, the marsh is divided up into even more sections including also a middle marsh zone. The Wadden Sea marshes have no upland-transition zone, instead sheep-grazed dikes form the landward borders. Marsh zonations are an artificial classifications, vary among geographic locations and it should kept in mind that transition areas between the zones are smooth. Surface depressions collect fresh water during rainfall and can cause small-scale patchy patterns of salinity differences and consequently vegetation patchiness. Some surface depressions become pools and ponds with permanently stagnant water becoming possibly more saline than sea water due to evaporation. With increasing salt-marsh succession creeks can silt up forming elongated salt pans in the higher or middle marsh (Steers, 1977).

Where soil drainage is low, water-logging can lead to anoxic conditions, which is the case in the dense soils of salt marshes (Teal and Kanwisher, 1966). Although the soils of the vegetated marsh surface contain higher amounts of plant detritus than the soils in the unvegetated salt-marsh creeks, both are characterized by a vertical sequence of different sediment layers. On the surface, the soil consists of an oxic and a suboxic layer only a few millimetres to centimetres deep, which is coloured brown by iron hydroxide ($Fe(OH)_3$) (Wilhelmsen and Dittmann, 2004). This oxidized surface is separated by the RPD-layer (Redox-Potential-Discontinuity-Layer) from the sulfidic zone below (Wilhelmsen and Dittmann, 2004). This anoxic zone is coloured black by iron monosulfide (FeS) and deeper in the sediment it reacts with hydrogen sulphide (H_2S) to pyrite (FeS_2) colouring the sediments grey (Wilhelmsen and Dittmann, 2004). The anoxic zone is mostly uninhabitable for benthic organisms (Neira and Rackemann, 1996), except those areas aerated by e. g. worms coating their burrows with mucus, whereas the oxidized zone is inhabited by a variety of micro- and macro-organisms.

Shallow areas with low turbidity and soft sediments, such as salt marsh creeks, the pioneer zone or low marsh, accumulate organic matter from the marine system or with the ebb tide from the vegetated marsh surface, fuelling microbial decomposition processes (Blagodatskaya and Kuzyakov, 2008). The nutrients mobilized this way and the light availability attract benthic primary producers, in particular diatoms, in the top sediment layers (Leach, 1970; Cloern, 1987; Billerbeck et al., 2007). Thus, not only the salt-marsh areas vegetated with halophytes are highly productive, but also the unvegetated microhabitats covered with microepiphytobenthos (Cloern, 1987; Emerson, 1989). Possibly due to enhanced light availability the productivity of microepiphytobenthos is highest during ebb tide exposure (Pomeroy et al., 1981). The duration of ebb tide exposure is most prolonged at the upper edge of the intertidal zone, where i. a. salt marshes can be found. Detritus, microbes and microalgae offer food for the benthic meio- and macrofauna in the salt-marsh creeks. Moreover, microbes and microalgae reduce erosion and sediment resuspension (Madsen et al., 1993; Austen and Witte, 2000). Furthermore, crawl trails of small bivalves, snails and worms can reduce the surface flow velocities via surface roughening by indentations, faecal pellet excretion, or via mucous secretion (Nowell et al., 1981; Thiel et al., 1984). Thus, the flora and fauna inhabiting the sediments further stabilize the soil and contribute to enhanced accretion rates. After the vegetation period in summer, vascular plant detritus adds to the accretion of the marsh surface covered finally by sediments delivered by winter storm floods. The storm floods can also cause cliffs on the marsh edge and ice drift can raze the vegetation and further shape the marsh. The appearance of the marsh draining creeks differs between and within salt-marshes (Steers, 1977). They can be narrow and steep-sided with a U-shaped cross section or wide and shallow with a V-shaped cross section. Unvegetated meandering creeks create cliffs and slip-off slopes on the creek banks. The surface vegetation decelerates the currents during flooding and enhances an unequal sediment deposition (Nolte et al., 2018) amplifying the patchiness of microhabitats within the salt marsh. This way a complex landscape at the interface of land and sea is formed.

Ecosystem services

Salt marsh ecotones are valued for a variety of ecosystem services. The anaerobic conditions deeper in the soil reduce decomposition of the deposited organic material and thus increase carbon sequestration (Freeman et al., 2001). Although the total global area of salt marshes is significantly smaller than that of e.g. tropical forests, salt marshes bury comparable total amounts of carbon per year due to a higher carbon burial rate (Mcleod et al., 2011). Therefore, salt marshes can contribute in climate change mitigation. With regard to the predicted sea level rise caused by global warming, salt marshes can become more important for coastal defence strategies in the future, because they can absorb wave energy during storm flood events (Dijkema et al., 1990; Franziska Rupprecht, 2015). Due to their high rates of primary production they are also valued for livestock grazing (Bakker et al., 2003; Yang et al., 2008; Gedan et al., 2009) and are important for coastal food webs (Rozas et al., 1988; Laffaille et al., 1998; Laffaille et al., 2002; Maier et al., 2014; Sheaves et al., 2015). Salt marshes provide habitats for a variety of species. While the regularly flooded sediments are inhabited by the marine endobenthic fauna, the vegetated marsh surface is populated by a variety of invertebrates, i. a. semi-terrestrial amphipods, insects, spiders and mites, and collembolans (van Klink, 2014). Birds use salt marshes for feeding, either catching the marsh arthropods or grazing the vegetation, or as a breeding habitat (Brindley et al., 1998; Hanson and Shriver, 2006; Wilson et al., 2007; Ma et al., 2011; Maier, 2014b). Furthermore, salt marshes are used as grazing areas by mammals, such as mice, rabbits, hares, and deer (Beeftink, 1977; MacDonald, 1977; Pfeiffer and Wiegert, 1981). Their effect on salt marshes is, however, assumed relatively low, in contrast to that of domestic undulates, which are stocked at higher densities and thus change vegetation patterns considerably (Beeftink, 1977; Kiehl et al., 1996; Esselink et al., 2002; Davidson et al., 2020). Also mammalian predators are attracted by the prey resources of salt marshes. For example in Georgia salt marshes (USA) rice rats (*Orzomys palustris*) feed mainly on crabs (*Sesarma spp.* and *Uca spp.*) but also on a variety of arthropods and exploit eggs and chicks from bird nests as raccoons (*Procyon lotor*) and minks (*Mustela vison*; Pfeiffer and Wiegert, 1981) do. MacDonald (1977) reported weasels, racoons and skunks as the most important mammalian predators in Californian salt marshes (USA). In the Wadden Sea the red fox (*Vulpes vulpes*) is the main predator in salt marshes with effects on the breeding success of birds (Møller, 1975; Koffijberg et al., 2006). Some marshes, especially at lower latitudes, are also inhabited by reptiles, such as crocodiles, turtles, lizards, and sea snakes (Campbell, 1972; MacDonald, 1977; Hart and Lee, 2006; Nifong and Silliman, 2013). Finally, also fishes and crustaceans utilize the salt marsh during tidal flooding (Boesch and Turner, 1984; Cattrijsse and Hampel, 2006; Whitfield, 2017) or even remain in marsh pools and ponds, and small rivulets during low tide (MacKenzie and Dionne, 2008; Rozas and Minello, 2010; Rieucau et al., 2015; Allen et al., 2017). Their population dynamics can even depend on this habitat type, which becomes apparent from the fact, that in some regions fishery yields depend upon the availability of salt marshes as nurseries for the exploited species (Turner, 1977; Boesch and Turner, 1984; Orth and van Montfrans, 1990; Minello and Webb, 1997; Rozas et al., 2005; Minello et al., 2012) or due to important food web links (Quan et al., 2007; Raoult et al., 2018; Jinks et al., 2020).

Nekton habitat

Multiple studies worldwide valued salt marshes as nurseries for fishes and crustaceans due to their relative low predator and high prey abundances (e. g. Weinstein, 1979; Cattrijsse et al., 1997; Halpin, 2000; Minello et al., 2003). Densities of piscivorous fishes are low in the shallow salt marshes compared to deeper areas (McIvor and Odum, 1988; Boswell et al., 2019). Rozas and Hackney, Courtney, T. (1984) hypothesised that – despite the high availability of small prey fish and crustaceans – the physicochemical conditions in shallow marsh creeks are unfavourable for larger predatory fish, because they are less tolerant to rapid diel oscillations of temperature and oxygen levels (Hackney et al., 1976). Additionally, it is frequently reported that small nekton can hide within the submerged vegetation of salt marshes, thus, reducing predation mortality (Rozas and Odum, 1988; Savino and Stein, 1989a; Mattila, 1992; Paterson and Whitfield, 2000). Another important argument for the nursery value of salt marshes for nekton are the abundant food resources. Multiple studies reported that fish visited salt marshes for feeding (Hollingsworth and Connolly, 2006; Platell and Freewater, 2009; Nemerson and Able, 2020) and left this habitats with fuller stomachs (Rozas and LaSalle, 1990; Allen et al., 1994). The flooded vegetated marsh surface, that provides abundant terrestrial arthropods as prey, is especially valued for its foraging conditions (Rozas and LaSalle, 1990; West and Zedler, 2000). Hence, nekton entering flooded salt marshes can consume marine prey resources, such as zooplankton and benthos, but can additionally extent their diets towards the terrestrial prey resources (Kneib, 1982a; Laffaille et al., 2000b; West and Zedler, 2000). Nekton exploiting prey resources of salt marshes, e. g. terrestrial prey, could thus relax diet competition in the marine ecosystem. Fish and crustaceans foraging in inundated salt marshes might also benefit from the abiotic conditions. In the low flow velocities in the salt marshes, they need less energy for locomotion (Liao, 2007), and reduced turbidity through less suspended particles (Postma, 1961) enhances visual and olfactory orientation, e. g. to find food or avoid predators (Weissburg and Zimmer-Faust, 1993; Abrahams and Kattenfeld, 1997; Robertis et al., 2003; Smee and Weissburg, 2006; Smee et al., 2008). But in the very shallow intertidal zone in salt marshes, conditions can be harsh as well (Daiber, 1977). Especially, in the upper reaches of salt-marsh creeks temperatures of the small water body may increase and oxygen may drop to levels uninhabitable by fish (Hackney et al., 1976; Desmond et al., 2000; Green et al., 2009). However, within the physiological limits of the organisms, high temperatures combined with sufficient oxygen concentrations and a high prey availability, increases the metabolic rate, which translates into fast growth (Houde, 1989; Munk, 1993; Attrill and Power, 2002; Pörtner, 2002; Attrill and Power, 2004) and, eventually, a higher probability to survive and reproduce (Pauly, 1980;

Gislason et al., 2010). These abiotic habitat characteristics are increasingly pronounced with decreasing depth. Thus it is not astonishing, that Rozas and Odum (1987c) and Hettler (1989) found in a freshwater marsh in Virginia, and a salt-marsh in North Carolina, USA, respectively, the highest abundances of small nekton species in the upper reaches of the marsh creeks – an area avoided by their predators (Rozas and Hackney, Courtney, T., 1984). The combination of low predation pressure and good growth conditions is rarely found in marine habitats, exposing organisms most often to a trade-off between survival and fulfilment of their energy demands. Salt marshes relax this dilemma, which is why they are considered a good growth environment and thus nurseries for fishes and crustaceans (Halpin, 2000; MacKenzie and Dionne, 2008).

The Wadden Sea salt marshes

The nursery value of salt marshes and other coastal habitats can vary considerably among geographic regions (Beck et al., 2003). Salt marshes in the Wadden Sea located along the southern North Sea coast differ in multiple ways from other the well-studied marshes for example at the US coasts (Cattrijsse and Hampel, 2006). Today´s Wadden Sea salt marshes cover ca. 400 km² (Esselink et al., 2017). Salt marshes can be classified into different types depending on their location and origin (Dijkema, 1987; Allen and Pye, 1992; Esselink et al., 2017). In the Wadden Sea mainly four classes of salt marshes occur, (1) back-barrier salt marshes, (2) hallig salt marshes, (3) coastal mainland salt marshes, and (4) brackish estuarine mainland marshes. Back-barrier salt marshes are located at the lee of the barrier islands. These marshes evolved naturally due to their sheltered position. At least along the Dutch and Lower Saxony Wadden Sea coast they often still possess natural creek systems and a transition zone towards the dunes on the luv of the barrier islands. However, in areas of human settlements and on the islands of the North Frisian coast, the back-barrier salt marshes were often modified with dikes and artificial drainage systems to prevent storm floods. Along the North Frisian coast between the barrier islands and the mainland, smaller islands called “*halligen*” can be found. These are higher elevated patches of the former mainland separated centuries ago from the coast by storm floods. They are covered completely by salt marshes with some artificial flood-proof mounds with buildings. The hallig salt marshes are often protected by summer polders, drained with an artificial creek system and are used for livestock grazing. Thus, although located on islands, the physiography and vegetation of the hallig salt marshes are similar to the mainland salt marshes (Esselink et al., 2017). The coastal and estuarine mainland salt marshes cover the largest areas and are predominantly of artificial origin (Esselink et al., 2017). In the Middle Ages embankments were built to reclaim land from the sea (Lotze, 2005). Brushwood groynes were built along the coast to catch more sediment and salt marsh drainage was enhanced via ditches (Bakker et al., 2002). This way accretion was accelerated and embankments were gradually shifted towards the sea squeezing the salt marshes surrounded by sea and dikes into a diminishing area. The last land reclamation in the German Wadden Sea for agricultural use was completed in 1954, when the “Friedrich-Wilhelm-Lübke-Koog” at the North Frisian coast was built by embanking directly the tidal flat without prior accretion measures (Reise, 1998). In the following years still several hundred square kilometres were diked for coastal protection reasons (Wilhelmsen and Dittmann, 2004). The today´s mainland salt marshes developed based on those anthropogenic sediment accretion measures, but the total spatial extent of salt marshes decreased significantly during the last centuries (Probst, 1996; Lotze, 2005; Airoldi and Beck, 2007; Esselink et al., 2009; Gedan et al., 2009). The remaining salt marshes were strongly modified compared to their natural appearance. Since Medieval times the salt-marsh creeks were dredged and straightened to drain the land (Knottnerus, 2005). Today a regular and rectangular systems of short and straight creeks assures an optimal dike drainage. Even earlier than the constructional modifications of the salt marshes, the vegetated marsh surface served for livestock grazing in the Neolithic (Knottnerus, 2005; Lotze et al., 2005). Sheep and cattle grazing in the last centuries modified vegetation and arthropod communities (Meyer et al., 1995; Esselink et al., 2002) – with possible effects on fish diets (Laffaille et al., 2000b; Friese et al., 2018a; Chapter 5, but see Joyeux et al., 2017, who found no effect). Reed marshes (*Phragmites spp.*), which covered historically the brackish upland transition zone were completely lost during the dike building. The accretion measures of the last centuries caused the marshes being dominated by late-succession plant communities (Esselink et al., 2009). The high elevated vegetated surface of Wadden Sea salt marshes is consequently rarely flooded. But in US freshwater marshes areas with submerged vegetation were favoured by shrimps and fishes over unvegetated areas (Rozas and Odum, 1987b, 1987a). Submerged vegetation is assumed a key habitat characteristic of salt marshes providing shelter and food (Weisberg and Lotrich, 1982; Rozas and Odum, 1988; Rozas and Reed, 1993). In the Wadden Sea salt marshes, however, fish entering this habitat are – except for winter storm floods – restricted to the unvegetated salt-marsh creeks or negligible small areas of inundated pioneer zone. Furthermore, the pioneer zone in the Wadden Sea is dominated by *Salicorna spp.* which grows with relatively large spacing rarely providing hiding opportunities. *Spartina spp.*, which is valued in the low marsh in the US as feeding habitat and predator refuge for nekton (Minello and Webb, 1997), is rarely abundant in Wadden Sea salt marshes (Esselink et al., 2017). The low marsh in the Wadden Sea is dominated by C3-plants with a higher stem density than *Spartina spp.* (Bouma et al., 2010; Franziska Rupprecht, 2015). An increased stem density can increase the refuge value of the marsh (Savino and Stein, 1989b), but when the vegetation becomes too dense it can hamper the nekton to swim far into the marsh as they might not be able to leave in time with ebb tide (Hampel, 2003).

In the German Wadden Sea salt marshes livestock grazing and dredging was significantly reduced with the foundation of the National Parks of Lower Saxony, Hamburg, and Schleswig-Holstein in 1986, 1990, and 1985, respectively (Stock, 2003; CWSS, 2017). But despite those protection measures the natural structure of the salt marshes has not recovered almost 35 years later.

Some investigations on the use of salt marshes by nekton were conducted before this PhD-project. The first description on the utilization of marine Wadden Sea salt marshes by fish was conducted by Dänhardt et al. (2011a) at the northern part of the Dieksanderkoog. This study was followed by several Bachelor and Master theses investigating the habitat quality of Wadden Sea salt-marsh creeks for nekton (Winkler, 2012; Ruhbaum, 2013; Schareck, 2014), some conducted within this PhD project (Twardy, 2015; Burgund, 2017; Conradt, 2017). While the Wadden Sea marshes were rarely studied, at least some brackish marshes in the adjacent river estuaries were investigated. In the beginning of the 2000s the value of brackish marshes in the Westerschelde estuary in the Netherlands for fishes and crustaceans was studied extensively (Hampel, 2003; Hampel et al., 2003a, 2003b; Hampel et al., 2004; Hampel and Cattrijsse, 2004; Hampel et al., 2005; Cattrijsse and Hampel, 2006; Hampel et al., 2009). Recently, also the value of a restored brackish marsh in the Weser estuary in Germany for fish was explored (Scholle et al., 2017). However, the conditions of estuarine brackish marshes differ markedly from marine coastal salt marshes. The salinity gradient in river deltas of, e. g. the rivers Rhine, Ems, Weser, Elbe and Eider, has a major effect on the species composition in these habitats. As species composition and abundance in river deltas differ from marine salt marshes also ecosystem processes must be assumed to differ. Therefore, results from the brackish marshes cannot be transferred to the marine Wadden Sea salt marshes.

The Wadden Sea is a highly dynamic and structurally complex ecosystem consisting of various interconnected habitats. Understanding the functioning and linkages between the different habitat types is an important step towards successful conservation measures. Several long-term fish monitoring programmes in the Wadden Sea provide species-specific abundance trends on fish (Tulp et al., 2017). However, these valuable observations miss some habitat types and do not yield insights into functional aspects. For example, species-habitat relationships allow explaining species occurrence in space and time, which is a prerequisite to evaluate potential conflicts with human activities. One of the most important human activities in German Wadden Sea salt marshes is grazing of sheep, cattle and horses. Livestock grazing is known to affect sedimentation (Andresen et al., 1990; Nolte et al., 2013), plants (Andresen et al., 1990; Kiehl et al., 1996; Kleyer et al., 2003), arthropods (Andresen et al., 1990; Meyer et al., 1995; Rickert et al., 2012; van Klink et al., 2013) and birds (van der Graaf et al., 2002; Bos et al., 2005; Erb, 2012; Mandema et al., 2013), and is used as a major management tool in Wadden Sea salt marshes (Nolte, 2014). But knowledge on the impact of livestock grazing on fishes was still missing before this PhD project, although a study from France indicated negative effects on the foraging opportunities of fish (Laffaille et al., 2000b).

Within marine-estuarine habitat mosaics (Nagelkerken et al., 2015), salt marshes represent an element valuable as feeding and growing environment for fish (Laffaille et al., 2001; Quan et al., 2007; Larkin et al., 2008; Mazumder et al., 2011). Despite the known importance of salt marshes for nekton in other regions, this species group was rarely studied in the Wadden Sea salt marshes and due to the lack of knowledge mostly ignored in management decisions. Investigation on the importance of salt-marsh creeks for fish were already demanded in the trilateral Wadden Sea plan in 2010. To fill the general knowledge gap of the importance of salt marshes for nekton, but also of the impact of anthropogenic modifications of Wadden Sea salt marshes, this PhD study was initiated as a part of the research project INTERFACE (Interaction of fish, plants, carbon & sediment: management & ecosystem functions of Wadden Sea salt marshes).

Outline of the Thesis

Following the argumentation of Sheaves et al. (2006), who advised against a classification of complex systems as either important or not important, the aim of this thesis is not to assess, whether Wadden Sea salt marshes are valuable for nekton or not, but to provide a first mechanistic understanding of species-habitat interactions and potential benefits and threats these habitats could provide. The four empirical studies of Chapter 2 to 5 address the five factors for habitat selection and quality according to Craig and Crowder (2002; predation, abiotic factors, bioenergetics, food resources and competition) and, additionally, analyse the human impact in terms of sheep grazing.

Chapter 2 reviews the dominant nekton species utilizing the Wadden Sea salt marshes. Furthermore, the chapter investigates whether fishes and crustaceans tend to migrate towards the marsh creeks, in terms of a directed movement and habitat selection (Harden Jones, 1968), or whether they ended up in the marsh creeks accidentally or randomly, e. g. via passive drift. Finally, seasonal and diurnal abundance patterns and length frequency distributions are analysed. Consequently, this chapter reveals who uses and who avoids the salt-marsh creeks and can thus also evaluate the predation pressure in the habitat.

Chapter 3 describes the abiotic conditions in German salt-marsh creeks and evaluates the benefits and threats for different nekton species, size classes and life stages. Hence, this chapter adds to explaining the abundance patterns found in Chapter 2.

Chapter 4 evaluates the foraging opportunities of the German salt-marsh creeks for fish. The short- and long-term body conditions of four fish species were measured and their diet compositions analysed. Moreover, prey densities of benthic and planktonic prey resources were quantified. These data sources together with the predator abundances from Chapter 2, were used to investigate the foraging strategies as well as potential prey limitations and resource competition.

Chapter 5 analyses the impact of sheep grazing on the diets of fish visiting the salt marshes. It investigates which fish species consume during which seasons which terrestrial prey resources. The study tested the hypothesis, that terrestrial prey consumption differs among fish species, seasons and grazing treatments (grazed and ungrazed salt marshes). Furthermore, the relative abundances of terrestrial prey and marine prey in grazed and ungrazed salt marshes were compared. And finally, the chapter evaluates whether the accessibility, determined by storm flood events, or the abundance, determined by sheep grazing, is more important for consumption of terrestrial prey resources by fish.

Chapter 6 summarizes the results from the four empirical studies (Chapter 2 to 5) and puts them into context. The chapter looks at the importance of individual microhabitats within the salt marsh and then at the importance of salt marsh on a larger scale, i. e. within the seascape. Finally, it hints at future research questions and management implications, that can be deduced from the findings of the thesis.

2

Preference, avoidance or coincidence? How fish and crustaceans utilize intertidal salt-marsh creeks in the German Wadden Sea

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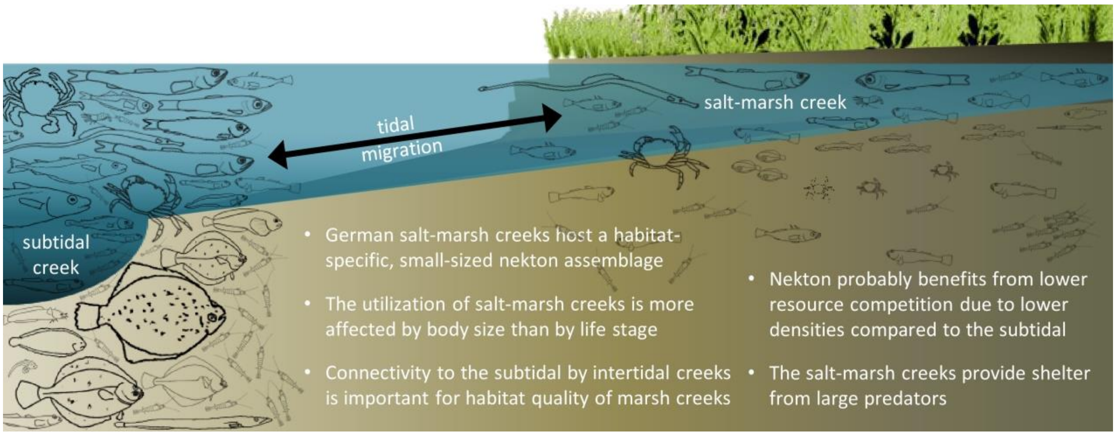

- German salt-marsh creeks host a habitat-specific, small-sized nekton assemblage
- The utilization of salt-marsh creeks is more affected by body size than by life stage
- Connectivity to the subtidal by intertidal creeks is important for habitat quality of marsh creeks
- Nekton probably benefits from lower resource competition due to lower densities compared to the subtidal
- The salt-marsh creeks provide shelter from large predators

Abstract

Worldwide, salt marshes have proven important or even essential for a wide variety of marine nekton. But in the world´s largest intertidal wetland, the Wadden Sea, their role for nekton is surprisingly unexplored. Building on extensive field sampling, we present an inventory of fish and crustacean species utilizing German Wadden Sea salt marshes and investigate their habitat utilization and affinity. Ten species dominated the nekton assemblage of the salt-marsh creeks both in frequency of occurrence and in relative abundance. Repetitive samplings resulted in highly variable catches, probably caused by the abundance in the subtidal. However, when occurring in high numbers, e. g. common goby (*Pomatoschistus microps*) and brown shrimp (*Crangon crangon*) were depleted with the nine consecutive hauls indicating a high habitat affinity. Seasonal and diurnal quantitative sampling revealed seasonal shifts within the nekton community and significant higher densities during night than day for eight out of the ten dominant salt-marsh nekton species. Compared to the subtidal not only the species composition differed significantly but also the size composition. The majority of fish in the marsh creeks were small (97% < 4.5 cm), consisting of larvae, juveniles and adults of small species. Thus, the utilization of salt-marsh creeks seems predominantly be triggered by size than by life stage. The absence of aquatic and avian piscivores indicates that salt-marsh creeks function for small nekton as refuge from predators. The difference of the nekton community of the marsh creeks from the subtidal raises the demand for habitat-specific monitoring programmes and further research on the connectivity and interactions between different habitat types, both considering seasonal and diurnal abundance variabilities.

Introduction

Habitat selection affects an organism’s probability to survive and reproduce on the one hand directly via habitat-specific rates of predation mortality, and on the other indirectly via an enhanced energy budget facilitating growth and reproduction (Hettler, 1989; Johnson, 2007; Allen et al., 2017; Boswell et al., 2019). Thus, habitats combining shelter from predators with favourable abiotic conditions and good foraging opportunities will ultimately increase an animal’s biological fitness (Clark and Shutler, 1999).

For fish and decapod crustaceans, salt marshes provide such services (Boesch and Turner, 1984; Mattila, 1992; Beck et al., 2001; MacKenzie and Dionne, 2008). At the same time, some properties of the confined small water bodies of the salt-marsh creeks represent risks to aquatic animals, e. g. temperature extremes or beaching during low water. Nekton species may prefer, avoid (lack of otherwise abundant species) or occur randomly in salt-marsh creeks. Geomorphology, hydrodynamics and hydrology differ considerably between salt-marsh creeks and ditches and the open waters, constituting a specific set of habitat characteristics by which aquatic animals are attracted, which they avoid or towards which they are indifferent.

Salt marshes are described as important habitats for fish and crustacean in various studies worldwide (e. g. Boesch and Turner, 1984; Quan et al., 2007; Whitfield, 2017; Jinks et al., 2020). Information of the ecological role of salt marshes for nekton is, however, still rare in the world's largest intertidal wetland, the Wadden Sea, (Mathieson et al., 2000; Cattrijsse and Hampel, 2006) and only just recently coming into focus (Friese et al., 2018a; Chapter 5). Wadden Sea salt marshes are structurally and historically unique and differ substantially from marshes e. g. in North America, Australia, South Africa, China and also at other European coasts (Boesch and Turner, 1984; Cattrijsse and Hampel, 2006). They have been modified since centuries for coastal protection and agriculture (Bakker et al., 2002; Airoldi and Beck, 2007). Sediment accretion was facilitated by installing brushwood groynes, and extensive networks of ditches were dug to foster drainage (Bakker et al., 2002). Embankments for coastal protection were gradually relocated seawards to reclaim land for agriculture (Bakker et al., 2002). As a result of these modifications, extensive marsh areas are in a relatively late successional stage today (Esselink et al., 2017), compared to salt marshes elsewhere (Cattrijsse and Hampel, 2006). The relatively high elevation prevents the vegetated marsh surface from flooding, and only the intertidal salt-marsh creeks are flooded twice a day and run completely empty during ebb tide. The flooded vegetated marsh surface is usually considered a profitable nekton habitat (Kneib, 1987; Paterson and Whitfield, 2000; MacKenzie and Dionne, 2008), but knowledge on how unvegetated marsh creeks are used by aquatic animals is rather fragmentary. The most drastic disruption of a natural gradient in the area was cutting off the hinterland by dykes, which reduced the salt-marsh area along the Wadden Sea substantially (e. g. Bakker et al., 2002; Esselink et al., 2017). Since fast drainage of the marsh is essential for dyke protection, naturally meandering salt-marsh creeks were straightened in the past. Another measure of dyke stabilization is livestock grazing with multiple effects on natural processes: grazing changes soil characteristics (Nolte et al., 2013), nutrient flows (Müller et al., 2013) and plant communities (e. g. Esselink et al., 2002), affects breeding birds (e. g. Mandema et al., 2013) and invertebrate communities (e. g. Andresen et al., 1990), and is even capable of modifying the diets of fishes entering the salt-marsh creeks during flood (Laffaille et al., 2000b; Friese et al., 2018a; Chapter 5).

The aim of the present study was to understand seasonal and diurnal utilization of Wadden Sea salt-marsh creeks by nekton and whether utilization patterns can be explained by preference, avoidance or coincidence. Based on a multiannual set of presence-absence and relative abundance data, we provide – to our knowledge – the first inventory of fish and crustaceans in German Wadden Sea salt marshes. In a second step, specific habitat affinity was investigated by means of depletion and replenishment patterns of species typically found in Wadden Sea salt-marsh creeks. Thirdly, for studying habitat specificity, seasonal and diurnal dynamics of nekton density and length frequency we sampled four creeks of a single marsh every month for one year. For comparison, reference data from the adjacent tidal and subtidal areas were also collected. Possible effects of grazing on the nekton community were examined by sampling two creeks in a sheep-grazed and in an ungrazed marsh, respectively. Finally, the findings of these diverse analyses were integrated to classify the observed habitat utilization patterns as preference, avoidance or coincidence. As the marsh creeks were dominated by few species the functional redundancy of biological traits was analysed as an indicator of the ecosystem´s resilience to species loss.

The new insights provide an important knowledge on a species group usually underrepresented in conservation and management (often as a result of lack of knowledge). Nekton inhabiting the salt-marsh creeks may not only be affected but also affect itself the ecosystem functioning of salt marshes, e. g. by representing a link to other subtidal habitats. Our results may assist to make future conservation efforts more holistic and meet the demands of the ecosystem approach.

Material and Methods

General overview of nekton assemblages in German Wadden Sea salt marshes

Metadata of all available datasets from the German Wadden Sea coast were compiled, including the grey literature (Tab. 2.1) to give a general overview of the salt marsh nekton assemblage. A total of 522 hauls collected from 2010 to 2018 and originating from 12 different salt marshes formed the basis of the overview (Tab. 2.1 and Fig. 2.1). All samples were obtained using fyke nets made of identical material and mesh size (6 mm), differing only in stowage height (1.50 m, 1.00 m and 0.60 m). Fykes were located mid-stream in the main nekton travel corridors (Boswell et al., 2019). Catch rates were standardized as individuals per tide (low water to next low water). Since this is only a coarse approximation of sampling effort, we confined our analyses to presence-absence and relative abundance data, representing species being dominant and occurring frequently in the German Wadden Sea salt marshes.

Functional habitat utilization patterns

Patterns of habitat utilization – preference, avoidance or coincidence – were analysed using depletion trajectories followed during 9 consecutive day and night hauls in October 2010, and May, June and August 2011, respectively. Sampling was carried out with two fyke nets of 1.50 m stowage height in two major salt-marsh creeks at Dieksanderkoog Nord (DSKN, Fig. 2.1, Dänhardt et al., 2011a). Three types of theoretical habitat utilization were defined (Fig. 2.2). Case 1 represents depletion without replenishment, indicating species with a relatively low migration radius or with no or small source population in the subtidal from which replenishment of the creek can occur or slower replenishment than reductions by the sampling. Species exhibiting this type are presumed to be highly connected to and, thus, have a high affinity for the salt-marsh creeks. Case 2 represents random replenishment, typical for e. g. species with a larger migration radius or a patchy source population. In case 3, caught individuals are replaced already with the next high tide with conspecifics being sufficiently abundant, mobile, close to and attracted by the marsh creek to fill the gap left by the fyke catches. Such a pattern indicates a strong habitat affinity and a rich source population for recovery within relatively short periods and can be an indicator for density dependent habitat use (see also Cain and Dean, 1976). Case 1 and case 3 could also be interpreted as special cases of case 2.

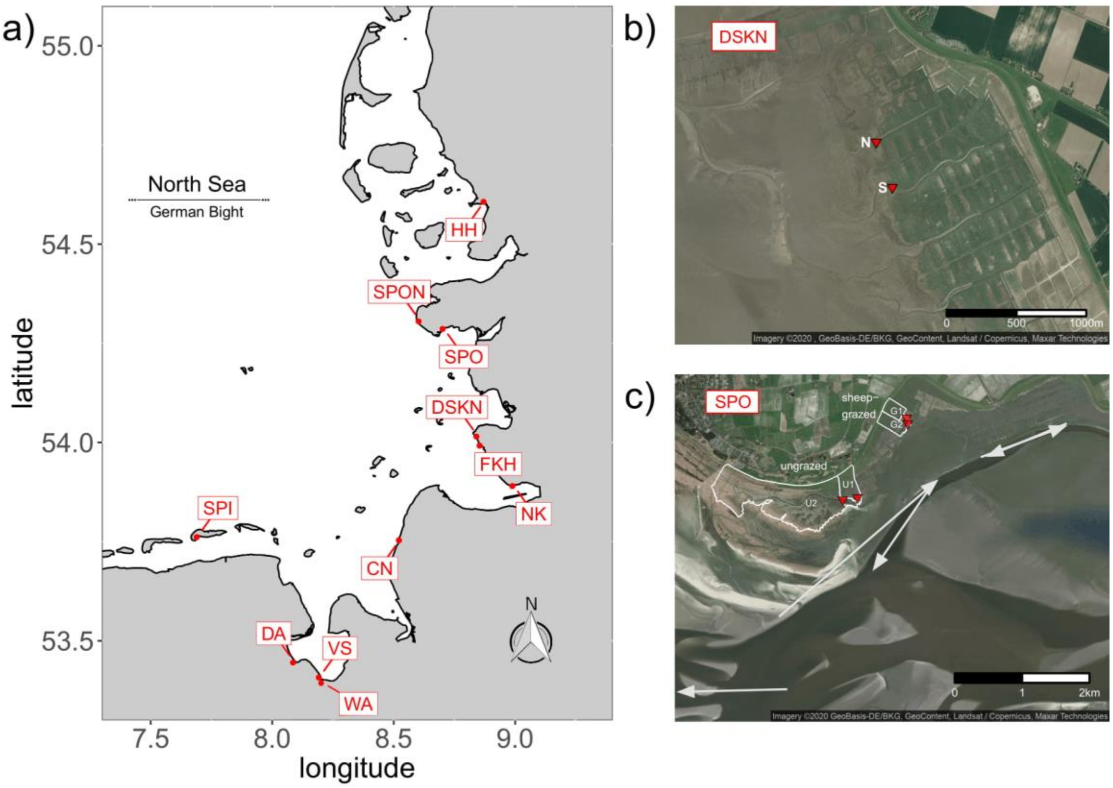

Fig. 2.1: Sampling locations a) along the German North sea coast 2010-2018, SPI: Spiekeroog, DA: Dangast, VS: Vareler Schleuse, WA: Wapelersiel, CN: Cappel-Neufeld, NK: Neufelder Koog, DSKN: Dieksanderkoog Nord, FKH: Friedrichskoog Hafen, SPO: St. Peter-Ording, SPON: St. Peter-Ording Nord, HH: Hamburger Hallig; b) DSKN: sampled for habitat utilization patterns in 2010-2011 with the fyke net positions in the northern creek (“N”) and the southern creek (“S”); c) SPO: sampled for quantitative abundance analyses in 2015-2016 including watershed areas of each creek in the ungrazed marsh (U1, U2) and in the sheep-grazed marsh (G1, G2), red triangles indicate fyke net positions and arrows indicate trawl transects for reference samples from the subtidal in July 2015.

Diurnal, seasonal and small-scale spatial patterns of nekton densities

Diurnal, seasonal and small-scale spatial patterns of nekton densities were recorded during a one-year field campaign in a marsh near St. Peter-Ording (Fig. 2.1), where standardized samples from four marsh creeks and reference samples from the adjacent subtidal were obtained monthly at spring tide between March 2015 and February 2016 (no sampling in November 2015 and January 2016. Two creeks draining a sheep-grazed and an ungrazed marsh each were sampled to detect possible grazing effects on the nekton community. In each of these marsh types a large fyke with a 1.5 m stowage height was applied on one creek and a smaller fyke with a stowage height of 1.0 m in the other (Supplement A, Fig. A.1). Although both net types had the same mesh size (6 mm), the meshes of the large fyke net were more tightened as only one ring kept them open instead of three in the smaller fyke net. Subsequently the larger fyke nets tend to catch smaller sized and larger amounts of nekton. By applying these two different net types and one of each in the grazed (G) and ungrazed (U) marsh, catch efficiency was increased and diversified. As a standard procedure, each month in each creek a day and a night catch was conducted to track diurnal habitat utilization patterns. Fykes were set and emptied during ebb tide. For each haul, total weight and species abundance were recorded. In addition, individual standard length (to the mm below) of fish was measured. Subsamples were taken when catch size was too large to be handled in an appropriate time. Since herring *C. harengus* smaller 4 cm and juvenile plaice *Pleuronectes platessa* could not reliably be identified in the field, vertebrae or caudal fin rays of subsamples were counted in the laboratory (Munk and Nielsen, 2005).

Monthly reference presence-absence data from the adjacent subtidal were obtained from April to October 2015 (no data in June 2015), from a commercial shrimper, employing two 4 m beam trawls (0.4 m stowage height, mesh size 11 mm in the cod end), trawled at 2-3.5 knots. To obtain quantitative catch numbers and length measurements we chartered the boat on July 15th 2015. Haul durations varied from 15 min up to 1 h 30 min. In July 2015 hauls lasted 22 min on average while during the rest of the year they lasted 49 min on average.

Data analyses

Fyke catches from the sampling campaign 2015-2016 were standardized to number of fish per volume (m^3) by dividing absolute catch numbers by the filtered water volume (Friese et al., 2018a; Chapter 5). Catches that could not be quantified due to net malfunctioning were excluded (Supplement A, Tab. A.2). Catch rates were additionally provided as individuals per area (m^2) to allow for comparison with other studies (Supplement A, Tab. A.3) and with the beam trawl catches from the adjacent subtidal. However, as fyke nets are a passive gear a filtered area cannot be calculated.

Tab. 2.1: Data sources for the analyses of nekton occurrence in German Wadden Sea salt marshes. Abbreviations correspond to Fig. 2.1.

data source	year	area	month												number of hauls
			Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	
Dänhardt et al. (2011a)	2010	DSKN										51			51
	2011	DSKN					71	60	8	80					219
Dänhardt, A. (unpublished data)	2012	NK								8					8
		DSKN								15					15
		FKH								3					3
Winkler (2012)	2011	DA								7		9			16
		VS								5	3	10			18
		WA									14	4			18
Ruhbaum (2013)	2013	CA					4								4
Schareck (2014)	2013	SPON				7								18	25
		CN					1								1
Dänhardt, A. and Hufnagl, M. (unpublished data)	2015	SPO							18						18
	2016	SPI							12						12
Friese et al. (unpublished data)	2014	CA				2				2					4
		DSKN				2			2						4
		SPO				2			8	3		3			16
		HH				2									2
		VS							2						2
Friese et al. (2018b)	2015	SPO			8	12	8	8	8	8	8	8		8	76
	2016	SPO		8											8
Friese, J. (unpublished data)	2018	SPO										2			2
number of hauls			0	8	8	27	84	68	58	131	25	87	0	26	**522**

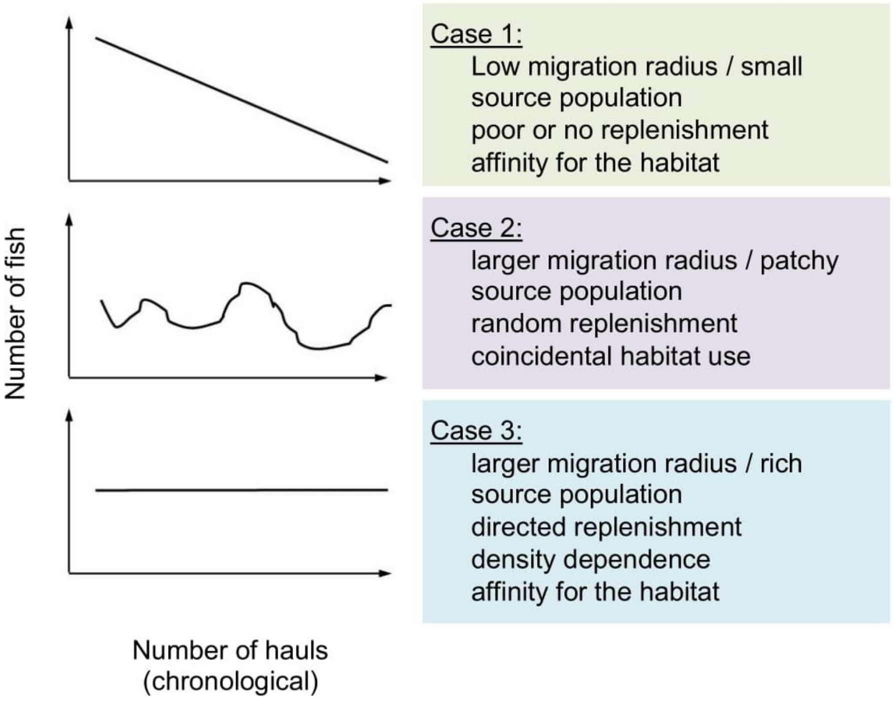

Fig. 2.2: Theoretical model cases of habitat utilization patterns

But calculating numbers per area can be done by dividing the total numbers present in the creek by the flooded area at high tide. Numbers caught with the fyke net does not have to be equal with the numbers totally abundant in the creek. Therefore two different calculation methods were applied for this additional area-based standardization: (1) a minimum density, assuming that caught numbers equal total numbers in the creek, and (2) a maximum density, extrapolating the catch numbers within the fished runoff water volume to the unfished water volume while assuming equal distribution (Supplement A, Tab. A.3).

Quantitative diurnal, seasonal, and small-scale spatial abundance analyses were carried out for the nine most common species of the salt-marsh creeks (six fish species *Gasterosteus aculeatus, Sygnathus rostellatus, Pomatoschistus microps, Pomatoschistus minutus, Clupea harengus, Osmerus eperlanus,* and three crustacean species *Carcinus maenas, Crangon crangon, Palaemon spec.*). *Pomatoschistus* (post)larvae cannot be distinguished by morphological characteristics (Larmuseau et al., 2008). They were thus combined to *Pomatoschistus spp.* for seasonal size composition analysis, which focussed on the appearance of the young-of-the-year, while for all other analysis the unidentified goby (post)larvae were classified as *P. microps,* because on the one hand they occurred in relatively now numbers in the catches (mesh size 6 mm) and on the other as *P. microps* was the dominating goby species, the bias was kept as low as possible by this approach. Paired Wilcoxon signed rank tests were run to investigate spatial and diurnal abundance differences.

Size classes of fish in the salt-marsh creeks and the subtidal were compared via catch rates (numbers per 1000 m², calculated as minimum density, see above) per size class. Due to different catch methods and larger mesh size in the subtidal, the abundance of smaller individuals cannot be compared. However, we assume that the larger individuals, caught efficiently with 11 mm beam trawls, were also caught efficiently with the 6 mm fyke nets. Decreasing water levels in the salt-marsh creeks reduce the space left between the fyke net wings and the creek bank, leading to a decreasing probability of passing the net, especially as most fish prefer the deeper mid-stream areas of the creek (Boswell et al., 2019). Therefore we assume that the size-specific abundance of larger fish caught in the subtidal can be compared to the salt-marsh creeks despite different catch methods.

Nekton communities in the salt marshes and in the subtidal were compared with a cluster analysis based on presence-absence data due to the different catch methods. Only those months, for which data from both habitats were available were included in the analysis (April, May, July, August, September and October 2015). Sørensen index of dissimilarity with unweighted pair group method with arithmetic mean (UPGMA) was used for clustering.

Functional redundancy of biological traits (Petchey and Gaston, 2002) was evaluated by analysing the decrease of functional diversity (FD) with decreasing species richness. FD is the diversity of functional traits, which are ecosystem-relevant components of the phenotypes of the species analysed (Tilman, 2001; Petchey and Gaston, 2006). The selection of these traits has a major impact on the results of the functional redundancy and the results of the analysis refers only to those traits included (Petchey et al., 2009). Our analysis included categories of seven traits (Supplement A, Tab. A.4; Franco et al., 2008; Neal and Pizzolla, 2008; Breine et al., 2010; Rice et al., 2013; Florin et al., 2014; Luna, 2019) which were combined using fuzzy coding (Chevenet et al., 1994; Beauchard et al., 2017). Fuzzy coding is used because assignment of certain trait categories to species differs between literature sources. These different trait categories per trait and species were combined by fuzzy coding using values from 0 (= no affinity to the trait category) to 1 (= high affinity to the trait category) adding up to 1 per trait and species. The species-trait-matrix containing these fuzzy codes was then multiplied with the presence-absence data per haul, resulting in fuzzy codes of 0 when species are absent. Using the *R* function *Xtree* (Schumacher, 2003) FD was calculated as the total branch length of a dendrogram built by clustering based on Sørensen index of dissimilarity with UPGMA (Petchey and Gaston, 2002). FD was repeatedly calculated per haul dropping randomly 1 to (n-1) species to simulate species loss, where n is the total number of species present per haul. Random species subsets were repeated ten times per haul and species number.

All data analyses were performed in the open-source software *R* version 3.5.1 (R Core Team, 2018). An overview of used *R* packages is given in the Supplement A (Tab. A.1).

Results

General overview of nekton assemblages in German Wadden Sea salt marshes

C. maenas, *C. crangon* and *Palaemon spec.* were the most frequent crustaceans, occurring in 88, 60 and 32 % of all hauls, respectively (Tab. 2.2). Concerning the fish species, *G. aculeatus* was recorded most frequently in the salt-marsh creeks, followed by *S. rostellatus*, *O. eperlanus*, *C. harengus*, *P. microps*, *P. minutus* and *Alosa fallax* (Tab. 2.2). These most frequent nekton species were also dominating the catches in terms of their percentage of the total catch numbers per haul (Fig. 2.3). In the same order as their frequency of occurrence in the hauls, *C. maenas*, *C. crangon* and *G. aculeatus* had the highest mean percentage per haul (Fig. 2.3). With the fourth highest mean percentage per haul *P. microps* was a major component of the catch composition followed by *S. rostellatus*, *C. harengus*, *O. eperlanus*, *A. fallax*, *Palaemon spp.* and *P. minutus* (Fig. 2.3).

Functional habitat utilization patterns

Catches in consecutive hauls were highly variable (Fig 4). However, high catch numbers of *C. crangon* and *P. microps* (> 100 individuals) coincided with catches of *C. crangon* decreasing in consecutive hauls by 94.5 %, 81.5 % and 76.6 % in May, August and October and of *P. microps* decreasing by 85.8 % and 98.0 % in October (when ignoring the first night catch) and August, respectively (Fig 4). These observations are best represented by case 1 (Fig 2.), indicating stationary species with a preference for the habitat. *G. aculeatus* was classified as a mobile species with a patchy source population in the subtidal (case 2, Fig. 2.2), because it was either randomly replenished at low catch numbers (October and August), or at high catch numbers, its abundance increased (in May) or decreased (in June, Fig. 2.4). *S. rostellatus* showed sudden increases in catch numbers in May, June and August indicating a mobile species with a patchy source population and a rather coincidental habitat use (case 2, Fig. 2.2; Fig. 2.4). In October 2010 catch numbers of *S. rostellatus* remained stable on a relatively high level despite fishing (fluctuating around ca. 73 and 171 individuals per catch in the northern and southern creek, respectively; Fig. 2.4), indicating a steady replenishment from a rich source population with a strong affinity to enter the marsh creeks. Despite abundance fluctuations, *C. harengus* was eventually depleted in October and August, when it occurred in low numbers (case 1, Fig. 2.2; Fig. 2.4). However, in June and July they tended to became more abundant with increasing fishing effort, suggesting not only a patchy but increasingly rich source population in the subtidal with a high affinity to enter the marsh creeks (case 2, Fig. 2.2; Fig. 2.4). Catch numbers of the anadromous *O. eperlanus* remained relatively stable across hauls in October and August, indicating a steady replenishment from the subtidal source population and a high affinity to the marsh creeks (case 3, Fig. 2.2; Fig. 2.4). In May and June, however, when catch numbers were relatively low, catch numbers either increased or decreased within consecutive hauls indicating a patchy source population in the subtidal (case 2, Fig. 2.2; Fig. 2.4). The anadromous *Alosa fallax* was only caught in August and its abundance pattern, a positive replenishment followed by a depletion, indicates a mobile species with a patchy source population (case 2, Fig. 2.2). In total, only *C. crangon* and *P. microps* were classified as species with a low migration radius and a high habitat affinity, because the depletion caused by repeated fishing could not be replenished by the individuals coming from elsewhere to the sampling area. Despite some random depletion patterns, the other analysed species had a probably larger migration radius and used the habitat rather coincidentally.

Tab. 2.2: Seasonal frequency of occurrence of all nekton species caught in Wadden Sea salt marshes from 2010-2018 sorted by total frequency of occurrence.

month	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Dec	Total
number of hauls (N)	8	8	27	84	68	76	131	25	87	8	522
fish species	Frequency of occurrence [%]										
Crustacea											
Carcinus maenas	50.0	75.0	74.1	92.9	95.6	72.4	91.6	100.0	93.1	87.5	88.31
Crangon crangon	100.0	87.5	51.9	76.2	33.8	64.5	55.7	32.0	70.1	100.0	60.34
Palaemon spec.	0.0	62.5	66.7	13.1	45.6	55.3	31.3	24.0	10.3	75.0	32.38
Hemigrapsus sanguineus	0.0	0.0	0.0	0.0	0.0	13.2	1.5	12.0	4.6	12.5	3.83
Eriocheir sinensis	0.0	0.0	0.0	0.0	17.7	0.0	1.5	0.0	0.0	0.0	2.68
Liocarcinus holsatus	0.0	0.0	3.7	0.0	0.0	1.3	3.1	0.0	3.5	0.0	1.72
Macropodia rostrata	0.0	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.19
Fish											
Gasterosteus aculeatus	87.5	87.5	85.2	83.3	70.6	59.2	42.8	48.0	27.6	100.0	57.47
Syngnathus rostellatus	12.5	37.5	48.2	31.0	23.5	52.6	59.5	36.0	58.6	25.0	45.79
Osmerus eperlanus	62.5	25.0	33.3	22.6	41.2	26.3	43.5	68.0	48.3	75.0	39.27
Clupea harengus	62.5	12.5	70.4	44.1	38.2	40.8	21.4	16.0	21.8	87.5	33.91
Pomatoschistus microps	100.0	100.0	92.6	8.3	11.8	40.8	26.7	64.0	34.5	100.0	33.72
Pomatoschistus spec. (larvae)	0.0	0.0	0.0	41.7	2.9	13.2	25.2	4.0	59.8	0.0	25.48
Pomatoschistus minutus	37.5	50.0	18.5	3.6	2.9	10.5	7.6	32.0	13.8	50.0	11.30
Alosa fallax	0.0	0.0	0.0	0.0	0.0	0.0	35.1	4.0	0.0	0.0	9.00
Pleuronectes platessa	0.0	37.5	44.4	8.3	2.9	2.6	3.1	4.0	2.3	0.0	6.32
Platichthys flesus	0.0	0.0	3.7	0.0	4.4	2.6	9.9	4.0	11.5	12.5	5.94
Sprattus sprattus	12.5	0.0	11.1	9.5	1.5	2.6	2.3	20.0	3.5	0.0	4.98
Pungitius pungitius	37.5	0.0	3.7	0.0	0.0	4.0	1.5	16.0	3.5	75.0	4.21
Anguilla anguilla	0.0	0.0	0.0	1.2	0.0	2.6	0.0	36.0	5.8	0.0	3.26
Chelon labrosus	12.5	0.0	14.8	0.0	1.5	0.0	0.0	0.0	3.5	25.0	2.11
Buglossidium luteum	0.0	0.0	0.0	0.0	0.0	9.2	0.8	0.0	0.0	0.0	1.53
Belone belone	0.0	0.0	0.0	0.0	2.9	4.0	0.8	0.0	0.0	0.0	1.15
Engraulis encrasicolus	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	2.3	12.5	1.15
Gobiidae	0.0	0.0	0.0	0.0	0.0	7.9	0.0	0.0	0.0	0.0	1.15
Chelon ramada	0.0	0.0	0.0	0.0	0.0	0.0	0.0	20.0	1.2	0.0	1.15
Pomatoschistus lozanoi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	4.6	0.0	0.96
Scardinius erythrophthalmus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.0	2.3	0.0	0.96
Abramis brama	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.0	0.0	0.0	0.77
Ammodytidae	0.0	0.0	3.7	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.77
Perca fluviatilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.0	0.0	12.5	0.77
Rutilus rutilus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.0	0.0	0.0	0.77
Scophthalmus rhombus	0.0	0.0	0.0	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.77
Trachurus trachurus	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	1.2	0.0	0.77
Zoarces viviparus	37.5	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.77
Myoxocephalus scorpius	0.0	0.0	11.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.57
Solea solea	0.0	0.0	0.0	0.0	1.5	0.0	1.5	0.0	0.0	0.0	0.57
Liparis liparis	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	1.2	0.0	0.38
Triglidae	0.0	0.0	0.0	0.0	0.0	2.6	0.0	0.0	0.0	0.0	0.38
Atherina presbyter	12.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.19
Blicca bjoerkna	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.19
Ciliata mustela	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.19
Gymnocephalus cernua	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.19
Sander lucioperca	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.0	0.0	0.19

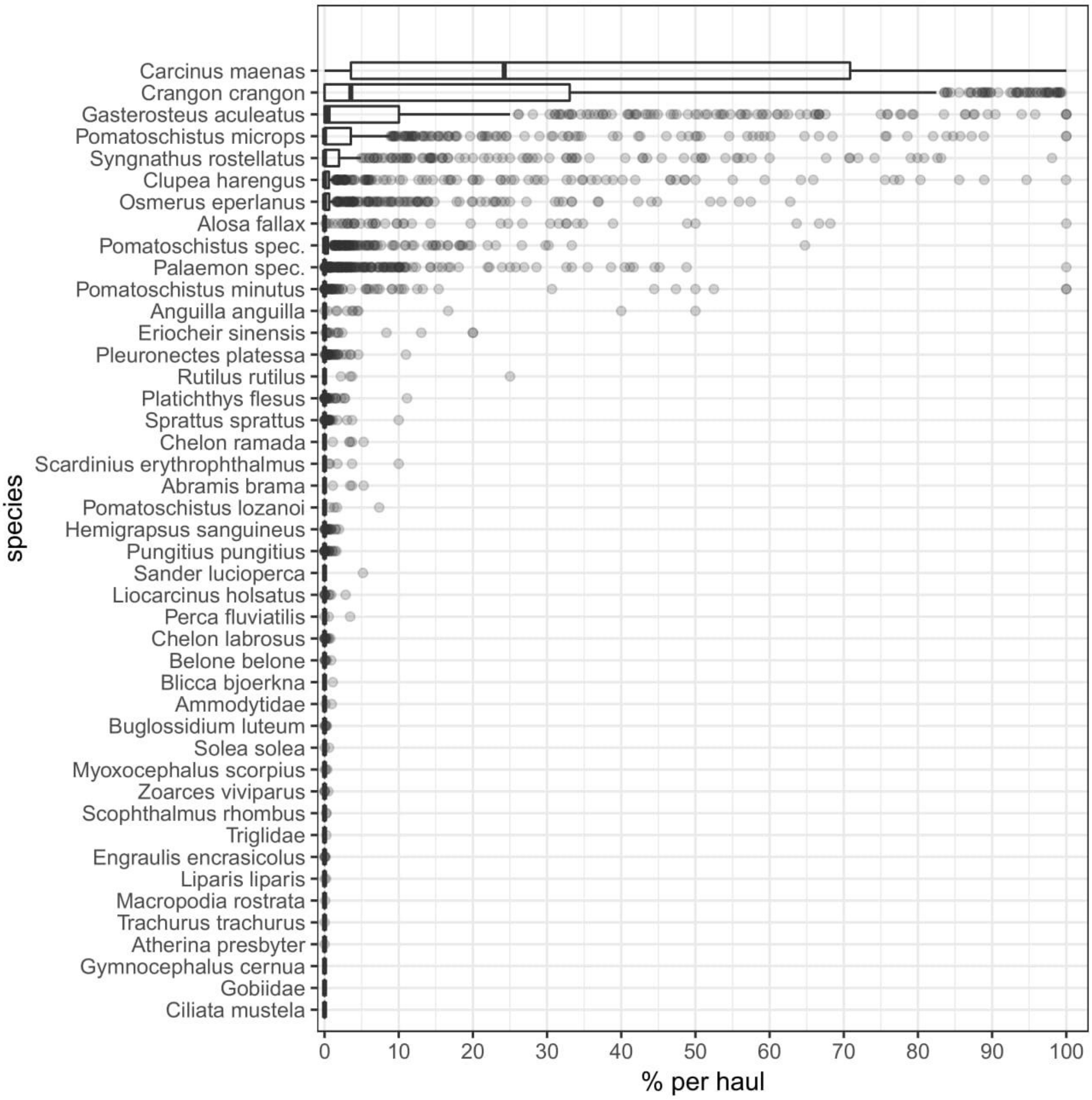

Fig. 2.3: Species dominance per haul based on multiannual data compilation (2010-2018, including 522 hauls). Each point refers to the percentage a species contributed to the total catch (in numbers) per haul.

Small-scale spatial, diurnal, seasonal and size-specific abundance patterns

The fyke nets in the creeks *G1*, *G2*, *U1*, and *U2* filtered on average 40.6 (± 7.4) %, 51.0 (± 7.9) %, 37.1 (± 6.3) %, and 28.6 (± 5.3) % of the runoff water volume, respectively. Highest densities of the nine most common nekton species were observed in the creek *G2* in the grazed salt marsh followed by the largest creek *U2* in the ungrazed salt marsh and finally the two smaller creeks with the smaller fyke nets (average individuals per 1000 m^3: *G2*: 9999; *U2*: 3259; *G1*: 1474; *U1*: 288; Supplement A, Tab. A.5 to Tab. A.8). In the creeks in the grazed salt-marsh located in a funnel-shaped shoreline significantly higher nekton densities (in particular *C. maenas*, *G. aculaetus*, *Palaemon spec.*, *P. microps*, and *S. rostellatus*) were observed than in the creeks of the ungrazed salt-marsh located closer to the tip of the Eiderstedt peninsula (Paired Wilcoxon signed rank test: V = 150, p-value = 0.0129; Supplement A, Tab. A.5).

At night the abundance of *C. maenas*, *C. crangon*, *G. aculaetus*, *P. microps*, *P. minutus, O. eperlanus, and S. rostellatus* in the marsh creeks were significantly higher than during day (by on average 134 %, 14910 %, 177 %, 20269 %, 4184 %, and 158 % respectively; for p-values see Supplement A, Tab. A.8). Abundance of *C. harengus and Palaemon spec.* was similar between day and night.

There were pronounced seasonal patterns in species composition and densities, with highest densities in October with in total 16 ind. m^{-3} caused by the high abundance of *C. crangon* (Fig. 2.5). Abundance of *C. crangon* decreased from March to May and subsequently increased until October and decreased again in the winter month December and February (Fig. 2.5, Supplement A, Fig. A.2). *Palaemon spec.* displayed a variable abundance during the whole year but disappeared during winter (Fig. 2.5, Supplement A, Fig. A.2). *C. maenas* occurred in highest densities from June to October (Fig. 2.5, Supplement A, Fig. A.2). The abundance of *G. aculeatus* in contrast increased during winter until early spring and was most abundant in April (Fig. 2.5, Supplement A, Fig. A.2). *S. rostellatus* peaked in July and August and disappeared suddenly afterwards. *P. microps* occurred in the highest numbers (Fig. 2.5, Supplement A, Fig. A.2). Its abundance decreased from March until June, followed by four months of high abundance from July till October and low abundance in December and February. *P. minutus* disappeard during the first three sampling months (Fig. 2.5, Supplement A, Fig. A.2). The density of *C. harengus* fluctuated strongly but highest densities were found from April to July (Fig. 2.5, Supplement A, Fig. A.2). Also the density of *O. eperlanus* varied strongly but on a lower level and with highest densities from July to October (Fig. 2.5, Supplement A, Fig. A.2).

In total, 97.3 % of the fishes caught in the marsh creeks in St. Peter-Ording from March 2015 until February 2016 had a standard length of 0.5-4.5 cm (Fig. 2.6a). The larger fish caught in the subtidal were absent in the marsh creeks (Fig. 2.6). Within the whole sampling year, the largest specimen caught were three *P. flesus* (15.2 cm, 21 cm and 21.8 cm) and one *C. harengus* (21 cm). The small fishes represented different life stages and were composed of larvae, postlarvae, juveniles and adult fishes of species with a small maximum length. Although fish larvae were likely underrepresented due to gear effects (mesh size 6 mm), they occurred in the catches and their length frequency distributions revealed a seasonal shift in larvae species occupying the marsh creeks. From March to May *P. platessa* postlarvae entered the salt-marsh creeks (Supplement A, Fig. A.3), accumulating in the small rivulets during low tide. In April, high numbers of postlarval *C. harengus* appeared in the creeks and became increasingly abundant until July, while *P. platessa* larvae gradually disappeared (Supplement A, Fig. A.3). In June, larvae and juveniles of *Pomatoschistus spp.* appeared in the fyke net catches and increased in length until

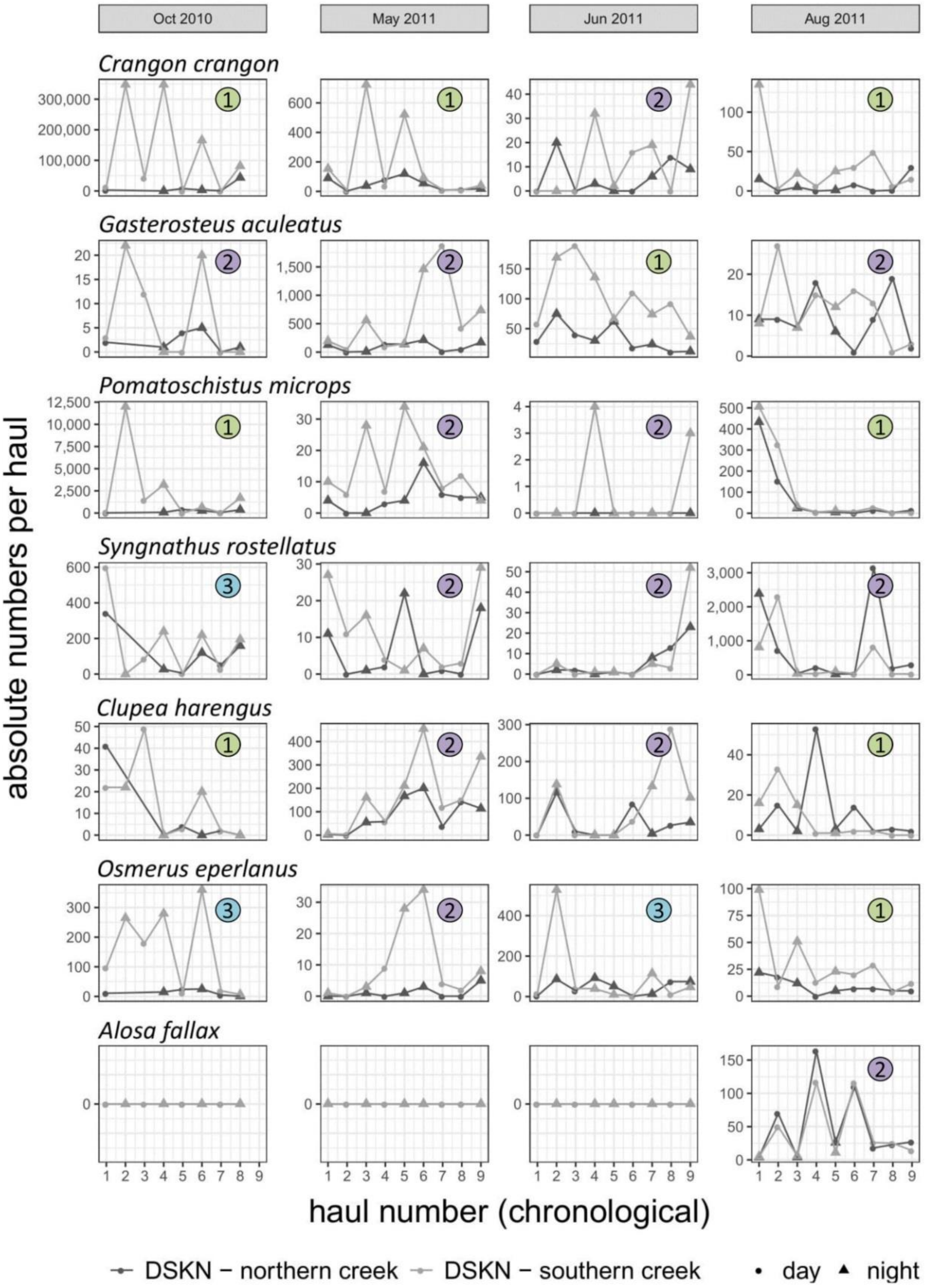

Fig. 2.4: Habitat utilization patterns of the selected Wadden Sea salt-marsh nekton species. Depletion or replenishment is indicated by the absolute numbers of individuals caught in consecutive fyke net hauls. Numbers in circles refer to the best match with the theoretical patterns of habitat utilization defined in Fig. 2.2.

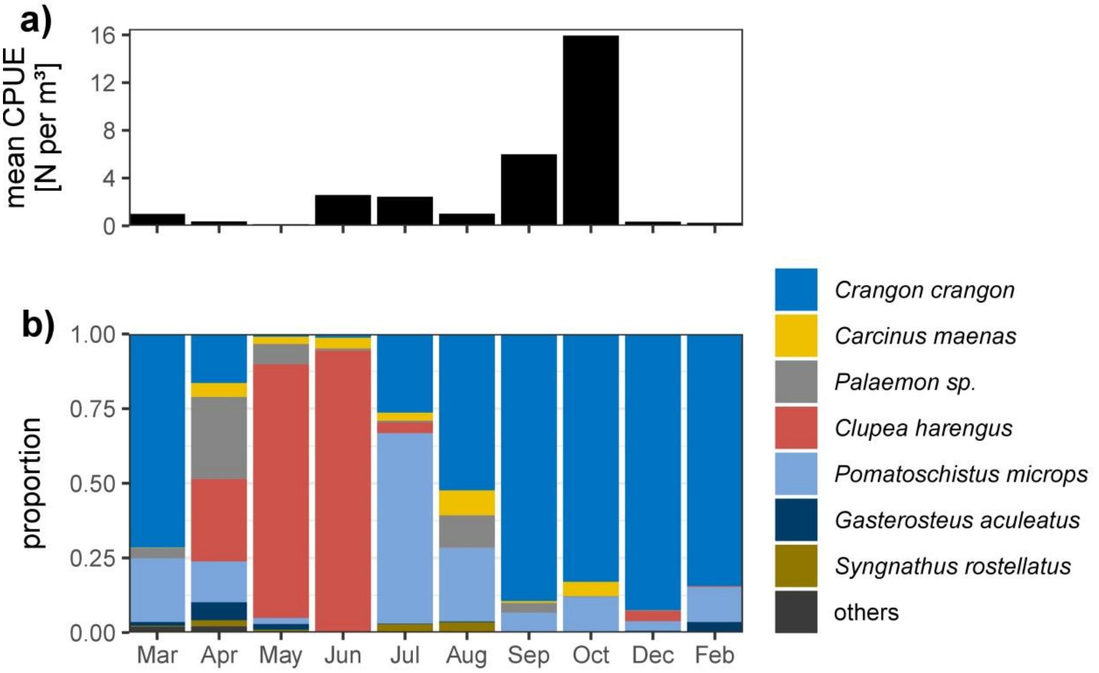

Fig. 2.5: Seasonal a) total abundance of nekton (mean catch per unit effort CPUE) and b) catch composition. The category “others” includes *Ammodytidae*, *Belone belone*, *Chelon labrosus*, *Engraulis encrasicolus*, *Hemigrapsus sanguineus*, *Myoxocephalus scorpius*, *Osmerus eperlanus*, *Perca fluviatilis*, *Platichthys flesus*, *Pleuronectes platessa*, *Pomatoschistus minutus*, *Pungitius pungitius*, *Solea solea*, *Sprattus sprattus*, *Zoarces viviparus.*

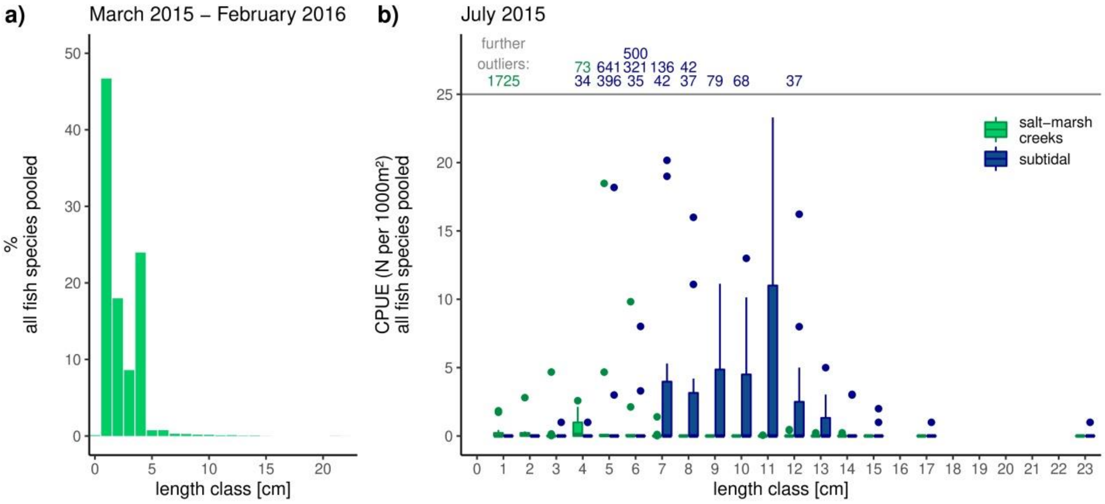

Fig. 2.6: Standard length frequency distribution of all fish species caught a) from March 2015 – February 2016 in the salt-marsh creeks near St. Peter-Ording and b) in July 2015 in the salt-marsh creeks and in the adjacent subtidal area. Please note the differing mesh sizes and applied net types. Salt-marsh creeks: fyke nets, 6 mm mesh; Subtidal: beam trawl nets, 11 mm mesh

October (Supplement A, Fig. A.3). The length distribution of *G. aculeatus* showed similar seasonal patterns like the gobies, but juveniles were only caught in small numbers (Supplement A, Fig. A.3). In July, a new cohort of *S. rostellatus* appeared in the salt-marsh creeks, increased in size but decreased in abundance until October (Supplement A, Fig. A.3). Among the fish species found most frequently and abundantly in the marsh creeks, *O. eperlanus* did not show a specific seasonal length distribution pattern, but occurred in various length classes year round (Supplement A, Fig. A.3). Larvae and postlarvae of *Chelon labrosus* (22 individuals, 16-32 mm), *Myoxocephalus scorpius* (9 individuals, 14-18 mm), *Zoarces viviparus* (6 individuals, 35–58 mm) *Ammodytidae* (3 individuals, 44-52 mm), *Belone belone* (2 individuals, 32-34 mm) and *Solea solea* (1 individual, 15 mm) were caught only occasionally and in very low numbers.

Community analysis

The species composition differed significantly between the salt-marsh creeks and the adjacent subtidal (Fig. 2.7, Supplement A, Tab. A.9). Three of 5 custacean species and 11 of 27 fish species were found in both habitats, with *C. maenas*, *Palaemon spec.*, *G. aculeatus* and *P. microps* occurring more frequently in the salt-marsh creeks, and *C. harengus, O. eperlanus, P. flesus, P. platessa, P. minutus, S. solea, S. sprattus and S. rostellatus* being encountered more frequently during sampling the subtidal (Supplement A, Tab. A.9). Altogether, in the subtidal the frequency of occurrence was

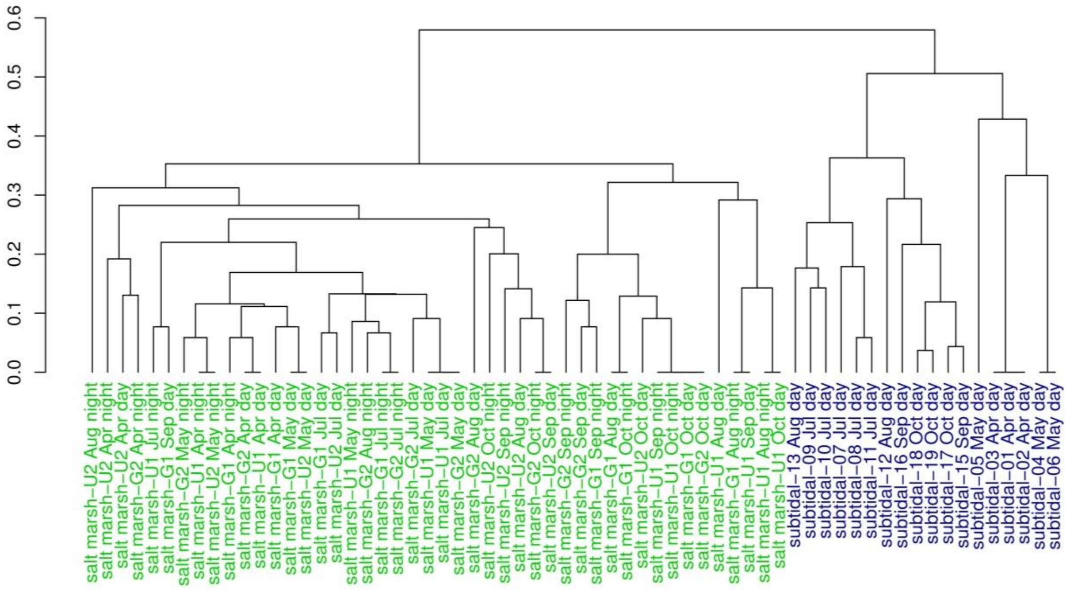

Fig. 2.7: Cluster analysis of the nekton communities in salt-marsh creeks (green) and in the adjacent subtidal areas (blue) based on presence – absence data from April, May, July, August, September and October 2015 and calculated using the Sørensen index of dissimilarity

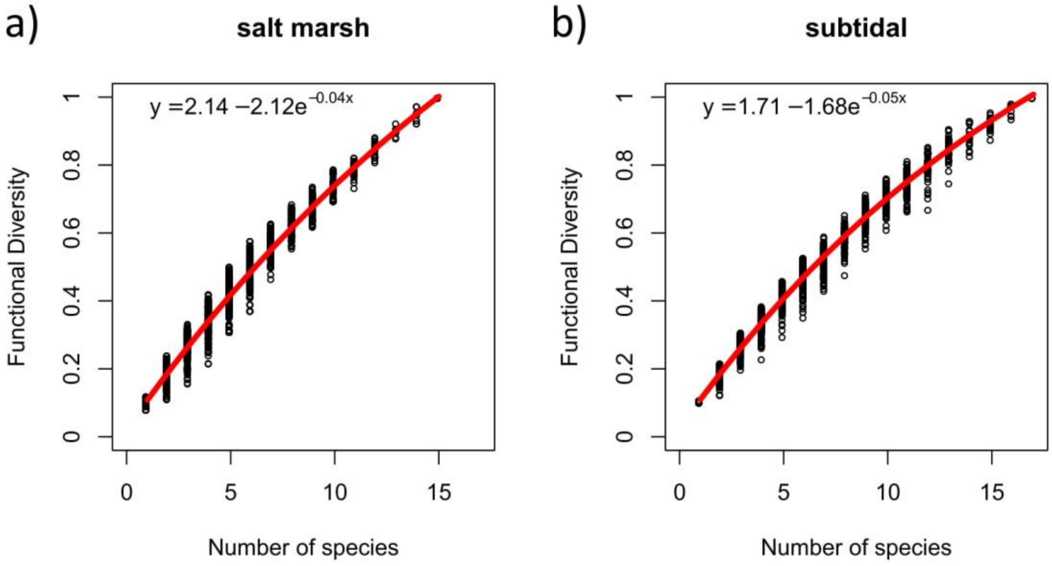

Fig. 2.8: Relationship between functional diversity and species richness a) inside the salt-marsh creeks and b) in the open water of the adjacent subtidal. Calculations were performed according to Petchey and Gaston (2002) and are based on presence-absence data per haul including those months were data were available from both habitats (April, May, July, August, September and October 2015). The traits used are described in the Supplement A, Tab. A.4.

more evenly distributed across species than in the salt-marsh creeks (Supplement A, Tab. A.9). Within the entire reference period, we caught 20 species in the salt-marsh creeks and 26 in the subtidal. On average, we found 7.3 (± 2.5) species per haul in the marsh creeks, but 11.0 (± 3.5) in the subtidal. Twelve species found in the subtidal were never observed in the salt-marsh creeks, apparently avoiding this habitat (Supplement A, Tab. A.9). The combined information on frequency of occurrence, temporal habitat utilization patterns and species-specific abundance indicates a high affinity for the salt-marsh creeks by at least *C. maenas, C. crangon, G. aculeatus, P. microps, S. rostellatus, C. harengus* and *O. eperlanus*.

The relationship between functional diversity and species richness was analysed to evaluate the ecosystem´s resilience to species loss. In both habitats, an immediate decrease of functional diversity with decreasing species richness became evident and indicates a low functional redundancy (Fig. 2.8). The decline in functional diversity was slightly steeper in the salt-marsh creeks (Fig. 2.8).

Discussion

Salt-marsh creeks along the German Wadden Sea coast host a specific, species-poor and small-sized nekton assemblage. Our results support previous findings from other salt marshes, that specific life stages of few generalist species utilize this habitat type

(Sogard and Able, 1991; Cattrijsse et al., 1994; Visintainer et al., 2006). Frequency of occurrence, repetitive samplings, and species-specific abundance implied that especially *C. maenas*, *C. crangon*, *G. aculeatus*, *P. microps, S. rostellatus, C. harengus* and *O. eperlanus* have a preference for salt-marsh creeks. The nekton community in the subtidal differed significantly from the marsh creeks. Not all species that occurred in the marsh were efficiently caught in the subtidal due to gear effects. However, the absence of certain species in the marsh is unlikely to be caused by gear effects alone, as the probability of net avoidance is low in the spatially constrained marsh creeks. In conclusion, certain species indeed avoid the marsh creeks while others prefer it. Although the marsh creeks are inhabited by less species than the subtidal, both systems were similarly characterized by a low functional redundancy, meaning that in both systems the ecosystem functioning is similarly sensitive to loss of species (Petchey and Gaston, 2002; Rice et al., 2013). As the nekton community is dominated by short-lived species, inter-annual abundance variations are expected to be high, as the few year-classes are more sensitive to variations in reproduction success (Bjørkvoll et al., 2012). Another finding of the study is the narrow size composition of fish. While many studies worldwide highlight the nursery value of salt marshes for nekton (e. g. Cattrijsse et al., 1997; Paterson and Whitfield, 2000; Beck et al., 2001; Fonseca et al., 2011; Whitfield, 2017), this habitat type attracts early life stages of large-sized species as well as adults of small-sized species. Obviously, habitat requirements and preferences are more similar between nekton of similar size than within species. The abundance of early life stages was underestimated (mesh size: 6 mm), but the mass occurrences of *P. platessa*, *C. harengus* and *Pomatoschistus* postlarvae and the small size distribution of *C. crangon* (Burgund, 2017) indicate that this habitat has also a nursery value for at least these species. Cattrijsse et al. (1997) reported that postlarval *C. crangon* migrates actively into a Dutch estuarine salt-marsh creek to utilize this prey-rich and predator-poor habitat as a nursery. Thus, especially the role of the salt marsh for small size classes, which were not efficiently caught during this study, should be further investigated to elaborate the relative ecological relevance of species identity and body size.

Catch composition in fyke nets can be biased by escapes through the opening and predation within the gear (Breen and Ruetz, 2006). However, the tidal flow, decreasing water levels during the fyke net catches and the funnel insert of the nets reduce the escape probability. Furthermore, no signs for predation within the net were found during stomach content analysis (Friese et al., 2018b; Friese, unpublished data). The observed abundance difference between the grazed and ungrazed marsh are more likely to be caused by the marsh geomorphology than by the grazing management. The funnel-shaped coastline at the grazed marsh guided the nekton into the marsh creeks, while the access pathways to the creeks in the ungrazed marsh were less direct. Additionally, compared to the grazed marsh, both creeks in the ungrazed marsh were wider resulting in a lower percentage of fished runoff water and a higher probability of net avoidance. *C. maenas* is known to be attracted by fykes, but its catch numbers can still be used for relative abundance changes as catchability is supposed to remain more or less equal.

Predation pressure is a major factor structuring animal occurrence as in the short-term survival is more important than feeding (Fernö et al., 1998). The presence of predators can result in immediate mortality and hinder organisms from feeding (Werner et al., 1983), like it was shown for *G. aculeatus* by Ibrahim and Huntingford (1989a). Thus habitat selection is often subject to a trade-off between predator avoidance and optimal foraging (Hugie and Dill, 1994). In German salt-marsh creeks, predation by aquatic predators is probably relatively low for fish and crustaceans as indicated by their species and size compositions. Shallow areas are inhabited usually by smaller fish than deeper areas in which larger piscivorous fish are present (Ruiz et al., 1993; Paterson and Whitfield, 2000; Gibson et al., 2002). Only small fractions of fish larvae and small *C. crangon* were found in the stomachs of *P. microps* and *G. aculeatus* in the analysed salt-marsh creeks (Friese et al., 2018a; Chapter 5). *Pomatoschistus spp.* are known to be important predators of juvenile *C. crangon*, but their daily rations are low compared to other predators (e. g. Tiews, 1978). Another potential predator for the salt-marsh nekton is *C. maenas* due to its omnipresence, abundance and size. Berghahn (1984) described *C. maenas* as a slow-moving predator that did not recognise *P. platessa* larvae at distances above 5 cm and if they did, they failed to catch it. Although fish was found in stomachs of *C. maenas*, it was probably carrion (Ropes, 1968) and thus predation by *C. maenas* is likely of minor importance. *C. crangon* is an important predator of *P. platessa* larvae (van der Veer and Bergman, 1987), but considering the size composition of *C. crangon* in the analysed marsh creeks (Burgund, 2017), for most of them the 1.5 - 2 cm large *P. platessa* larvae are probably too large. The foraging behaviour of potential avian predators especially within flooded German salt-marsh creeks is still unknown. We suppose that the marsh creeks are on the one hand too deep for wading birds specialized to forage on the uncovered tidal flats on macrobenthos (Manderson et al., 2004) and restricted to waters no deeper than their leg length (Whitfield and Blaber, 1979) and on the other hand too shallow for seabirds specialized on plunge diving. This assumption is underpinned by an enclosure experiment in a higher marsh pool in the USA, where fish mortality was not caused by bird predation (Kneib, 1982b). Compared to the subtidal and tidal flats the predation pressure by both aquatic and avian predators is therefore assumed relatively low for the nekton in the German salt-marsh creeks. Possibly to fully benefit from the reduced mortality in this habitat (Talbot and Able, 1984; Kneib, 1987; Cattrijsse et al., 1994), some fish and crustacean even stay in the marsh in shallow pools or rivulets at low tide. We found juvenile *Pomatoschistus sp.* and miniature schools of juvenile *G. aculeatus* in small marsh ponds (in St. Peter-Ording, 2015, pond size ca. 2-3 m² and ca. 20-30 cm depth) and, like Berghahn (1984), we observed *P. platessa* larvae staying during low tide in the rivulets with less than 5 cm depth.

Small-sized fishes, like we found in the salt-marsh creeks, occupy key roles in the centre of food webs (e. g. Fauchald et al., 2011; Pockberger et al., 2014; Bergström et al., 2015). Modelling results suggest that *P. microps* is a keystone species in sandy tidal flats and seagrass meadows increasing the energy transport towards higher trophic levels (Pockberger et al., 2014). A high ecological importance in the Wadden Sea was attributed to both goby species, *P. microps* and *P. minutus*, due to their high abundance (Herrmann et al., 1998; Vorberg and Breckling, 1999). They are important predators for the lower trophic levels, such as *C. crangon* (Tiews, 1978; Kuipers and Dapper, 1984), and important prey for fish (e. g. Ntiba and Harding, 1993; Pockberger et al., 2014), birds (e. g. Dänhardt et al., 2011b; Jouta et al., 2018), and seals (e. g. Hall et al., 1998). *G. aculeatus* is among the most abundant fish species in the Wadden Sea in winter and also serves as prey for seabirds and larger fish (Vorberg and Breckling, 1999). In the Baltic, the three-spined stickleback is an important mesopredator capable of setting off trophic cascades that change the entire ecosystem (Bergström et al., 2015). In the North Sea, however, this species is rarely caught, and much of its biology and its trophic role is largely unknown (Yang, 1982; Daan, 2015), probably due to its affinity to habitats inaccessible to standard monitoring gear (Tulp et al., 2017).

The nekton communities and ecosystem processes of European marshes not only differ from e. g. North American marshes (Cattrijsse and Hampel, 2006), but also among each other (Laffaille et al., 2000a; Mathieson et al., 2000; Hampel et al., 2003b). In their comparison of various European marshes Mathieson et al. (2000) highlighted *Platichthys flesus* and *Anguilla anguilla* as the most widely recorded species. In the analysed German marshes, however, they occurred in less than 6 % and 4 % of the hauls respectively. Juvenile sea bass, *Dicentrarchus labrax*, is dominant in further westerly European marshes (e. g. Laffaille et al., 2000a), in the German marsh creeks, however, not a single record of this species is known, although this species is not uncommon in the Wadden Sea coast (Tulp et al., 2017).

The differing nekton communities in the subtidal and the salt-marsh creeks indicate that certain species actively visit the salt-marsh creeks while others avoid them. Using stable isotopes, Green et al. (2012) even demonstrated that fish were able to visit particular marshes repeatedly and therefore showing high site fidelity. Decreasing abundances of *C. crangon* and *P. microps* within repetitive samplings at Dieksanderkoog Nord in 2011 (Fig. 2.4; Dänhardt et al., 2011a) indicate a relatively small and stationary population with a relatively high site fidelity (Fig. 2.2). Similarly, Cain and Dean (1976) discovered a depletion of individual species within repetitive samplings in intertidal salt-marsh creeks in the United States. They also interpreted these depletion patterns as indicators for relatively small locally-fixed populations with low exchange with adjacent areas and thus a high affinity to a specific habitat. However, both patterns of either a decrease in abundance or a steady replenishment during repetitive samplings (case 1 and case 2, Fig. 2.2) could also be caused by a coincidental habitat use reflecting the population source in the subtidal (case 2, Fig. 2.2). A decrease in abundance in the marsh creeks could for instance be caused by a decreasing population source in the subtidal, e. g. by migration. Another assumption that should be considered when interpreting the depletion/ replenishment patterns is the time scale, along which fished out individuals are replaced with conspecifics from a source outside the marsh creeks. Especially in species with low mobility, this dynamics could take longer than five days. Despite these limitations, depletion experiments can be useful for analysing habitat affinity, especially with a combination of approaches also considering frequency and abundance data.

Nekton migrates into shallow coastal areas, like salt-marsh creeks, in spring and summer and spent the cooler seasons in deeper areas (Rountree and Able, 1992; Green et al., 2009; Schulte et al., 2020). However, *G. aculeatus* appears at the Wadden Sea coast especially during the cold season from autumn to spring (our data; Vorberg and Breckling, 1999). Studies rarely sample winter periods, but in our study the marshes were populated even during winter by e. g. *C. harengus*, *G. aculeatus*, *P. microps* and *C. crangon*. In winter flooded marshes even offer improved foraging opportunities through longer accessibility and increased habitat size (Friese et al., 2018a; Chapter 5). From March to May large quantities of *P. platessa* larvae visited the marsh creeks reflecting its transition to the benthic lifestyle in the Wadden Sea in this season (e. g. Pihl and Rosenberg, 1982; Berghahn, 1984). These larvae were growing in size in consecutive months indicating that the salt marshes might be a favourable nursery area for *P. platessa*. The abundance of *S. rostellatus* showed a smaller peak in April and a larger in July and August. These two abundance peaks of *S. rostellatus* were also found in the Dutch Wadden Sea (Hovenkamp and van der Veer, 1993; Beyst et al., 1999; Hiddink and Jager, 2002). The abundance peak in July and August is caused by the arrival of a new year class and coincides with the peak abundance of the seagrass (*Zostera*) beds from June to September (Folmer et al., 2016), with which *S. rostellatus* is associated and which occurred in front of the analysed salt marsh. *S. rostellatus* is maladapted to extreme temperatures in summer in shallow areas like salt-marsh creeks, because its temperature optimum is rather narrow ranging from 14.0 to 14.2 °C (Power and Attrill, 2003). They are assumed to be poor swimmers (Hiddink and Jager, 2002), and thus may have drifted passively with the tides to the marsh creeks. *C. crangon* abundance increased from May till October, probably because the new summer cohort joins the shallow water populations (Evans and Tallmark, 1984; Burgund, 2017; Temming et al., 2017). This seasonal abundance pattern is typical for *C. crangon* in the Wadden Sea (e. g. Hufnagl et al., 2010). Diurnal abundance patterns were most pronounced for *C. crangon* and *P. minutus* reflecting their night-active lifestyle (Ehrenberg and Ejdung, 2008; Hufnagl et al., 2014).

The nekton density in the salt-marsh creeks was relatively low compared to abundances reported from other Wadden Sea areas (e. g. Breckling and Neudecker, 1994; Vorberg and Breckling, 1999). Abundance data in the literature are highly variable and fragmentary because a spatiotemporally resolved monitoring of the diverse Wadden Sea habitat mosaic is lacking. Therefore, abundance patterns of the marsh creeks can only exemplarily be compared to other Wadden Sea studies. While we found mean densities of *P. microps* in salt-marsh creeks of 100 individuals per 1000 m^2 (abbreviated as ind. 1000 m^{-2} in following), del Norte-Campos (1995) reported similarly densities of less than 0.1 to more than 130 ind. 1000 m^{-2} in shallow tidal areas. During low tide in shallow intertidal creeks or tidal pools *P. microps* can occur in densities of more than 10000 ind. 1000 m^{-2} (Doornbos and Twisk, 1987; Hinz, 1989; Vorberg and Breckling, 1999), in the marsh creeks during high tide, however only a maximum density of 2937 ind. 1000 m^{-2} was observed. *P. minutus* occurred in the marsh creeks with average densities of 1 ind. 1000 m^{-2}, similar values as observed by Breckling and Neudecker (1994) in deeper channels during night. But in small intertidal creeks they can occur with up to 800 ind. 1000 m^{-2} (Breckling, 1999). *C. harengus* occurred with densities of 152 ind. 1000 m^{-2} on average and 6019 ind. 1000 m^{-2} on maximum in the marsh creeks. Similar densities were reported by Hinz (1989) with almost 6000 ind. 1000 m^{-2} near Friedrichskoog, Germany. *G. aculeatus* occurred with 2 ind. 1000 m^{-2} on average up to 19 ind. 1000 m^{-2} on maximum of in the marsh creeks. Vorberg and Breckling (1999), however, reported densities of *G. aculeatus* of 30 ind. 1000 m^{-2} in the inner Meldorf Bight. The most abundant nektonic species in the marsh creeks was *C. crangon* with densities of 519 ind. 1000 m^{-2} on average to almost 14000 ind. 1000 m^{-2} on maximum. These densities are still low compared to other reports from the Wadden Sea (e. g. up to 30000 ind. 1000 m^{-2} in Saathoff, 2018, to more than 1.8 million ind. 1000 m^{-2} in Berghahn, 1984). The low nekton density does not mean that marsh creeks are a low-quality habitat (van Horne, 1983; Kristan, 2003). In contrast, those individuals that find their way to this specific habitat may benefit from reduced competition and the low predation pressure. Small habitats, like the salt-marsh creeks, with only a few inhabitants could also be more important for a population than larger habitats, if their inhabitants have a better survival chance, a better fitness and a higher chance of reproduction (Dahlgren et al., 2006). The habitat value depends on its overall contribution to the adult population and not on its size (Dahlgren et al., 2006).

The size of Wadden Sea salt marshes was not always as small as today. Paleogeographic reconstructions indicate that the spatial extent of these salt marshes was approximately as large as the tidal areas before embankments were built in the middle ages (e. g. Vos and Knol, 2015). Therefore this habitat type was probably more important for marine organisms prior to anthropogenic habitat destruction. But nekton habitat was not only quantitatively lost, also the geomorphological diversity of salt-marsh creeks was reduced during the last centuries in favour of optimal dyke drainage (Bakker et al., 2002). The habitat complexity can affect habitat utilization, e. g. the degree of branching of salt-marsh creeks at the US west and east coasts correlated positively with species richness (Rozas et al., 1988; Hettler, 1989;

Visintainer et al., 2006). Beside the historical habitat loss and modifications, and despite nature conservation efforts, the Wadden Sea salt marshes also face an uncertain future. If it comes to a sea level rise that salt marshes could not compensate by sediment accretion, then they are at risk to be squeezed between dikes and erosion cliffs caused by storm floods. Regularly increased marsh flooding might increase crab burrowing, thus decrease soil stability and facilitate marsh degradation, as caused by *C. maenas* in New England, USA (Crotty et al., 2017; Raposa et al., 2018; Raposa et al., 2019). This biological factor might not be of concern in Wadden Sea salt marshes today – although we already observed multiple burrows of *C. maenas* at Vareler Schleuse (Jadebusen) in 2014. But to avoid misleading predictions of the resilience of salt marshes to future storm floods it should be taken into account, that the Wadden Sea salt marshes are also a habitat for burrowing crabs.

Conclusion

The German Wadden Sea salt marshes are part of a tidally driven pulsing ecosystem (e. g. Rozas, 1995) and are only temporarily accessible for nekton. Obstructions, like sheet pile walls as at the marsh entrance at Spiekeroog port (unpublished data by Dänhardt and Hufnagl, 2016), or long access paths from the subtidal can reduce residence time and potential benefits (Dänhardt et al., 2011a). The different nekton densities we found between the grazed and ungrazed salt marshes is most likely caused by different accessibility. The connectivity with low tide refuges in adjacent areas affects the habitat quality of salt-marsh creeks for nekton. Seagrass meadows in front of the marsh, like in our study area, reduce low tide mortality of fish (Irlandi and Crawford, 1997) and *C. maenas* megalopa larvae (Moksnes et al., 1998) and thus increase the habitat quality of the connected marsh. Also, turbid tidally mixed waters in the subtidal in front of a marsh could provide shelter for animals coming out of the marsh creeks with the ebb tide (e. g. Abrahams and Kattenfeld, 1997). Some species, like *C. harengus* and *P. platessa* use the sheltered marsh creeks only during early life stages and migrate to deeper areas as they grow. Their migration pathways connect the different habitats and highlight the need for an integrated management of the whole seascape (Nagelkerken et al., 2015). Mesopredators, e. g. sticklebacks and gobies, transport organic matter not only vertically upwards in the food chain but also horizontally from coastal to offshore areas. They use the salt-marsh creeks not only as a refuge from predators but also as feeding habitat (Friese et al., 2018a; Chapter 5). But with ebb tide they have to leave this highly productive and protected area (Lefeuvre et al., 2000) and become available as prey in the subtidal. For a successful habitat conservation, a functional understanding of which species utilizes which habitats for which reasons during which time and by which migration routes is essential (Sheaves, 2009; Tulp et al., 2017). The seasonal and diurnal habitat utilization patterns and the characteristics of the salt-marsh nekton community provided in this study, help to answer some of those questions but also raise the demand for habitat-specific monitoring programs. Further research on the role of salt marshes as nurseries for juvenile *C. crangon* and fish larvae is needed. Knowledge on the functional connectivity of the salt marshes with other Wadden Sea habitats is necessary to successfully protect the ecosystem functioning of the marsh, its interconnected habitats and the access pathways in between. The spatiotemporal availability of the protected marsh habitat for small nekton could be increased by protection and promotion of wide networks of ramified meandering salt-marsh creeks including accessible, large, long and deep creeks with increased flooding periods. Two large salt-marsh creeks ca. 10 km north of our sampling site at Westerhever, were planned to be filled with sediment to facilitate water logging and thus increase biodiversity and reduce bird predation by foxes. However, this would destruct a rare nekton habitat. Future salt marsh management decisions should take into account that salt-marsh creeks do not only serve for dike drainage but are valuable habitats for small nekton.

3

Another piece of the puzzle: abiotic habitat properties of German salt-marsh creeks benefit small fishes and crustaceans

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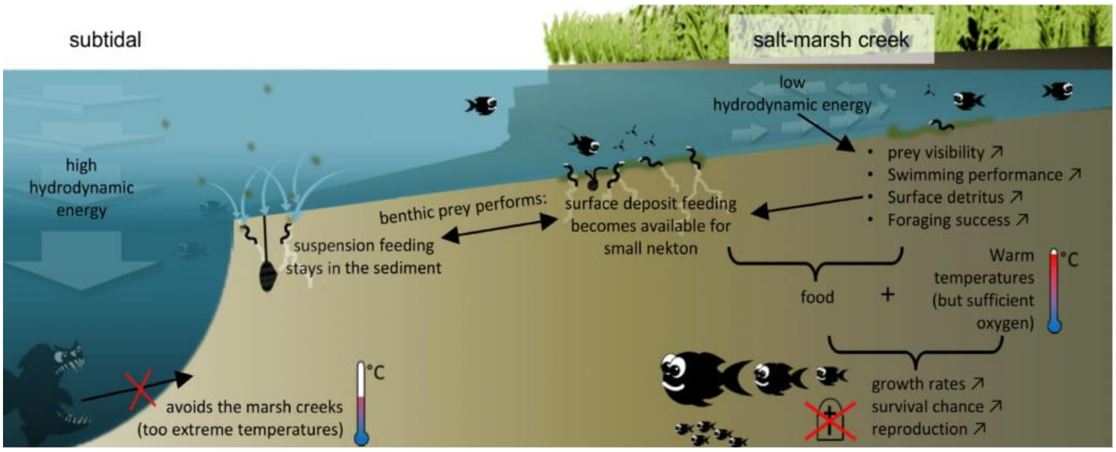


Abstract

Inundated salt marshes are valued as nekton habitat due to their low predator and high prey abundance. But habitat quality depends also on abiotic properties. We measured hydrological (temperature, oxygen concentration) and hydrodynamic (flow velocity, turbidity, sediment grain size) parameters in four German salt-marsh creeks and compared these with the adjacent tidal flat and subtidal area. Water temperatures in the salt-marsh creeks varied with season, daytime and over the tides. In contrast to deeper subtidal areas, the small water body in the marsh creeks adapted rapidly to air temperatures, resulting in relatively cool water temperatures in winter and relatively warm temperatures in summer. Despite high summer temperatures, the oxygen concentration in the creeks remained year round within the tolerance range of most fishes and crustaceans (above 5 mg / L), probably due to tidal mixing and primary production. Furthermore, the water body in the salt-marsh creeks was sheltered by the vegetated marsh surface from wind and waves and thus characterized by low flow velocities (0.15 ms^{-1}), as well as lower turbidity and finer sediments than in the subtidal. As the specific set of habitat characteristics in the marsh creeks could explain utilization of this habitat by nekton, we performed a constrained redundancy analysis including temperature and turbidity as explanatory variables. Turbidity explained almost 21 % of the variation in nekton species occurrence, while temperature accounted for only 2 % of the variation. Compared to larger animals, small-sized nekton, which dominated the salt-marsh nekton community, is more capable to deal with extreme temperatures and will profit more from reduced currents than larger animals. Despite the limited accessibility for aquatic organism, intertidal salt-marsh creeks appear to provide favourable habitat for small nekton due to increased growth potential during seasonally higher temperatures, reduced swimming effort, and increased prey visibility and availability in the muddy sediments.

Introduction

Salt marshes are often valued as nurseries for fish and crustaceans due to their low predation pressure and high food availability (Boesch and Turner, 1984; Craig and Crowder, 2002). Beside predator, prey, and competitor densities, the abiotic environment is similarly important for the energy budget of fishes and crustaceans affecting growth rates, physical fitness, and finally survival chance and reproductive success (Beck et al., 2001). Animals tend to select their habitats according to these benefits but depend on abiotic conditions within their physiological tolerance range (Craig and Crowder, 2002).

Salt-marsh creeks are confined and shallow water bodies located at the upper edge of the littoral zone. Thus, their geomorphology, hydrodynamics and hydrology differ considerably from open waters. While salt-marsh creeks are embedded in a large-scale coastal habitat mosaic connected by tidal currents and migratory nekton, the marsh creeks itself consist of a structurally complex mosaic of microhabitats (McIvor and Odum, 1988; Minello et al., 2003; Kaneko et al., 2019). Environmental conditions can vary within a few centimetres within the creeks caused e. g. by varying water depths, flow velocities (side ditches, small islands, meanders causing cut banks and slip-off slopes) and light availability (shadows caused by vegetation overgrowing the marsh edge). The abiotic habitat properties of salt-marsh creeks vary not only spatially but also temporally on a tidal, lunar, daily and seasonal cycle. Thus, salt-marsh creeks are a structurally complex and highly dynamic environment providing both stressors and benefits for its inhabitants.

Various factors influence the flow dynamics in the salt-marsh creeks. On the one hand the tidal flow slows down around high water at the upper edge of the littoral zone (e. g. Wang et al., 1999; Fagherazzi et al., 2008), and due to frictional resistance in the creeks (Healey et al., 1981). But on the other hand the confined space in the creek beds might accelerate ebb and flood currents locally. Also the weather conditions and lunar cycle affect the flow velocities in the marsh creeks (Bayliss-Smith et al., 1979). Submerged vegetation and the unflooded marsh areas can shelter the water body from wind and waves and again reduce the currents (Healey et al., 1981; Reed et al., 1985). The flow dynamics in turn affect fishes and crustaceans in multiple ways. Position maintenance and swimming becomes increasingly energy-demanding with increasing flow velocities (Schmidt-Nielsen, 1972; Liao, 2007). High flow velocities and water turbulence increase the amount of suspended particles and thus the turbidity (Postma, 1961). This can hamper visual and olfactory orientation of nekton, e. g. to find food or avoid predators (e. g. Weissburg and Zimmer-Faust, 1993; Abrahams and Kattenfeld, 1997; Smee et al., 2008). Flow velocities affect sediment deposition, which translates into a specific sediment composition structuring the distribution of benthic species and those associated with them (Weinstein et al., 1980). Areas with low turbidity accumulate soft sediments and organic matter and attract benthic primary producers in the top layers (Leach, 1970; Cloern, 1987; Billerbeck et al., 2007), making them highly productive (Cloern, 1987; Emerson, 1989) and valuable e. g. as nursery habitat for nekton (Pihl and Rosenberg, 1982).

However, areas of low flow velocities are often simultaneously characterized by shallow water depth. Small water bodies have a lower thermal capacity (Oczkowski et al., 2015) and thus shallow areas in the Wadden Sea can heat up more rapidly in summer than deeper areas (e. g. Berghahn, 1984). Dark muddy sediments reflect less radiation than coarser sand (Lyzenga, 1978; Dube, 2012) and thus warm up faster and – when located at the upper edge of the tidal zone - longer during ebb tide. During hot summer days the incoming tide is heated up by the solar radiation from above and additionally, but probably to a lesser extent by the warm sediments from below (Collar et al., 2020). With increasing water temperature, the metabolic rate of animals increases and thus their oxygen demands. But simultaneously, the solubility of oxygen in the water decreases with increasing temperature. In winter, due to the lower heat storage capacity of the small water bodies and the long exposure time of the sediments to the cold air temperatures, water temperatures of shallow salt-marsh creeks can decrease rapidly. Fishes and crustaceans are ectotherms using behavioural thermoregulation, which means they endeavour to select habitats suitable for their specific temperature requirements (Neill, 1979). But both, high and low temperature extremes as well as temporary oxygen shortage may cause physiological stress in certain species or life stages, possibly resulting in habitat avoidance (Froeschke and Stunz, 2012).

Likewise, nutrient runoff and good light availability in shallow salt-marsh creeks increase primary production, oxygen concentrations (de Wilde and Kuipers, 1977; Berghahn, 1984) and, eventually, prey abundance. Within the physiological limits of the organisms, high prey abundance, high temperatures and oxygen concentrations increase the metabolic rate, which, together with rich food supply, translates into fast growth (Houde, 1989; Munk, 1993; Attrill and Power, 2002; Pörtner, 2002; Attrill and Power, 2004) and, eventually, a higher probability to survive and reproduce (Pauly, 1980; Gislason et al., 2010).

But these characteristics of salt marshes and their function and value as habitat for fishes and crustaceans differ worldwide (Cattrijsse and Hampel, 2006). In the Wadden Sea, one of the largest tidal areas in the world (Common Wadden Sea Secretariat, 2012) with over 40.000 ha of salt marshes (Esselink et al., 2017), the role of salt-marsh creeks as a nekton habitat is surprisingly unknown (Cattrijsse and Hampel, 2006; but see Friese et al., 2018a or Chapter 5). To fill this gap, we (1) characterize four selected salt-marsh creeks typical for the German Wadden Sea as fish habitat by means of hydrographic (temperature, oxygen levels) and hydrological (water level, flow velocity, turbidity, sediment grain size) parameters, (2) contrast these properties to those found in the adjacent subtidal and, eventually, (3) relate them to observed occurrence and abundance patterns of nektonic species and life stages. To our knowledge, this is the first detailed compilation of tidal, diurnal and seasonal dynamics of abiotic features affecting habitat use, habitat value and habitat availability of nekton, thus providing a reference potentially useful or even valuable for future interpretation of observed abundance and utilization patterns of aquatic species and their different life stages in this temporary habitat.

Material and Methods

Study site

We measured several abiotic habitat parameters (namely temperature, salinity, oxygen concentration, water levels, flow velocity, turbidity, sediment grain size) at spring tide in four salt-marsh creeks and the adjacent tidal and subtidal areas near St. Peter-Ording, Schleswig-Holstein, Germany (Fig. 3.1). Due to technical limitations not all parameters could be measured during all samplings in all locations. Locations b, d, f, h and j (Fig. 3.1) were sampled and measured regularly on a monthly basis from March 2015 till February 2016 (excluding November and January). In July 2015 additionally the subtidal locations m and n (Fig. 3.1) were examined by ship. The locations a, c, e, g, l, j and k (Fig. 3.1) were only sampled in 2017 for sediment grain size analysis.

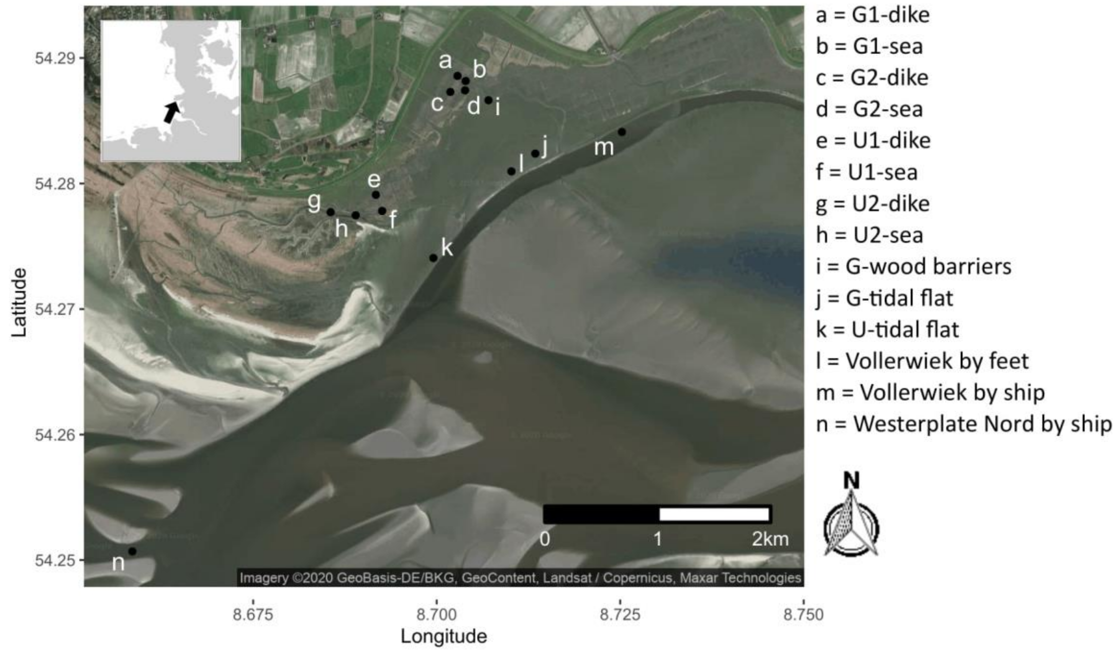


Fig. 3.1: Study area near St. Peter-Ording, Germany. Locations a, b, c and d in creeks within a grazed marsh; Locations e, f, g and h in creeks within an ungrazed marsh; Locations l, j, and k on the tidal flat, sampled only for sediment grain size analysis; Location l on the tidal flat, sampled monthly; Locations m and n sampled only in July 2015

Temperatures and water levels

The annual temperature profiles and water levels were logged every 5 min in each creek using Cera-Divers D1702 combined with a Baro-Diver D1500 (Schlumberger Water Services). They were installed as recommended by the manufacturer, hanging in a tube about 5-15 cm belowground in the middle of the creeks close to the fyke net positions. This way they were protected from flotsam and despite the varying water levels proper measurements could be achieved. The measurements were interrupted at the beginning of January to save the data logger from ice drift and installed again with the last field campaign in February 2016, which explains the gap in the data record in Fig. 3.2. Air pressure measurements using the Baro-Diver D1500 failed in July 2015. These data were necessary to calculate the water levels from the pressure measurements of the Cera-Divers D1702. The air pressure at mean sea level from the weather station at St. Peter-Ording of the Deutscher Wetterdienst (access date: 25.08.2016, station-ID: 4393) was used to fill the gap, after proving the consistency with the Baro-Diver measurements. Details on measurement methods and devices of the Deutscher Wetterdienst can be accessed online via the Climate Data Center (cdc.dwd.de/portal/). Water temperatures higher in the water column were manually measured with a WAM 235 Analysis instrument (Dostmann electronic GmbH).

Salinity and Oxygen concentration

Salinity and oxygen concentration was measured using a WAM 235 Analysis instrument (Dostmann electronic GmbH). As this device cannot measure both salinity and oxygen concentrations simultaneously, we decided to measure oxygen continuously and salinity sporadically. Dissolved oxygen (DO) in mg / L was corrected for salinity (S) using the formula provided by the manufacturer of WAM 235 (Eq. 3.1):

$$DO_{corr} = DO \times \left(1 - \frac{S}{100}\right) \qquad \text{Eq. 3.1}$$

Previous salinity measurements in German salt-marsh creeks in 2014 demonstrated that salinity was relatively stable (Twardy, 2015). As salinity could not be measured continuously in our study, we used the estimated mean salinity of 32 for this correction. We aimed to measure one tidal cycle per creek and sampling campaign, however due to technical problems with the logging function data are incomplete. As the available data from various months and locations still give us insight about the oxygen conditions in the habitat, we included all available data sets despite their deficiencies. For a general overview of the oxygen concentrations in German salt-marsh creeks, we provide oxygen concentrations averaged per tide from various literature sources (Dänhardt et al., 2011a; Winkler, 2012; Ruhbaum, 2013; Dänhardt, A. and Hufnagl, M., unpublished data; Friese et al., unpublished data) including 54 measured tides in 2011, 2013, 2014, 2015 and 2017 from several locations along the German Wadden Sea coast (Dangast, Vareler Schleuse, Wapelersiel, Cappel-Neufeld, Dieksanderkoog Nord, St. Peter-Ording, Hamburger Hallig). Oxygen measurements were averaged per tide as some data sets included continuously logged measurements while others only included single manual measurements.

Flow velocities

Flow velocity was exclusively measured in the salt-marsh creeks (locations b, d, f and h; Fig. 3.1) from March till June 2015 using a manually operated vane wheel flow sensor (höntzsch Instruments µP-ASDI).

Turbidity

During pre-investigations in 2014 secchi disks were visible to the ground of the shallow marsh creeks and therefore too inaccurate to measure turbidity. As turbidity and suspended matter correlate linearly in coastal waters, e.g. the Wadden Sea (Postma, 1961; Otto, 1966; Rügner et al., 2013), we measured total suspended solids (TSS) in g / mL as proxy for turbidity. Samples were taken in each of the four salt-marsh creeks approximately between high and low water and in the subtidal creek "Ehstensieler Fahrwasser" for reasons of accessibility approximately during low water. Due to limited sample processing capacity and the homogeneity of the measurements, we limited our sampling to two samples of 200 mL per location, however samples from March 2015 are missing and from April to June 2015 only one larger sample (250-500 mL) was measured (Tab. 3.1). In the laboratory water samples were filtered using a pre-weighted Whatman® GF/F filter (Cat No 1825-025, Ø 25 mm). The filters were dried beforehand at 85 °C for 25 hours on average, cooled down in a desiccator and weighted using Sartorius 1773MP8 Analytical Balance. After the filtration filters were processed the same way with a longer drying time of 33 hours on average. TSS was calculated as the difference of the filter weight before and after filtration and standardized for the filtrated water volume.

Tab. 3.1: Sample sizes of measurements of total suspended solids (TSS)

area \ month	Apr	May	Jun	Jul	Aug	Sep	Oct	Dec	Feb
G1	1 x 300 mL	1 x 250 mL		2 x 200 mL					
G2	1 x 500 mL								
U1	1 x 300 mL								
U2									
Vollerwiek by feet									
Vollerwiek by ship									
Westerplate Nord by ship									

Sediments

Sediment cores with a diameter of 6 cm and a depth of 20 cm were taken on 21^{st} of February 2017 to complete the 2015/2016 data set. It was assumed that sediment compositions did not change significantly in the meantime. In each of the four salt-marsh creeks 10 cores were taken close to the dike and close to the mouth of the creek respectively (Fig. 3.1, location a-h). Additionally, we took 10 cores on the tidal flat in front of the ungrazed, and in front of the grazed marsh and close to the grazed marsh at a wooden barrier each (Fig. 3.1, location i-l). All 110 samples were frozen at -20 °C until processing. Sediment particle size distributions were analysed by laser measurements using *FRITSCH ANALYSETTE 22 MicroTec plus* with a wet ultrasonic dispersion unit and the associated milling and sizing software *MaS Control version 1.0.0.013*. Measurements were conducted exploiting the full measuring range from 0.08-2000 µm. To prepare the samples for sizing each sediment core was diluted in warm water, well mixed and sieved over 2 mm mesh size. The fraction larger 2 mm was negligible and was therefore discarded. As organic matter content of the samples was assumed negligible, we omitted a treatment with H_2O_2. A subsample of ca. 100 mL was taken from each diluted and well mixed sediment core sample. While mixing this sample with a stirring bar, subsamples were pipetted into *FRITSCH ANALYSETTE 22 MicroTec plus* for measuring. The number of those pipetted subsamples and number of measurements for each subsample depended on the homogeneity of the single measurements and varied from 4 to 25. Single strongly deviating measurements were excluded from further analyses (13 out of 1119 measurements were discarded). The remaining subsample measurements were averaged per sediment core.

Data analysis

All data analysis were carried out in R version 3.6.2 (R Core Team, 2019).

The effect sizes of wind velocity and direction as well as the wave sheltered position of the salt-marsh creeks on the turbidity was quantified with an ANCOVA. Month was excluded from the model, because on the one hand only two measurements per month were available in the subtidal and on the other hand wind velocity changed over seasons (Fig. 3.6). In advance, the predictors (wind velocity, wind direction, and area, namely salt-marsh creeks and subtidal) were checked for multicollinearity via generalized variance-inflation factors (GVIF; Fox and Monette, 1992) using the R function *corvif()* by Zuur et al. (2009). GVIF values were adjusted for different degrees of freedom (*df*) to be comparable between explanatory variables (Eq. 3.2; Fox and Monette, 1992):

$$GVIF_{adj} = GVIF^{\frac{1}{2df}} \qquad \text{Eq. 3.2}$$

All above mentioned predictors were included into the initial model as no multicollinearity appeared. Within a step-wise selection based on the lowest Akaike Information Criterion (AIC), wind direction was removed from the model and an interaction term between wind velocity and area was included.

A redundancy analysis (RDA) was performed to evaluate the relationship between the nekton species community and the physical habitat properties. The species data were derived from Friese et al. (2020b; Chapter 2) and transformed to presence-absence data due to differing catch methods in the marsh creeks and the subtidal. Within the RDA, species data were scaled to unit variance. Rare species that occurred in less than 6 hauls were removed completely from the analysis. Additionally the brown shrimp *Crangon crangon* was removed from the analysis, as it occurred in each haul and thus the relationship between occurrence and the environment cannot be evaluated for this species. Only habitat-specific environmental parameters available for each haul, were included in the analysis. Initially, water temperature, TSS and the sediment grain size (as the percentage above and below 50 µm particle size) were considered. However, TSS and sediment grain size correlated strongly (Pearson correlation coefficient: 0.81, p-value < 0.0001). As the flow velocity affects the TSS and finally the sediment, TSS was chosen - together with temperature - for the RDA (as flow velocity was not measured in the subtidal). TSS and temperature were negatively tested for multicollinearity (VIF = 1). The environmental parameters can be described by a linear gradient as revealed by a detrended correspondence analysis (axis length ≤ 0.89 standard deviations). As the gradients are linear and not unimodal a redundancy analysis (RDA) was favoured over a canonical correspondence analysis (CCA). The model was calculated using the function *rda()* and the statistical significance of the canonical axes was tested according to Legendre et al. (2011) with a permutation test for rda (with 999 permutations) using the function *anova.cca()*, both functions from the *R* package *vegan* version 2.5-6 (Oksanen et al., 2019).

Results

Flooding

In the analysed salt marsh – like in most German marshes – the water stayed typically inside the salt-marsh creeks during flooding while the vegetated marsh surface remains dry, except some areas of the low marsh. During low tide the creeks emptied typically completely with variations due to the lunar cycle and wind. In winter low and high tide water levels were generally higher than during the rest of the year (Fig. 3.2a). During storm flood events even the vegetated marsh surface was flooded. Beside these extreme flooding events, frost periods during winter could cause the salt-marsh creeks not being flooded for several days (Fig. 3.2a). This happened at the turn of the year, when ice floes were piled up on the nearshore tidal flats by waves and tides creating a bank that hindered the water from entering the salt-marsh creeks (see red arrow in Fig. 3.2a).

Temperatures

The shallow salt-marsh creeks were characterized by a fluctuating seasonal temperature profile with highest temperatures in July and lowest in January (Fig. 3.2b). Water temperatures varied less than air temperatures but they followed in general a similar seasonal pattern (Fig. 3.2b). Most extreme temperatures were measured a few hours before low tide, when the creeks contained only small rivulets. The highest water temperatures we measured 2014 was 29.77 °C on July 24th, 4:45 pm (local time) and in 2015 27.9 °C on July 17th, 5:10 pm, both in a salt-marsh creek at St. Peter-Ording. The lowest water temperature we measured was 0.8 °C in another salt-marsh creek at St. Peter-Ording on October 11th, 2015 06:54 am (local time). In winter, from November to February, air and water temperatures tended to fluctuate

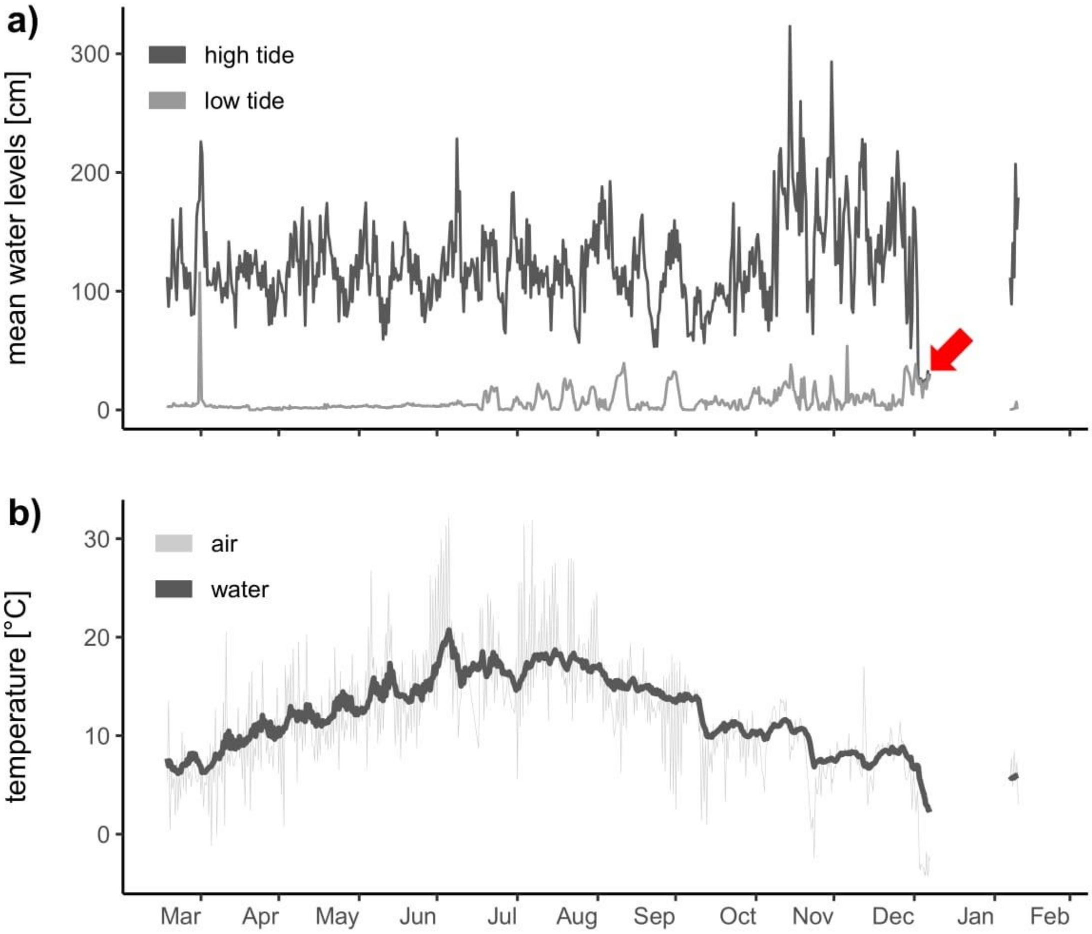


Fig. 3.2: Seasonal a) mean water levels at high low tide and b) mean air and water temperatures at St. Peter-Ording from March 2015 to February 2016 measured with Cera-Diver at the sea bed in the four salt-marsh creeks and a Baro-Diver as a reference for air temperature; the red arrow highlights a period, when the marsh creeks were not flooded at all.

less and water temperatures were more frequently higher than air temperatures (Fig. 3.2b).During summer, from July to August, this pattern was reversing (Fig. 3.2b). The tidal temperature profiles vary seasonally and during day and night (Fig. 3.3). During low water levels, water temperatures tend to resemble the air temperature (Fig. 3.3). When air temperatures increased over the day, water temperature increased as well – especially at low water levels (ca. < 50 cm, Fig. 3.3). When air temperatures were lower during night than during day (in July, September and October), the night-time water temperature profile diverges over the tide compared to the daytime profile (Fig. 3.3). While the water warmed up first, it started to cool down before high tide and continued to become even colder with ebb tide (Fig. 3.3).

Comparable temperature measurements from the subtidal and the salt-marsh creeks were only available in July 2015 at daytime at St. Peter-Ording. Temperatures in salt-marsh creeks were significantly higher (ca. 4 °C) than subtidal temperatures and they were more dispersed (Wilcoxon rank sum test with continuity correction: W = 7.5, p-value < 0.0001, Fig. 3.4a).

Oxygen concentrations

During the course of a tide at daytime in July and September 2015 oxygen concentrations remained constantly just above 5 mg / L, while they increased in the course of the tide in October (Fig. 3.3). At very low water levels (ca. < 25 cm) oxygen concentration varied strongly with increasing values (like in July and December) or decreasing values like e. g. October (Fig. 3.3). During night oxygen concentrations decreased in the course of the tide (Fig. 3.3). However, when water levels of less than ca. 25 cm were reached, they started to increase again (Fig. 3.3). Oxygen concentrations in the subtidal were significantly higher than in the salt-marsh creeks in July 2015 (Wilcoxon rank sum test with continuity correction: W = 4088.5, p-value < 0.0001, Fig. 3.4b). When comparing all available oxygen measurements in German Wadden Sea salt-marsh creeks derived from a multiannual data compilation, all oxygen measurements were above 5 mg / L (except two measurements in September 2011 at Wapelersiel, Fig. 3.5). The oxygen concentration was significantly, on average by 1.8 mg / L, higher during day than during night (Student's t-Test: t = 2.7929, df = 36.713, p-value = 0.004).

Turbidity

On average the measurements resulted in a flow velocity of 0.15 ms^{-1}. The low tide surf zone (“Vollerwiek by feet”) had the highest total suspended solids concentrations (abbreviated as TSS, used as a proxy for turbidity; Fig. 3.6a). Samples from the deeper areas in the subtidal (“Vollerwiek by ship” and “Westerplate Nord by ship”) had comparably clear water like the shallow marsh creeks (Fig. 3.6a). But those measurements from the deeper areas were only available in July 2015. In winter TSS

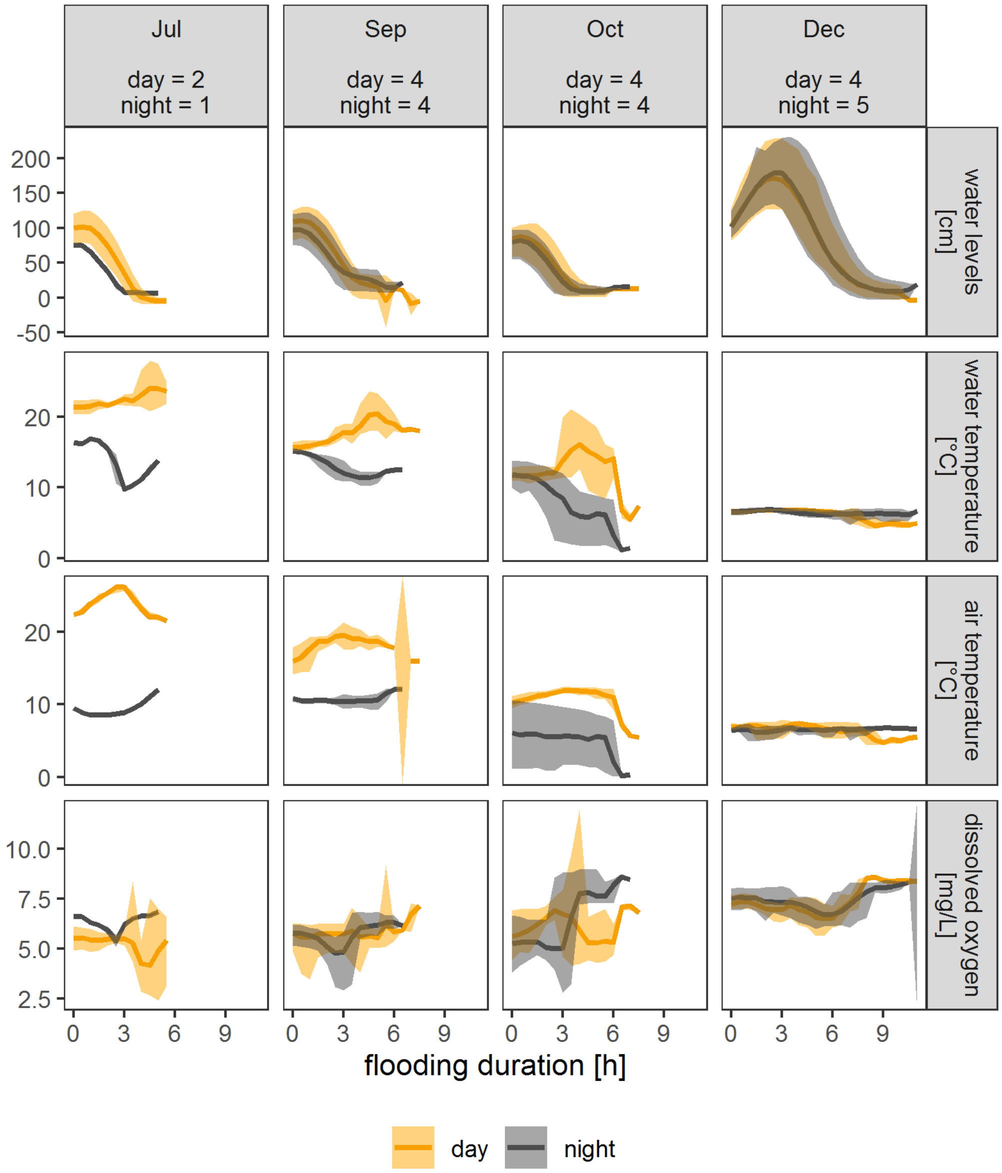


Fig. 3.3: Tidal temperature and oxygen profile during different seasons in 2015 (columns: July, September, October and December) and day and night. Each row contains a different variable (water levels, water and air temperature, dissolved oxygen). Units are given right-hand per row for each variable. Numbers of measured tides are given in the column headers. The bold lines represent means and the shaded areas show the range of minimum and maximum values.

concentrations increased compared to the rest of the year, except for June (Fig. 3.6b), which was characterized by high wind velocities (Fig. 3.6c). The seasonal TSS pattern in the subtidal (Fig. 3.6b, blue circles) traced the median seasonal wind velocity (Fig. 3.6c). This pattern was less pronounced in the salt-marsh creeks (Fig. 3.6b, boxplots). The ANCOVA confirmed the impression, that TSS was less affected by the wind in the marsh creeks than in the subtidal (Fig. 3.7). The formula of the final model reads as follows:

$$TSS = -30.3 + 9.7 \times V - 14.6 \times A + 10.9 \times V \times A \quad \text{Eq. 3.3}$$

where V is wind velocity and A is area (salt-marsh creeks or subtidal). No relevant residual patterns and no residual outliers were found. However, the model residuals slightly violated the normal distribution. The model was significant with a p-value of < 2.2e-16 and had an adjusted R^2 of 0.52 and a residual standard error of 28.93 on 141 degrees of freedom. In contrast to the area, both, wind velocity and the interaction between wind and area were significant with a p-value of 4.24e-11 and 0.0003, respectively.

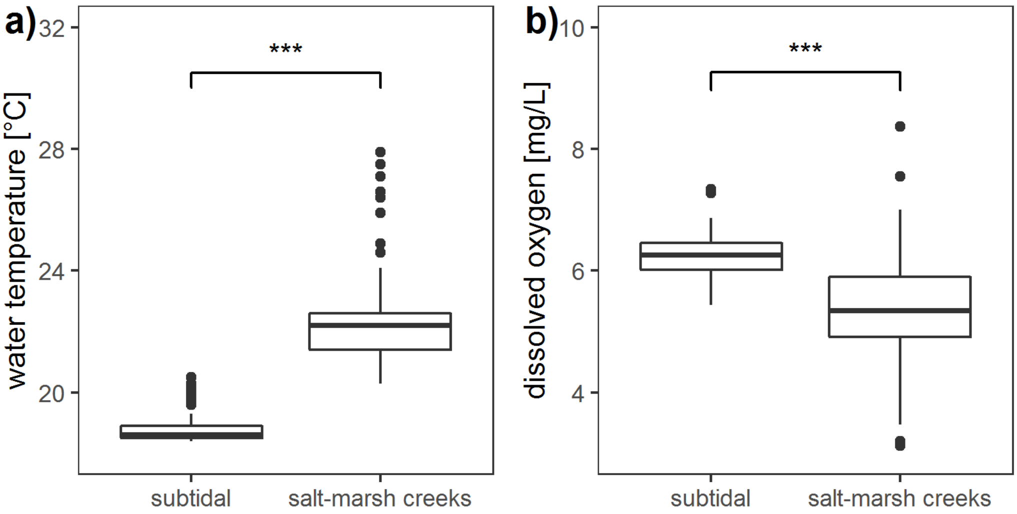


Fig. 3.4: Comparison of daytime a) water temperatures and b) oxygen concentration in the salt-marsh creeks (G2 and U2 pooled) at St. Peter-Ording (17.07.2015) and the adjacent subtidal areas (15.07.2015).

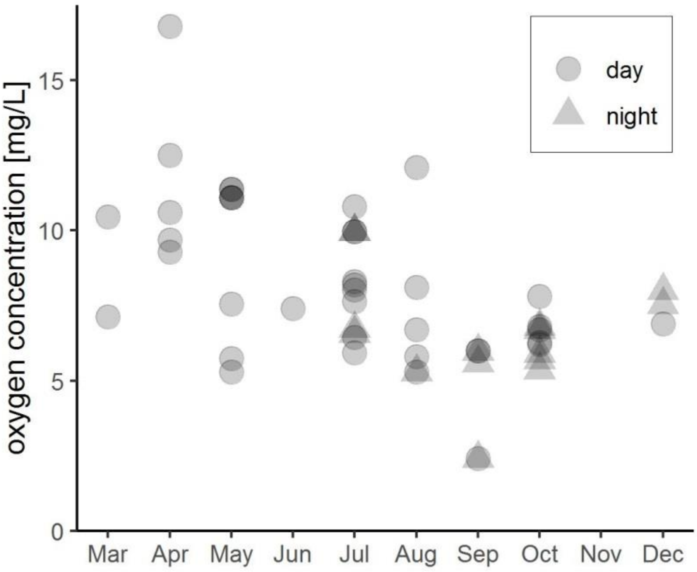


Fig. 3.5: Seasonal oxygen concentrations in German Wadden Sea salt-marsh creeks. The data include 54 measurements from 2011, 2013, 2014, 2015 and 2017.

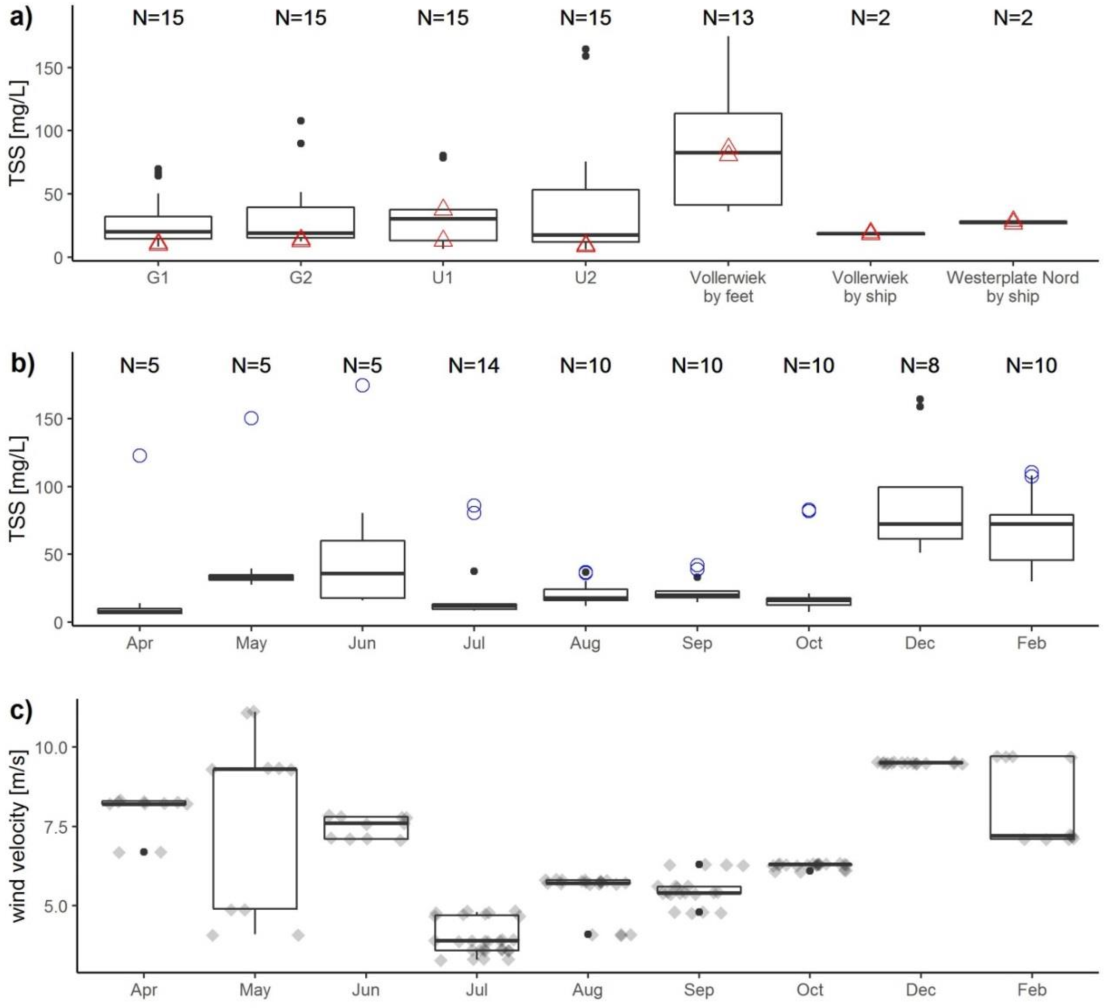


Fig. 3.6: Concentration of total suspended solids (TSS) as a proxy for turbidity a) per area, ship based samples (“Vollerwiek by ship” and “Westerplate Nord by ship”) were only available in July, therefore we highlighted all July samples with red triangles for comparability, and b) per month, marsh samples are shown as boxplot, the reference from the open tidal flat “Vollerwiek by feet” is shown as blue circles (2 samples per month, December is missing). Ship-based samples were excluded, as they are not available on a seasonal basis; c) seasonal wind velocity measured by Deutscher Wetterdienst DWD at the weather station St. Peter-Ording during TSS sampling. The grey lozenges represent the single measurements.

Sediments

Sediments in the salt-marsh creeks were composed of smaller grain sizes than sediments in the open tidal flats adjacent to the analysed marsh (Fig. 3.8). The salt-marsh creeks contained on average 97.76 (± 3.76) % particles smaller 50 µm while the sampling locations on the tidal flats contained on average 46.41 (± 16.41) % particles smaller 50 µm. The location inside the marsh creeks, close to the dike or close to the sea did not affect the sediment grain size composition. However, the sediments of the more wind and wave exposed creeks U1 and U2 tended to have larger grain sizes than the sediments of the creeks G1 and G2 which are located in a bay (Fig. 3.8).

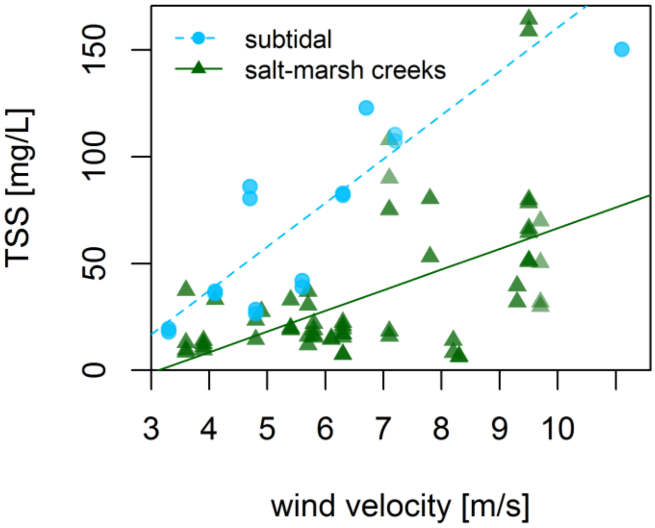


Fig. 3.7: Results of the ANCOVA showing how wind velocities affect the turbidity in the salt-marsh creeks and in the offshore reference sites.

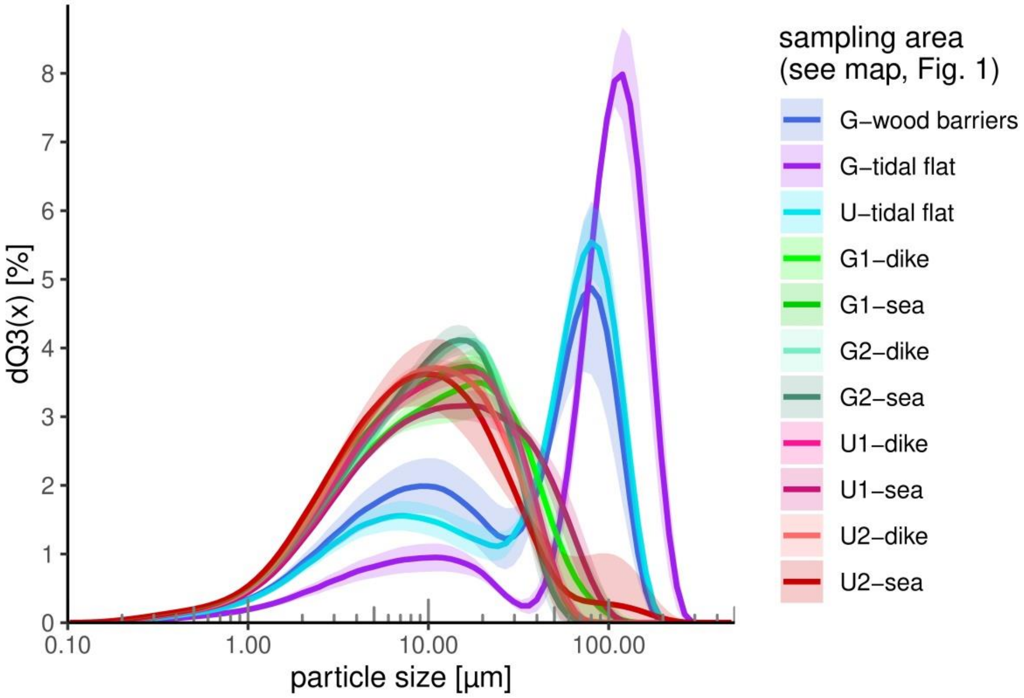


Fig. 3.8: Sediment grain size distribution (dQ3(x)) per sampling area. Lines show the average over 10 sediment cores each. Shaded regions show the standard deviation. The areas “G-wood barriers”, “G-tidal flat”, and “U-tidal flat” are located on the tidal flats adjacent to the salt marshes, all other areas presented in this graph are located in salt-marsh creeks.

Relationship between species occurrence and the abiotic environment

The RDA was statistically significant (p-value = 0.001) and the explanatory variables TSS and temperature could explain 23.0 % of the total variation in species occurrence. The first canonical axis (RDA1) was strongly positively correlated with TSS (0.9843), explained 20.66 % of the total variation and was statistically significant (p-value = 0.001). On the other hand the second canonical axis (RDA2) was negatively correlated with temperature (-0.9928), explained 2.4 % of the total variation and was not statistically significant (p-value = 0.083). Thus, turbidity was more important for species distribution than temperature. Salt marsh and subtidal sampling sites were associated with low and high turbidity, respectively (Fig. 3.9). Samples from summer months (July and August) tended to be associated with higher temperatures (Fig. 3.9). Samples from interim seasons, spring (April) and autumn (October) tended to be associated with higher temperatures when originating from salt-marsh sampling sites (circles) than those from subtidal sampling sites (triangles; Fig. 3.9). The shore crab (*Carcinus maenas*), the common goby (*Pomatoschistus microps*) and the three-spined stickleback (*Gasterosteus aculeatus*) were correlated with low water turbidity (TSS) and sampling sites in the salt marsh while being independent from water temperatures simultaneously (Fig. 3.9). Common prawn (*Palaemon sp.)* and Asian shore crab (*Hemigrapsus sanguineus*) were correlated as well but less intense with low water turbidity (TSS) and salt-marsh sampling sites, but showed stronger correlations to temperature (Fig. 3.9). Asian shore crab was associated with higher temperatures likewise as common dab (*Limanda limanda*), hooknose (*Agonus cataphractus),* and lesser sand eel (*Ammodytes tobianus*), which however, occurred in more turbid subtidal waters (Fig. 3.9). In contrast, common prawn was associated with cooler temperatures, similarly like herring (*Clupea harengus*), but not as strong as Nilsson´s pipefish (*Syngnathus rostellatus;* Fig. 3.9). The occurrence of Nilsson´s pipefish correlated most strongly with temperature and not at all with turbidity (Fig. 3.9). However, one should keep in mind, that for one thing temperature could explain less than 2.4 % of the total variation and for another thing the slim body shape of this fish species caused a low catchability (mesh size: 6 mm in the salt marsh and 11 mm in the subtidal; Friese et al., 2020b; Chapter 2). Smelt (*Osmerus eperlanus*) and fivebeard rockling (*Ciliata mustela*) correlated positively with turbidity and temperature in subtidal sampling sites (Fig. 3.9). In contrast to the morphologically similar herring, sprat (*Sprattus sprattus*) occurrence was strongly positively correlated with high water turbidity in the subtidal while being unaffected by temperature (Fig. 3.9). The sand goby (*Pomatoschistus minutus*) showed an opposite pattern compared to its close relative the common goby (Fig. 3.9). It had a similarly low correlation with temperature, but was associated with subtidal sampling sites of high water turbidity, while common goby seemed to prefer inshore habitats of low turbidity (Fig. 3.9) – indicating spatial niche segregation. The occurrence of the flat fishes plaice

(*Pleuronectes platessa*) and flounder (*Platichthys flesus*) was associated with turbid subtidal sampling sites and relatively independent from water temperatures, although plaice tended to slightly cooler temperatures than flounder (Fig. 3.9).

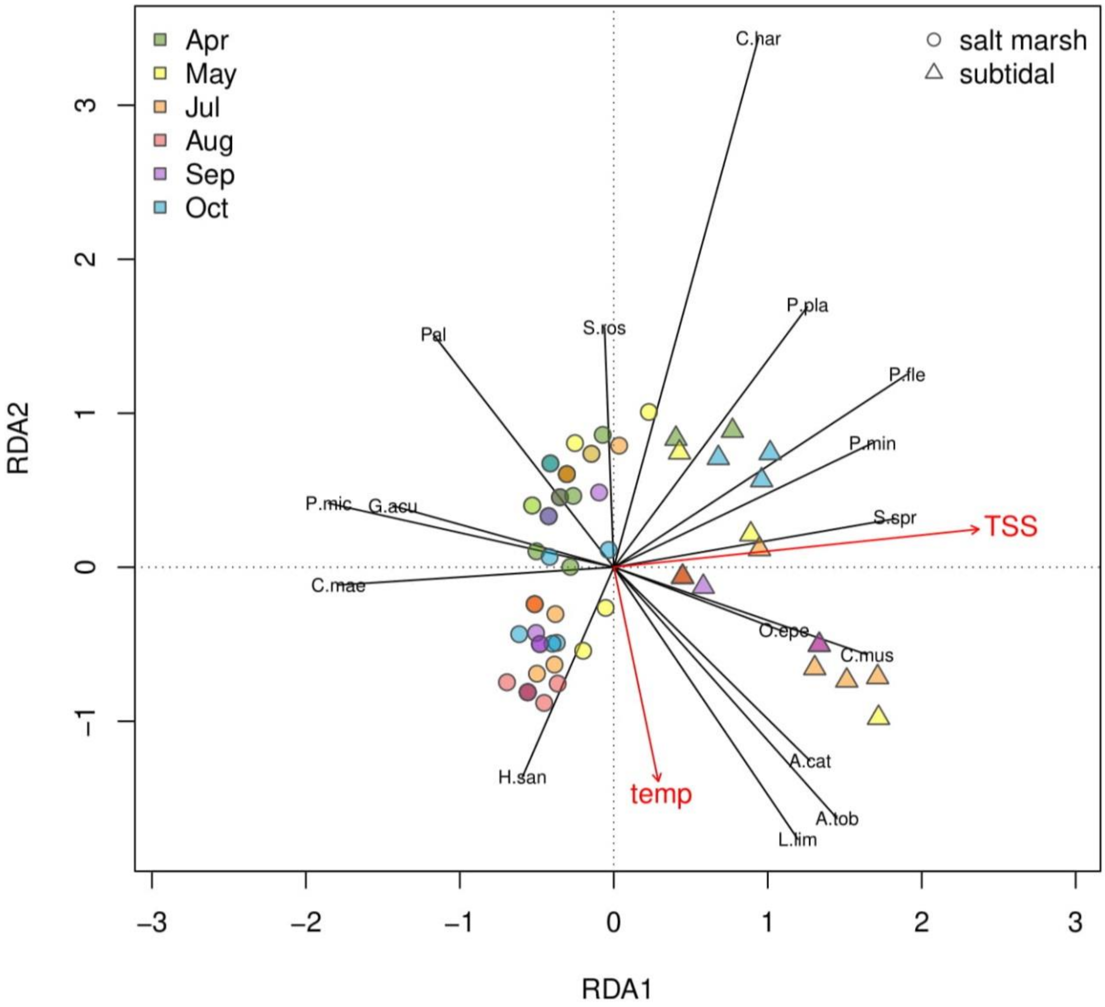


Fig. 3.9: Triplot of the redundancy analysis (RDA) using type I scaling and based on presence-absence data with two explanatory variables TSS (= total suspended solids, as a proxy for water turbidity) and temp (= temperature) and species as response variables. Species abbreviations: C.mae: *Carcinus maenas*, P.mic: *Pomatoschistus microps*, G.acu: *Gasterosteus aculeatus*, Pal: *Palaemon sp.*, S.ros: *Syngnathus rostellatus*, C.har: *Clupea harengus*, P.pla: *Pleuronectes platessa*, P.fle: *Platichthys flesus*, P.min: *Pomatoschistus minutus*, S.spr: *Sprattus sprattus*, O.epe: *Osmerus eperlanus*, C.mus: *Ciliata mustela*, A.cat: *Agonus cataphractus*, A.tob: *Ammodytes tobianus*, L.lim: *Limanda limanda*, H.san: *Hemigrapsus sanguineus.* Sampling sites are marked as circles when originated from the salt marsh and as triangles when originated from the subtidal; colours indicate the respective sampling months.

Discussion

Hydrology

Temperature

Water temperatures changed rapidly in the salt-marsh creeks depending on air temperature and solar radiation. We observed extreme temperatures in the marsh creeks with a frozen seabed in January 2016 and water temperatures approaching 30 °C in July 2014. Berghahn (1984) even reported water temperatures exceeding 32 °C in tidal pools on mudflats in the Wadden Sea in summer. Temperatures fluctuated during the tides depending on water levels and sun exposure (Berghahn, 1984; Deegan, 1990; Kneib, 1997b; Boswell et al., 2019) and vary therefore strongly between the time of the tide, the daytime and the season. Especially on hot summer days this can cause physiological stress for aquatic organisms as time for acclimation is short. Ectotherms, like fishes and crustaceans, depend strongly on temperature. Fishes and crustaceans visiting the marsh creeks regularly must have a relatively large thermal window to sustain the rapid temperature fluctuations. The extreme temperature variations might explain the predominance of *P. microps* versus *P. minutus* in the marsh creeks. *P. microps* has a wider temperature and salinity tolerance range than *P. minutus* (Dolbeth et al., 2007), and is therefore probably more capable of dealing with the conditions in the shallow marsh creeks. Indeed, *P. microps* can sustain temperatures of up to 34 °C (Freitas et al., 2007) and *C. crangon*, which is also among the most abundant species in the marsh creeks (Friese et al., 2020b; Chapter 2), resists temperatures below 0 °C (Reiser et al., 2014) and up to 30 °C (Freitas et al., 2007). On the other hand, flatfish like *P. platessa* and *P. flesus*, which seemed to rather avoid the marsh creeks (Friese et al., 2020b; Chapter 2), have an upper thermal limit of 26 °C (Freitas et al., 2007). As temperatures can increase suddenly in the marsh creeks, entering this habitat is especially risky for species that are less tolerant towards high temperatures or sudden temperature changes. For reason of energy efficiency most fish use tidal transport to enter and leave the marsh creeks (Szedlmayer and Able, 1993). But when temperatures exceed the thermal tolerance of a species, it would have to spend additional energy for swimming to leave the marsh creeks ahead of the ebb flow. In combination with the high temperatures, the energetic costs for such an escape could be fatal. Although, very high temperatures are extreme events occurring only during few tides in summer, these events are not always predictable as weather conditions can change rapidly. For species unable to deal with these extreme events, the marsh creeks can become an ecological trap. Juvenile fishes have in general a larger thermal window than larvae or adult fish (Pörtner and Farrell, 2008), and are thus probably better adapted to sudden temperature changes in the marsh creeks. Furthermore, the optimal temperature for feed conversion decreases with increasing fish size (Björnsson et al., 2001; Handeland et al., 2008). Thus, smaller fishes and crustaceans tend to prefer warmer temperatures while larger individuals prefer cooler temperatures (McCauley and Huggins, 1979; van Donk and de Wilde, 1981; Pedersen and Jobling, 1989). For instance, juvenile *C. crangon* (< 40 mm), which were the most abundant size class of in the marsh creeks (Burgund, 2017), have the highest growth rates at 20-26 °C, while growth rates of adults (40-60 mm) are highest in considerably cooler water of 14-20 °C (Hufnagl and Temming, 2011b). Hence, juveniles benefit from high summer temperatures in the marsh creeks, while adults are stressed in the same environment. As the body size is an important factor in thermoregulation, life stages of fish tend to disperse over different habitats. This spatial segregation of life stages can thereby avoid cannibalism. Especially in spring, when temperatures in the marsh creeks rise faster than in deeper areas, nekton in the marsh creeks can benefit via an increased metabolic rate, that could enable higher swimming speeds (Peck et al., 2006). Higher temperatures also improve fast-start performance of fish, as shown in laboratory experiments for mummichog (*Fundulus heteroclitus*), which is a characteristic fish species of salt marshes in the United States (Collar et al., 2020). However, in this experiment cooler acclimated fish performed better than warmer acclimated fish (Collar et al., 2020), indicating that high temperatures are only beneficial on the short-term. In the salt-marsh creeks high water temperatures occur only temporarily as the water body mixes at low tide with cooler water from the deeper regions. Thus, if the fishes in the German salt-marsh creeks behave similar like the mummichog, they could benefit from using two connected habitats: the subtidal, where they could acclimate to cooler temperatures and the salt-marsh creeks, where they could temporarily profit from higher swimming performance during days of high temperatures. The increased muscle power at higher temperatures (Johnston and Temple, 2002) can increase foraging success, and – together with the increased metabolic rate – lead to increased growth rates or accelerate gonad development, finally increasing the chance to survive and reproduce.

Oxygen

We hypothesized that oxygen concentration would drop during high temperatures, due to reduced solubility. Twardy (2015) reported reduced oxygen levels in salt-marsh creeks during high water temperatures (> 27 °C). However, like in the study of Twardy (2015) the measured oxygen concentrations in our study remained above 5 mg / L, which is required by most fish larvae (Saksena and Joseph, 1972; Silva and Tytler, 1973), adult fish (e. g. Otto and Zahn, 2008) and shrimps (Berghahn, 1984). Even in the multiannual compilation of oxygen measurements from fish-associated studies in German salt-marsh creeks, only two measurements by Winkler (2012) near Warpelersiel were below 5 mg / L. Obviously, diffusion, tidal mixing, and algal photosynthesis are sufficient to prevent the shallow marsh creeks from hypoxia. The strong variability in oxygen concentrations at low water levels might result from either a higher impact of surface diffusion or resuspended anoxic sediments due to increased turbulence in the small rivulets during low tide. But our data showed also, that during the night, when primary production stagnates, oxygen concentration can decline. Hypoxia can be important in the stagnant water in salt-marsh ponds, that are used by juvenile gobies (*Pomatoschistus sp.*) and juvenile three-spined sticklebacks (*Gasterosteus aculeatus*) (Friese et al., 2020b; Chapter 2). For example, in July 2014 a small salt-marsh pond at St. Peter-Ording was oversaturated with oxygen during daytime while oxygen concentrations dropped to critical levels for fish at night-time (R. Klinger, pers. comm.). In theory, nocturnal oxygen declines could be especially challenging for *C. crangon*, as its oxygen demand increases during night due to increased activity (van Donk and de Wilde, 1981). Still, *C. crangon* visited the analysed salt-marsh creeks predominantly during night-time (Friese et al., 2020b; Chapter 2) indicating that hypoxia was no limitation in habitat utilization. But juvenile fish and juvenile *C. crangon* are more tolerant towards low dissolved oxygen concentrations than adults and larvae (van Donk and de Wilde, 1981; Otto and Zahn, 2008; Elshout et al., 2013).

In conclusion, the extreme temperatures and potential sudden declines of oxygen in the shallow salt-marsh creeks are unfavourable for larger predators possibly leading to avoidance of this habitat type. Small-sized individuals are by contrast more tolerant, and thus better adapted to the salt-marsh environment.

Hydrodynamics

Flow velocity

We measured on average flow velocities in the marsh creeks of 0.15 ms^{-1}, which coincides with other studies reporting flow velocities in marsh creeks not exceeding 0.2 ms^{-1} on average and only rise to 0.5 ms^{-1} during spring tides or 0.8 ms^{-1} during storm tides (Bayliss-Smith et al., 1979; Reed et al., 1985). In the subtidal adjacent to the studied salt marsh, flow velocities of 0.5-0.7 ms^{-1} were reported (Schwemmer et al., 2009). Flow conditions affect the swimming performance and the energy budgets of nekton. Small fish reach lower swimming speeds with the same number of tail beats per second than large fish (Bainbridge, 1958) and need more energy to swim at the same speed (Schmidt-Nielsen, 1972). In fact the metabolic rate increases exponentially with the swimming speed (Tudorache et al., 2012). Information of maximum swimming speeds of fish is rare, but *P. minutus* for example obtains a maximum swimming speed of 0.27 ms^{-1} (Blaxter, J. H. S. and Dickson, 1959) or 0.5 ms^{-1} (Fonds, 1973). Similar maximum swimming speeds of 0.2 ms^{-1} and 0.3 ms^{-1} were measured for *Zoarces viviparous* and *Pholis gunnellus*, respectively (Blaxter, J. H. S. and Dickson, 1959), which are typical Wadden Sea species although rarely or not caught in the marsh creeks. Juvenile *P. platessa* achieve only 0.06 to 0.3 ms^{-1} (Blaxter, J. H. S. and Dickson, 1959). However, *C. harengus* - adapted to a pelagic life style – is even at postlarval and juvenile stages a good swimmer and achieves maximum swimming speeds of 0.5 to 3.0 ms^{-1} (Blaxter, J. H. S. and Dickson, 1959). The shrimp *C. crangon* achieves a maximum swimming speed of 0.4 to 1.1 ms^{-1} using tail flipping as an escape mechanism (Arnott et al., 1998); its standard swimming speed, however, can be assumed far below this value. Most of these small and rather slow-swimming fishes and crustaceans cannot swim against the subtidal flow velocities of 0.5-0.7 ms^{-1} (Schwemmer et al., 2009). Thus, in areas of high flow velocities escaping predators might be challenging for small nekton, because their escape radius is limited by the flow direction. While the fast currents in the deeper areas could increase mortality, the slow currents in the shallow marsh creeks could increase the chance for a positive energy budget. Nekton can drift passively with the tides into the salt-marsh creeks (Szedlmayer and Able, 1993) and forage there while the tidal flow decelerates and then reverses. Swimming effort during prey searching, position maintenance during prey detection, or fast-start performance during attacking prey, all of them cost less energy and are more likely successful at low flow velocities in the salt-marsh creeks – especially in sheltered areas within the creeks.

Turbidity

The low flow velocities in the marsh creeks are probably caused by the decelerating tidal stream close to the mean high tide water level and the vegetated marsh surface, that shelters the water body from the wind. Flow velocity affects sediment resuspension and settlement and consequently the turbidity of coastal waters. Due to the low flow velocities und thus increased sediment settlement (Butzeck et al., 2015) the water in the marsh creeks was relatively clear, while it was turbid at the adjacent low tide surf zone, probably due to tidal mixing. During winter (December and February) turbidity increased in the marsh creeks to similar values like in the subtidal mixing surf zone. This seasonal pattern with low turbidity in summer and high turbidity in winter is typically observed in the Wadden Sea (Philippart et al., 2013; Butzeck et al., 2015) and other European salt-marsh creeks (Green et al., 2009). Turbidity reduces the ability of both predator and prey to recognize each other by both olfactory and visual stimuli (e. g. Weissburg and Zimmer-Faust, 1993; Abrahams and Kattenfeld, 1997; Robertis et al., 2003). For example, *G. aculeatus* forages more efficiently in clear than in turbid waters, because prey can be detected from larger distances (Moore and Moore, 1976b). In the marsh creeks, the low turbidity and water depth allows the sunlight to penetrate down to the floor, improving – compared to the turbid subtidal – the foraging conditions of visually hunting epibenthivores (Friese et al., 2018a; Chapter 5).

Sediments

Because of the low flow velocities in the salt-marsh creeks, the sediments are finer there than in wave-exposed offshore areas. Moreover, salt marshes can only evolve at sheltered coasts, were sediments can accumulate and allow pioneer plants like *Salicornia spp.* to settle and to trap even more fine sediments (Steers, 1977). Laser particle-size measurements, like we used for our sediment grain size analyses, tend to underestimate clay fractions (Syvitski, 2007; Di Stefano et al., 2010). However, as the particle size composition peaked at ca. 10 µm in salt-marsh creeks and at ca. 100 µm at the tidal flats and as all samples were treated equally, this bias can be neglected. Fine sediments, like in the analysed salt-marsh creeks, are the preferred habitat of *P.*

microps (e.g. Magnhagen and Wiederholm, 1982b), which was more frequent and more abundant in the marsh creeks than *P. minutus* (Friese et al., 2020b; Chapter 2), that prefers deeper sandier subtidal areas (e.g. Magnhagen and Wiederholm, 1982b). The burrowing skills of some of the nekton species are higher in fine than in coarse sediments, e. g. small *C. crangon* (Pinn and Ansell, 1993). This burrowing improves its hiding from visual predators and thus increases its survival chance. *P. platessa* larvae, which occurred abundantly in the marsh creeks in April have increased growth rates in muddy compared to sandy shallow Wadden Sea areas (Berghahn, 1984). Muddy sediment offers also more benthic prey near the surface, where it can be accessed by small nekton. In areas with low flow velocities, where fine sediments can settle down, also more detritus can accumulate at the sediment surface and benthic algae have improved growth conditions, because they are less likely to be resuspended in the water column. This tempts the benthic infauna to switch from suspension feeding to surface deposit feeding (e. g. Taghon et al., 1980; Peterson and Skilleter, 1994). For example the mussel *Limecola balthica* can extent its siphon to vacuum up particles from the surface and this siphon can then be cropped by small nekton (e. g. Vlas, 1979; del Norte-Campos and Temming, 1994; Irlandi and Mehlich, 1996). Also the ragworm *Hediste diversicolor*, which was the most important prey for *P. microps* and *G. aculeatus* in the marsh creeks (Friese et al., 2018a; Chapter 5), has multiple feeding modes and switches from suspension feeding in sandy sediments, where high amounts of organic matter is suspended in the water column, to surface deposit feeding in muddy sediments, were more organic matter can be found on the surface than in the water (Esselink and Zwarts, 1989). However, the decision of *H. diversicolor* which feeding mode to apply, depends not only on the hydrodynamics and thus food availability, but is also affected by predation risk, which is higher in surface feeding (Schaum et al., 2013). In the marsh creeks, however, the nekton density is relatively low (Friese et al., 2020b; Chapter 2) and thus the potential energy gain by surface feeding probably outweighs the risk of falling prey. Consequently, the few fishes and crustaceans, that make their way to the marsh creeks, are likely to find abundant and accessible food there.

Thus, in conclusion the low flow velocities, clear waters and muddy sediments in the shallow salt-marsh creeks are favourable for small-sized individuals by increasing their chance for successful foraging and gaining a positive energy budget.

Relationship between species occurrence and the abiotic environment

Abiotic habitat properties determine habitat utilization of animals. A redundancy analysis revealed that the distribution pattern of fishes and crustaceans was more closely linked to flow conditions than to temperature. However, the low importance of temperature for species occurrence in the marsh creeks should be interpreted with caution. The temperature measurements in this study were not sufficient to describe the usual unimodal relationship of species occurrence and temperature, as data for extreme events were too rare. Thus, only a linear gradient was supported by the data. But especially temperatures at the upper and lower edges of the thermal tolerance windows limit species occurrence (Pörtner and Farrell, 2008), while temperatures within the thermal tolerance window affect the species in more subtle ways via their energy budget (Craig and Crowder, 2002). This is probably the reason, why we also found no correlation between nekton density and temperature. The temperatures in the marsh creeks varied seasonally, providing sometimes higher energetic benefits (e. g. increased growth potential at relatively warm temperatures and high prey availability) and sometimes higher energetic costs (e. g. higher metabolic rate at hot summer days with insufficient prey availability) than deeper areas with more constant temperatures. But in contrast to the variable temperatures, the low flow velocities, low turbidity and muddy sediments in the salt-marsh creeks were rather permanent habitat characteristics with relatively low variability. Although turbidity could explained ca. 20 % of the variance of species occurrence in the redundancy analysis, habitat selection is always determined by multiple factors and more than the importance of each factor, the interaction between different factors is relevant to understand species distribution patterns (Craig and Crowder, 2002).

Reconciling feeding and predator avoidance by means of switching between habitats

Due to the low predator abundance in the marsh creeks, small nekton can exploit there untroubled the rich prey resources (Friese et al., 2018a, 2020b; Chapter 2 and 5). Back in the subtidal at low tide, the well-fed nekton (Chapter 4) can stop foraging and fully concentrate on predator avoidance. Their attention and good nutritional condition could be key advantages to avoid chasing predators in the subtidal. Additionally, the high turbidity in the tidal mixing surf zone may help the small nekton to hide from predators during low tide (Abrahams and Kattenfeld, 1997). Thus, the small fish and crustaceans may benefit from low predation mortality during the whole tidal cycle while using two connected habitat types, the clear salt-marsh creeks and the adjacent turbid subtidal mixing surf zone. The importance of habitat connections was highlighted by Nagelkerken et al. (2015), who introduced the seascape nursery concept. Although our study indicates that salt-marsh creeks are not only nurseries but also valuable for small-sized and highly tolerant species, this habitat type is only temporarily accessible and its value depends decisively on the surrounding seascape. Thus, the Wadden Sea salt-marsh creeks are an example where the seascape nursery concept (Nagelkerken et al., 2015) should be applied and thus further research on migration patterns is necessary. Individuals that visit the temporarily available marsh creeks could increase their survival chance in comparison to conspecifics that used less favourable habitats during high tide. Consequently, despite the small spatial extent of salt-marsh creeks and their low nekton densities (Friese et al., 2020b; Chapter 2), the marsh-using nekton individuals could contribute substantially in sustaining population size (Dahlgren et al., 2006). In case the marsh-using mesopredators get eaten in the subtidal, they export the high productivity of the salt marshes to the surrounding habitats and higher trophic levels (Weisberg and Lotrich, 1982; Sheaves et al., 2015). Thus, salt marshes could also be valuable for those species and life stages that avoid the marsh creeks.

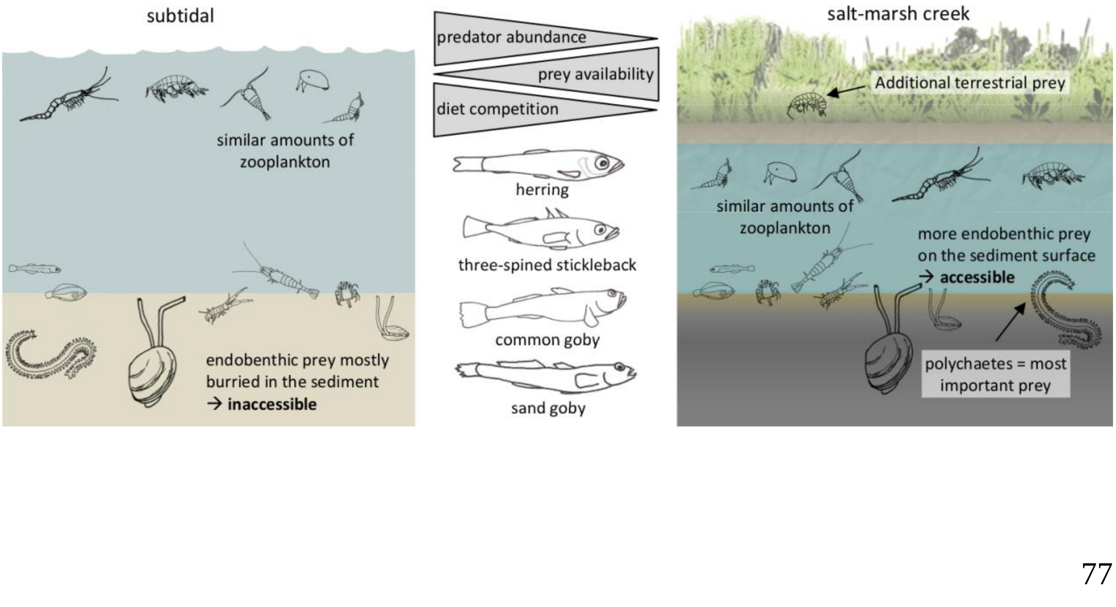
Conclusion

Our study highlights, that salt-marsh creeks can be demanding physical environments for fishes and crustaceans carrying the typical characteristics of the Wadden Sea to the extremes (e. g. rapid changes of hydrological parameters, flooding and desiccation, etc.; CWSS, 2017). Like other salt marshes they are utilized by the most tolerant species and life stages (e. g. Cucherousset et al., 2007). Especially the risk of high summer temperatures seems to be unfavourable for larger nekton and might explain the narrow nekton size range observed in the German marsh creeks (Friese et al., 2020b; Chapter 2). Small organisms and juveniles are more capable to deal with sudden temperature changes and at the same time profit more from the low flow velocities and seasonally higher temperatures in the marsh creeks, than larger nekton would do. In conclusion, the smaller nekton experiences less risks and more benefits in the marsh creeks, while larger nekton experiences there higher risks and less benefits. By analysing the abiotic environment of the marsh creeks, our study provided another piece of the puzzle to evaluate habitat quality of Wadden Sea salt-marsh creeks for nekton. As the low flow velocities are beneficial for small nekton, future salt-marsh restoration projects should take care to create aquatic microhabitats of low flow velocities, e. g. by building more naturally meandering creeks rather than artificial straight creeks. In case of the predicted increasing temperatures in the Wadden Sea (Hofstede and Stock, 2018), fishes and crustaceans that are well adapted to extreme environments, like those visiting the salt-marsh creeks regularly, might be on one hand among the winners of the changing environment. On the other hand temperatures in shallow waters may rise at rates three times higher than in deeper water (Oczkowski et al., 2015), thus shallow areas, like marsh creeks, might become uninhabitable even for the most tolerant species. Then the marsh specific nekton community would possibly be especially threatened, when forced to share deeper and cooler areas with predators and competitors. The salt-marsh creeks differ strongly from other Wadden Sea habitats, not only in their specific nekton community (Friese et al., 2020b; Chapter 2), but also in their physical habitat characteristics. The specific combination of abiotic conditions, we measured in the marsh creeks, occurs rarely in the Wadden Sea seascape. Protecting rare habitats, like salt-marsh creeks, and their connectivity within the seascape, conserves habitat diversity, consequently species biodiversity and ultimately increases ecosystem resilience.

4

Worms unlimited: high benthos density relaxes diet competition between fish in intertidal salt-marsh creeks

Julia Friese, Andreas Dänhardt and Axel Temming



Abstract

The submerged vegetation of salt marshes is worldwide valued as feeding habitat for fish. In Wadden Sea salt marshes, however, the vegetated marsh surface is rarely submerged and only the creeks are regularly flooded. Knowledge of the habitat-species relationship is crucial for an effective conservation of species. We present the first evaluation of the feeding habitat quality of these salt-marsh creeks for four characteristic species: herrings, three-spined sticklebacks, common and sand gobies. Habitat-specific dietary condition, stomach contents and potential food competition – based on diet overlap and predator and prey abundances – were compared between the salt marsh, sampling four intertidal salt-marsh creeks, and the adjacent subtidal. Long-term dietary condition was similar between the two habitats, while instantaneous feeding rates tended to be higher in the marsh creeks for herring, stickleback and common goby. The diets of sticklebacks and gobies were dominated by polychaetes in the marsh creeks and by zooplankton and various benthic crustaceans in the subtidal. Herring consumed mainly copepods in both habitats. Endobenthic prey was significantly more abundant in the muddy marsh creeks, whereas abundance of planktonic prey did not differ between the habitats. Despite a higher diet overlap, low predator and high prey abundances relaxed the competition for endobenthic prey in the marsh creeks. We conclude that habitats characterized by low flow velocities and, thus, muddy sediments, such as marsh creeks, provide small fish with favourable foraging conditions through high density of endobenthic prey. The extent and availability of profitable feeding habitats is a powerful driver of fish population dynamics. Historically, coastal protection resulted in an extensive loss of marsh areas and, with it, feeding habitat for fish. Today, it may be worthwhile for the conservation of fish in the Wadden Sea to protect and promote the development of large, long, deep and easily accessible salt-marsh creeks.

Introduction

Salt marshes are highly productive biotopes (Chapman, 1977). Located at the upper edge of the intertidal zone at shallow temperate coasts, their primary producer- and detritus-based food chains are fuelled by allochthonous nutrients from both the terrestrial and the marine system. Consequently, fish enter salt marshes for feeding as reported by various studies worldwide (Craig and Crowder, 2002; Hollingsworth and Connolly, 2006; Platell and Freewater, 2009; Fonseca et al., 2011). Especially the flooded marsh surface is regarded a profitable feeding ground for small and juvenile fish (Castellanos and Rozas, 2001; MacKenzie and Dionne, 2008). The submerged vegetation provides shelter from predators and at the same time marine and additionally terrestrial prey resources, such as e. g. insects and semi-terrestrial amphipods (Kneib, 1982a; Laffaille et al., 2000b). Thus, utilization of flooded salt marshes can result in enhanced growth rates of fish (Weisberg and Lotrich, 1982; Halpin, 2000). A predator refuge with simultaneously good foraging conditions is a rare combination for small fishes in marine ecosystems. Usually, small fishes face a trade-off between hiding and starving or feeding and risking predator contact (Sih, 1997). Hence, the quality of salt marshes as feeding and nursery habitat is considered high (Boesch and Turner, 1984; Beck et al., 2001; Whitfield, 2017). The majority of studies evaluating habitat quality of salt marshes for fish were conducted in marshes dominated by cordgrass (*Spartina sp.*), which are inundated every tide, have a low stem density, and are traversed by salt-marsh creeks that contain water even during low tide (Cattrijsse and Hampel, 2006). Accessibility of such marsh types for fish is much increased compared to marshes where water comes in and goes out solely via creeks and gullies.

The latter structural type dominates Wadden Sea marshes, whose vegetated surface is only flooded during winter storm floods and the salt-marsh creeks run completely empty during low tide (Cattrijsse and Hampel, 2006). As a consequence, fish visiting the Wadden Sea marshes have not only a larger travel distance from the subtidal low tide habitats to the salt marsh, but are also restricted to the bare and unvegetated salt-marsh creeks during most of the tides (Cattrijsse and Hampel, 2006). Additionally, these creeks are often straight, as they were meant to improve dike drainage, and short, as land reclamation of the last centuries squeezed the salt marshes between the sea and the dikes (Lotze et al., 2005). Until recently the value of Wadden Sea salt-marsh creeks for fish was largely unknown (Friese et al., 2018a, 2020b, 2020a; Chapter 2, 3, and 5). The salt-marsh creeks are used by various small fish (Friese et al., 2020b; Chapter 2) and their low depth and low turbidity provide good visual conditions for foraging (Friese et al., 2020a; Chapter 3). The low flow velocities and seasonally warmer temperatures than in deeper areas increases also their swimming skills (Friese et al., 2020a; Chapter 3) and thus their chance for a successful prey attack. Although, Friese et al. (2018a) showed, that the sheep-grazing management of the marsh negatively affected the diets of three-spined sticklebacks (*Gasterosteus aculeatus*) and common gobies (*Pomatoschitus microps*), which exploited terrestrial prey resources from the marsh surface during winter storm floods (see also Chapter 5), fish were not yet taken into account in the salt-marsh management.

Understanding species-habitat-interactions are important to include fishes into a holistic salt-marsh management in the future. Coastal habitats combining low predation pressure with high food availability can attract high densities of small and juvenile fish increasing diet competition and consequently decreasing foraging profitability of the habitat (Kneib, 1981; Craig and Crowder, 2002; Tableau et al., 2019). Although nekton density in German Wadden Sea salt marshes was found to be relatively low (Friese et al., 2020b; Chapter 2), diet competition depends not only on competitor density, but also on their diet overlap and on the prey density.

Investigations on resource use, availability and competition pressure of Wadden Sea salt marshes were missing, but are crucial to evaluate the feeding habitat value of these habitats for fish. The extent and availability of profitable feeding habitats affect fish population dynamics, either directly via enhanced growth rates and reproduction success of those fish using a profitable feeding habitat, or indirectly via food web links, when fish migrating from a profitable habitat are preyed by predators.

Our study aims to evaluate the seasonal quality of German Wadden Sea salt-marsh creeks as a feeding habitat for fish to fill this knowledge gap. We focused our analyses on four abundant fish species, the three-spined stickleback (*G. aculeatus*), the common goby (*P. microps*), the sand goby (*Pomatoschistus minutus*) and the juvenile herring (*Clupea harengus*). Measures of dietary condition (a. k. a. nutritional condition or body condition) can reflect the habitat quality as fish selecting profitable habitats will be more likely in a higher nutritional condition than fish that selected poor habitats (Amara et al., 2007; Johnson, 2007). The dietary condition of the four fish species was analysed inside and outside the salt-marsh creeks using the relative stomach content weight as short-term index. As long-term indicators for dietary condition the relative condition factor and the hepatosomatic index were determined. Furthermore, we investigated whether diet composition matched prey composition and density in the field. By combining stomach information and predator and prey densities, we assessed the degree of diet competition between the focal fish species in the marsh creeks. Finally, using a hypothetical scenario, we calculated whether the fish in the marsh creeks were in general able to decrease the prey resources of that habitat significantly. Based on our results, we evaluate the profitability of the Wadden Sea salt marshes, summarize the habitat characteristics that affect the profitability and translate our findings into applicable management recommendations.

Material and Methods

Collection and post-processing of samples

Four intertidal salt-marsh creeks of the *Eiderstedt* peninsula (54°17’N, 008°42’E) and the adjacent tidal and subtidal area were sampled during spring tide from March 2015 to February 2016 (excluding the months November and January). In the salt-marsh creeks fishes were passively caught with ebb tide using fyke nets. Fish samples from the subtidal were obtained from a commercial shrimper fishing with a five-meter beam trawl in a subtidal creek named *Vollerwieker Priel* (54°16’N, 008°42’E) adjacent to the marsh sampling area. Detailed descriptions on net specifications, geographical positions and effort standardization are given in Friese et al. (2018a, 2020b; Chapter 2 and 3). Fyke net catches from the salt marsh were sorted by species, separately weighted, counted and fishes were measured and frozen at -20 °C as fast as possible. Beam trawl catches from the subtidal were sorted by species and subsamples were immediately frozen at -20 °C. In July 2015, beam trawl catches were additionally weighted and counted prior freezing.

During each sampling campaign, the abundances of marine prey was quantified in the four salt-marsh creeks and in the adjacent tidal flats at the *Vollerwieker Priel* (54°16.863'N, 008°42.610'E). In July 2015, additional samples were taken further offshore at *Westerplate Nord* (54°15.046'N, 008°39.511'E). Macroendozoobenthos (MEZB) was sampled with five replicated benthos cores (20 cm deep, Ø 9 cm) in each location using sampling tubes and a plunger to retrieve the samples from the tubes. In March 2015, however, samples from the tidal flat are missing and at *Westerplate Nord* ten samples were collected. On the tidal flat, the cores were taken randomly within a radius of ca. 5 m. In the marsh creeks they were positioned randomly along a line elevated in cross-section approximately halfway between the creek bank and the creek centre. To consider small-scale flow velocity variabilities within the marsh creeks and, thus, potentially varying MEZB communities and densities, we sampled in each of the four marsh creeks additionally five replicates in March and June and three replicates each in July each close to the creek bank and in the creek centre, where maximum flow velocities occur. Due to the high silt content, the samples were first diluted in water and subsequently sieved on a 500 µm mesh on site. As the MEZB was dominated by only seven species and the focus was to quantify prey availability, species per sample were macroscopically identified and counted on site. Zooplankton was sampled by horizontally scooping a 2 or 3 L Niskin bottle against the current at 30 cm water depth. At least 30 L of scooped water was concentrated with an Apstein net (mesh < 63 µm) and preserved in 4 % borax buffered formaldehyde sea water solution (see Supplement B, Tab. B.1). In the laboratory, the zooplankton samples were sieved on a 355 µm mesh and transfused into a sorting fluid consisting of 0.5 % 1-Phenoxy-2-propanol, 5 % propane-1,2-diol and 94.5 % distilled water (Steedman, 1976). The zooplankton of each whole sample was counted and taxonomically classified using Bogorov counting chambers and a binocular. The densities of epibenthic harpacticoid copepods in the same salt-marsh creeks were analysed in July 2015 using small benthos cores of 2.7 cm diameter and 5 cm depth. The samples were fixed in 4 % borax buffered formaldehyde sea water solution and the harpacticoid copepods were extracted following a protocol of Somerfield and Warwick (2013). After sieving through a 63 µm mesh sieve, the copepods were separated from the sediment by centrifugation using a colloidal silica polymer (Levasil 200/40 – Obermeier) as a floating medium and kaolin as a separating layer. Afterwards the extracted harpacticoid copepods were counted. For details see Sommer (2016) and Bönisch (2017).

Dietary condition and stomach contents of fish

The dietary condition and stomach contents of preferably ten randomly chosen fishes of similar sizes were analysed per species and haul. The fish were thawed on ice. Prior to dissection regurgitation was recorded by checking the mouth for food residue. Standard length and wet body weight were measured to the nearest mm below and to the nearest mg, respectively. Immediately after extracting stomach, liver, and testes or ovaries with precision tweezers, microscopy scissors and scalpels, the three organs and the gutted fish were separately weighed to the nearest mg. For three-spined stickleback, the stomach was defined as the anterior intestine from the oesogaster to the sphincter. For herring and gobies, which lack a sphincter (Andersen, 1984), the stomach was defined to end at the first loop of the gastro-intestinal tract. The stomach was opened and the content was carefully removed with a scalpel on a Petri dish. The empty stomach was weighed to the nearest mg, while the stomach content was wetted with water to prevent desiccation. The stomach content was analysed using a binocular. Food items were identified to the lowest possible taxonomic level, when possible heads were counted, if heads were missing, a unique and definable fragment of a single prey organisms was counted as one, while a further progressed digestion obstructed prey counts, and finally the volumetric percentage composition of the different prey items and the mucus was visually estimated.

Data analyses

Long-term dietary condition

Relative condition factor K_n

As a proxy for the long-term energy reserves of the fishes we used the relative condition factor K_n. K_n is defined as the observed body weight W_i relative to a predicted size-specific standard body weight W_{pred} (see below):

$$K_n = \frac{W_i}{W_{pred}} \qquad \text{Eq. 4.1}$$

The fish`s condition is equal to a standard fish, when $K_n = 1$. The fish`s condition is better than a standard fish, when $K_n > 1$, and lower, when $K_n < 1$. The body weight of a fish is not only affected by its fat and protein content and its size, but also by its water content, the content of the whole intestinal tract and its maturity stage. W_i was calculated as the wet body weight W_{total} minus the wet stomach content weight $W_{stomach}$, the wet gut content weight W_{gut}, the wet gonad weight W_{gonads} and also minus the wet liver weight W_{liver}, as this organ was analysed separately using the hepatosomatic index (Eq. 4.2). All weights were measured in wet weight, because additionally muscle tissue was extracted from the gutted fish for another study (Friese et al., unpublished). Therefore, the gutted fish was incomplete and inappropriate for dry weight measurements.

$$W_i = W_{total} - W_{stomach} - W_{gut} - W_{gonads} - W_{liver} \qquad \text{Eq. 4.2}$$

The analysed herrings were juveniles and thus the sex determination, the wet gonad and liver weight was frequently missing, and hence set to zero.

The size-specific standard wet weight W_{pred} was calculated for each species and sex from the empirical weight-length relationship:

$$W_{pred} = k \times SL^b \qquad \text{Eq. 4.3}$$

where SL = standard length and k and b are parameters determined by fitting a linear model to the log-transformed empirical length (SL) and weight (W_i) data. The linear model was fitted with robust regression by iterated re-weighted least squares using M-estimation (R-function *rlm()*; Ripley et al., 2020). For juvenile herring, W_{pred} was calculated independent of sex. When sex determination of individual three-spined sticklebacks, common and sand gobies was not possible, W_{pred} was calculated using average values of k and b of both sexes. The length-weight-relationship and estimated values of k and b are given in Supplement B (Tab. B.2).

Hepatosomatic index HSI

As fish store major amounts of their energy reserves in their liver, the hepatosomatic index (*HSI*) was calculated as another proxy for the individual fish´s long-term dietary condition:

$$HSI = \frac{W_{liver}}{W_{pred}} \qquad \text{Eq. 4.4}$$

Short-term dietary condition

Relative stomach content weight S

The stomach content weight $W_{stomach}$ was calculated from wet weights as the difference between the full stomach weight and the empty stomach weight. All non-prey items such as parasites, sand, feathers, plants, and plastic were excluded from the stomach content weight ($W_{stomach}$). We assumed that the maximum possible stomach content weight increases linearly with fish size, as we were unable to measure it experimentally for each species, sex and size class within this study. To use the stomach content weight ($W_{stomach}$) as a proxy for stomach fullness, it had to be corrected for fish size. Therefore, the observed stomach content weight $W_{stomach}$ was expressed as a percentage of the predicted size-specific standard body weight W_{pred} (see Eq. 4.3) and was called the relative stomach content weight S.

$$S = 100 \times \frac{W_{stomach}}{W_{pred}} \qquad \text{Eq. 4.5}$$

Although regurgitation can lead to an underestimation of stomach contents, fish that regurgitated were not excluded from the analyses, because for one thing on average a quarter of the samples from the salt-marshes would have been lost (in the salt-marsh creeks 29.1 (± 36.0) % of the analysed fish regurgitated, while it were only 5.5 (± 11.9) % in the subtidal) and for another the standardized stomach contents of those fish that regurgitated were not significantly lower than of those that did not regurgitate (based on Wilcoxon rank sum test with continuity correction: herring: W-statistic = 1701, p-value = 0.5047, three-spined stickleback: W-statistic = 23595, p-value = 0.6283, common goby: W-statistic = 39263, p-value = 0.8497, sand goby: W-statistic = 1214, p-value = 0.8233 and Supplement B, Fig. B.1).

All condition indices (K_n, HSI, and S) refer to a standardized body weight W_{pred}, because the individually-measured body weight includes the specific condition of that specific individual fish. When using the individually-measured body weight as denominator, e. g. the same stomach content weight of fishes of the same size would result in either a comparably low relative stomach content weight S for fishes with a relatively high long-term condition or vice versa in a high relative stomach content weight S for fishes with a low long-term condition.

Size ranges of the analysed fish were rather narrow (except herring, Supplement B, Fig. B.2) and due to limited sample availability per area and month, no size-specific analyses were conducted.

Stomach contents

Evaluation of stomach contents followed Allen et al. (1994), who combined the frequency of occurrence (Hynes, 1950; Hyslop, 1980) and the estimated percentage abundance in the stomach to classify prey types as *present* (< 10 % of the stomach content), *common* (10-50 % of the stomach content) or *abundant* (> 50 % of the stomach content).

Density of prey resources

The analysis of prey densities focused on the main prey resources for the four predators, namely MEZB and zooplankton. Prey biomass was not analysed, because (1) for example for small fish feeding on bivalve siphons, the number of siphons matters, not the biomass of the whole bivalve, and (2) biomass measurements of MEZB and zooplankton would not be comparable due to higher measurement uncertainties in zooplankton caused by the low quantity of sample material. MEZB samples were analysed for density and species composition of bivalves and polychaetes. All non-endobenthic organisms found in the samples, such as e. g. fish larvae, crabs and shrimps, were excluded from the analysis. The mud shrimp (*Corophium volutator*) and the lugworm (*Arenicola marina*) occurred only occasionally in the samples. They were excluded from the analysis as their densities were assumed not reliable due to an inadequate sampling method for these species (e. g. a too large mesh size for the mud shrimp, see Crewe et al., 2001, and a too shallow and too small sampling volume for the lugworm, see e. g. Wells, 1945). Harpacticoid copepods live mainly on the sediment, but occur also in the water column and thus their density in the sediment (examined by Sommer, 2016 and Bönisch, 2017) as well as and in the zooplankton is given in Fig. 4.3. For simplification, only the spatiotemporal abundance patterns of most important prey types – based on the stomach content analysis – are shown in Fig. 4.3. Logistic and financial limitations hampered a sampling of all potential prey species and sizes classes, which is a common problem in ecological field studies, but it covers the most important prey types. A detailed overview over seasonal species composition in the zooplankton and MEZB samples in both locations, the marsh creeks and the subtidal, is provided in Supplement B (Fig. B.3). For reasons of readability, zooplankton species were grouped in Fig. B.3a (Supplement B). The abundances of individual species within these zooplankton categories are listed in Tab. B.3 (Supplement B).

Individual specialization on polychaete prey?

Polychaetes were the most important prey and also more abundant in the salt-marsh creeks than in the subtidal. Therefore, we hypothesised that individuals with the ability to specialize on this prey type could benefit more from the salt-marsh creeks, than their conspecifics. If fish are specialized on polychaetes, they would have more likely high amounts of this prey in both, the stomach and the gut, representing the diet on a shorter and a longer timescale, and they would have more likely a low diversity of stomach contents. The diversity of the stomach contents was calculated with the Simpson´s Index of Diversity *D* (Simpson, 1949) per individual fish, based on percentages:

$$D = 1 - \frac{\sum n(n-1)}{N(N-1)} \qquad \text{Eq. 4.6}$$

where *n* is the percentage of an individual prey type in the stomach and *N* is the sum of the percentages of all prey types in a stomach. The hypothesis, that fish would benefit from a specialization on polychaetes, was tested by investigating whether the relative stomach content weight *S* is positively correlated with the percentage of consumed polychaetes using the Pearson correlation coefficient.

Competition analysis

Diet overlap

Food competition was investigated using intra- and inter-specific diet overlap analysis. Only hauls with at least 5 individuals per predator were selected. The number of hauls per predator combination is given in Supplement B (Tab. B.4). Based on the stomach content compositions, 29 prey categories were defined (Supplement B, Tab. B.5). The Schoener Index (Krebs, 1999) was used as indicator for the diet overlap. As all diet overlap indicators are sample-size sensitive (Krebs, 1999), the Schoener Index P_{jk} (Eq. 4.7) was calculated by one-to-one comparisons of stomach contents of single predators derived by random sampling. The random sampling and calculation of P_{jk} were repeated 100 times per haul and predator combination, yielding a distribution of index values instead of only a single index value for each haul and predator comparison.

$$P_{jk} = 100 \times \sum_{i=1}^{n} minimum(p_{ij}, p_{ik}) \qquad \text{Eq. 4.7}$$

where P_{jk} is the diet overlap between predator j and predator k, p_{ij} and p_{ik} are the shares of resource i of all resources used by predator j and predator k, respectively, and n is the total number of resources used. For statistical analyses of whether the diet overlap differed between the salt-marsh creeks and the subtidal, for each intra- or inter-specific predator combination a negative binomial GLM was fitted, because the left-skewed distribution of the diet overlap P_{jk} did not allow for simple two-sample tests. The negative binomial GLM was fitted using the function *glm.nb()* from the R package *MASS* (Venables and Ripley, 2002).

Analysis of prey resource limitation

Diet competition only occurs when the shared prey resources are limited. In such a case, the relative stomach content weight S would decrease with increasing diet overlap, because less prey would be available for each competitor. Additionally, the relative stomach content weight S would decrease with increasing abundance of competing predators. To test these hypotheses, for each of the four predators, the relative stomach content weight S was related to the diet overlap P_{jk} and to the density of potential competitors in the creek. The density of each predator was based on Friese et al. (2020b; Chapter 2).

Prey resource limitation was analysed via the functional response of the consumption relative to the prey density in the habitat (Holling, 1959a, 1959b, 1965). The density of selected prey resources (bivalves, polychaetes, benthic harpacticoid copepods, the calanoid copepod *Temora spp.*, other copepods, and barnacle cypris larvae) was correlated to the mean percentage of each of them found in the stomachs of the four predators using Pearson’s product-moment correlation coefficient. When these prey resources would be limited, the amount consumed would increase with higher densities in the habitat (positive slope at all three Holling types). On the other hand, when they would not be limited, the consumed amounts would not correlate with the density in the habitat, because the consumption is for example limited by external and internal handling time (asymptote in all three Holling types; Holling, 1959b, 1959a, 1965; Whelan and Brown, 2005).

Finally, we examined whether the predators are hypothetically capable of depleting the prey resources of the salt-marsh creeks. This is possible, because the flooded salt-marsh creeks are kind of a “dead-end road” with a defined habitat volume and area per tidal flooding. First, the density of the prey resources per square meter (for the benthic organisms) and per cubic meter (for the zooplankton) was extrapolated to the total habitat area or volume at high tide (calculations described in Friese et al., 2018a;

Chapter 5), thereby obtaining the total number of the selected prey resources per salt-marsh creek and month. In the same way the total number of the four predators was obtained using their density (Friese et al., 2018a, 2020b; Chapter 2 and 5). In a second step, the possible amount consumed per predator, prey, creek and tide was calculated within two hypothetical scenarios. We hypothesized, that each single predator consumed as many organisms of the prey resource under consideration as they consumed (1) on average or (2) at maximum over the whole sampling period. In both of these scenarios it was assumed that only this single prey resource was consumed by all of the individuals of the predator species under consideration. Especially, the second scenario, in which predation pressure on single prey resources is maximized, reveals whether they are principally able to deplete substantial amounts.

All data analysis were performed using R version 3.6.2 (R Core Team, 2019).

Results

Dietary condition of fish

Both, long- and short-term dietary condition was highly variable among individuals (Fig. 4.1, Supplement B Fig. B.4 to Fig. B.6). The long-term dietary condition (indicated by K_n and *HSI*) of herring and three-spined stickleback were equal in the salt-marsh creeks and the subtidal (Fig. 4.1, Supplement B, Fig. B.5 and Fig. B.6). The two goby species tended to have a higher K_n and *HSI* in the subtidal than in the marsh creeks. However, comparisons per month and daytime revealed that only few cases were significant (Tab. 4.1, Supplement B, Fig. B.5 and Fig. B.6). In winter during day, the long-term dietary condition of herring and three-spined stickleback was also lower in the salt-marsh creeks than in the subtidal. A reverse situation, i. e. a higher long-term condition in the salt-marsh creeks than in the subtidal, was never observed. The specimen analysed in the salt-marsh creeks tended to be smaller than in the subtidal and all condition indices tend to increase with body size due to variance in homogeneity. Furthermore, all three condition indices are based on wet weights, therefore small differences should not be over-interpreted. In contrast to the long-term dietary condition, the short-term dietary condition (indicated by the relative stomach content weight) of at least three-spined stickleback and common goby tended to be higher in the salt-marsh creeks (Fig. 4.1, Supplement B, Fig. B.4). This difference was

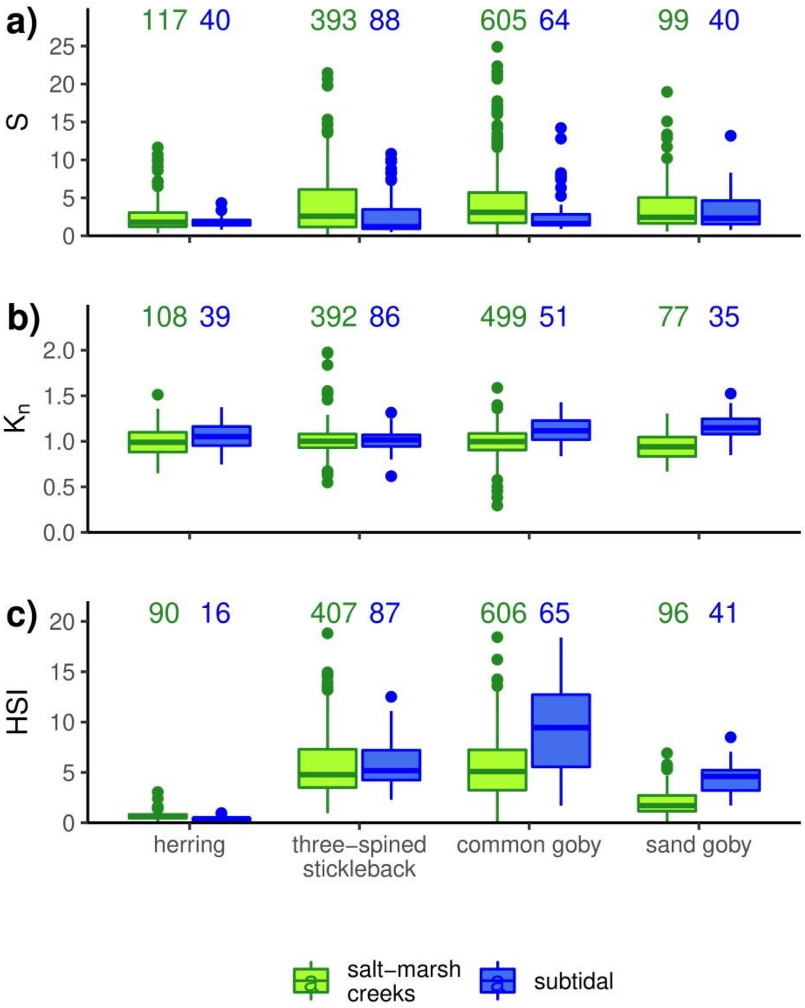


Fig. 4.1: a) Relative stomach content weight *S*, b) relative condition factor K_n, and c) hepatosomatic index *HSI* of the four fish species based on wet weights in the salt-marsh creeks and in the subtidal (without a temporal resolution). Sample sizes are given above each boxplot. For a seasonal and diurnal resolution see Supplement B, Fig. B.4 to Fig. B.6.

significant, when more than 30 fishes from the subtidal were available for the comparison (Tab. 4.1, Supplement B, Fig. B.4).

Diet composition

Herring

The diet composition of herring was relatively similar in the salt-marsh creeks and in the subtidal. However, they consumed higher amounts and more frequently mysids in the subtidal and more of the calanoid copepod *Temora spp.* in the salt-marsh creeks (Fig. 4.2). In the marsh creeks, herring diet was dominated by *Temora spp.* in winter (December and February), whereas other unidentified copepods were most important in spring (March and April) and early summer (May and June; Supplement B, Fig. B.7a). In early summer, almost 60 % of herring stomachs were filled with 10-50%

polychaetes (Supplement B, Fig. B.7a). In winter, the most frequent prey were harpacticoid copepods.

Three-spined stickleback

The diet of the three-spined stickleback was dominated by polychaetes, mainly common ragworm *Hediste diversicolor* in the salt-marsh creeks and by the mud shrimp *Corophium volutator* in the subtidal (Fig. 4.2). *H. diversicolor* dominated the diet of the three-spined stickleback in all seasons in the salt-marsh creeks accompanied by brown shrimp *Crangon crangon* in summer (May until August), by early life stages of crabs (Brachyura, probably *Carcinus maenas*) in late summer (July and August) and by the semi-terrestrial amphipod *Orchestia gammarellus* in winter (Supplement B, Fig. B.7b). From April to May also fish larvae (Actinopteri) of plaice and herring were found in their stomachs (Supplement B, Fig. B.7b). Another regularly observed prey type were parts of bivalve siphons, which occurred regularly during all seasons, when the three-spined stickleback was abundant in the marsh creeks (December to May, Supplement B, Fig. B.7b).

Tab. 4.1: Significant differences in dietary condition of the condition indices (relative stomach content weight *S*, relative condition factor K_n, and hepatosomatic index *HSI*) between the salt-marsh creeks and the subtidal. Seasons are classified as follows: spring: March, April; early summer: May, June; autumn: September, October, winter: December, February. Salt-marsh creeks are abbreviated as “marsh”. H1 refers to the H1-hypothesis tested with the Wilcoxon rank sum test with continuity correction, that is whether a condition index was significantly larger or smaller in the marsh than in the subtidal. Here only significant differences are shown, the full comparison of the three condition indices of the four fish species per season, daytime and location are provided in Supplement B, Fig. B.4 to Fig. B.6.

condition index	**species**	**season**	**daytime**	**location**	**Index value**			**number of analysed fish**	**Wilcoxon rank sum test with continuity correction**		
					mean	**standard deviation**	**median**		**W-statistic**	**p-value**	**H1**
relative stomach content weight S	common goby	autumn	day	marsh	5.75	4.26	5.00	81	2366	0.0000	S_{marsh} > $S_{subtidal}$
				subtidal	2.56	3.09	1.52	36			
	three-spined stickleback	spring	day	marsh	6.71	3.90	6.55	52	1422	0.0005	
				subtidal	4.26	2.70	4.24	39			
		winter	day	marsh	4.90	3.81	3.87	57	2032	0.0000	
				subtidal	0.98	0.28	0.95	40			
	herring	winter	day	marsh	3.26	2.49	2.49	56	1620	0.0001	
				subtidal	1.84	0.68	1.69	40			
relative weight K_n	common goby	autumn	day	marsh	1.12	0.09	1.11	58	407	0.0001	Kn_{marsh} < $Kn_{subtidal}$
				subtidal	1.22	0.12	1.21	28			
		spring	night	marsh	0.88	0.13	0.90	69	153	0.0008	
				subtidal	0.98	0.06	0.98	11			
	sand goby	spring	night	marsh	0.92	0.14	0.90	44	29	0.0000	
				subtidal	1.19	0.15	1.20	8			
	herring	winter	day	marsh	0.97	0.16	1.01	56	794	0.0122	
				subtidal	1.05	0.14	1.05	39			
Hepatosomatic Index HSI	three-spined stickleback	winter	day	marsh	3.70	1.40	3.36	57	639	0.0002	HSI_{marsh} < $HSI_{subtidal}$
				subtidal	4.56	1.20	4.45	39			
	common goby	spring	day	marsh	3.50	1.66	3.30	76	106	0.0153	
				subtidal	5.65	2.41	5.23	6			
			night	marsh	3.33	1.67	2.85	80	333	0.0194	
				subtidal	4.37	1.87	4.33	13			
		autumn	day	marsh	7.48	2.39	7.22	81	301	0.0000	
				subtidal	12.27	2.78	12.42	37			
	sand goby	early summer	day	marsh	1.12	0.83	0.85	3	0	0.0027	
				subtidal	4.54	1.08	4.69	11			
		spring	night	marsh	1.86	1.19	1.57	58	58	0.0001	
				subtidal	3.99	1.47	4.12	9			

Common goby

Year-around, common gobies fed mainly on polychaetes, especially *H. diversicolor*, in the salt-marsh creeks, while their diet in the subtidal was more diverse with a more frequent consumption of barnacles (*Cirripedia*) cypris larvae (Fig. 4.2, Supplement B, Fig. B.7c). In the marsh creeks, parts of bivalve siphons were also found in the stomachs, with increasing amounts towards autumn (Supplement B, Fig. B.7c). As for herring, harpacticoid copepods were most frequently observed in common goby stomachs in winter in the marsh creeks (Supplement B, Fig. B.7c). In summer, *C. crangon* and early life stages of *C. maenas* were found in the stomachs (Supplement B, Fig. B.7c). Especially in late summer, fish larvae, mainly gobies (*Pomatoschistus sp.*), were found in about 20 % of the stomachs, indicating cannibalism (Supplement B, Fig. B.7c).

Sand goby

The diet of the sand goby was relatively similar to the common goby, but with higher amounts and more frequent consumption of *C. volutator* and polychaetes, especially *H. diversicolor*, in the salt-marsh creeks and higher amounts of amphipods, probably mainly highly digested *Bathyporeia sp.*, and more frequent occurrence of zooplankton in the subtidal (Fig. 4.2). In spring, their diet in the salt-marsh creeks consisted mainly of *C. volutator* followed by polychaetes (*H. diversicolor*) and by bivalve siphons (Supplement B, Fig. B.7d). In early summer, their diet was dominated by *C. crangon*, and in winter, almost equal amounts of *C. crangon* and polychaetes were eaten by the sand gobies. The planktonic prey shifted from barnacle cypris larvae in spring and early summer towards *Temora spp.* in winter (Supplement B, Fig. B.7d).

Prey availability

Zooplankton density varied substantially between the salt-marsh creeks and the subtidal, however, these variations were inconsistent (Fig. 4.3). Monthly densities fluctuated also strongly, but some seasonal trends were observed (Fig. 4.3). Harpacticoid copepods occurred in the zooplankton in December in highest densities (Fig. 4.3). The density of *Temora spp.* peaked twice during the sampling period, first in June and then in December (Fig. 4.3). The other copepods and barnacle cypris larvae were most abundant in April (Fig. 4.3). All three benthic prey types, harpacticoid copepods (from benthic meiofauna samples), polychaetes and bivalves, occurred in significantly higher densities in the salt-marsh creeks than in the subtidal (harpacticoid copepods: W-statistic = 1265.5, p-value = 2.142e-06; polychaetes: W-statistic = 10940, p-value < 2.2e-16; bivalves: W-statistic = 8680, p-value = 6.705e-11). On average, the salt-marsh creeks contained ca. 5 times more benthic harpacticoid copepods, 27 times more polychaetes and ca. 10 times more bivalves. Densities of polychaetes increased from September to December. Bivalve density on the other hand peaked during summer from June to August (Fig. 4.3). The dominant

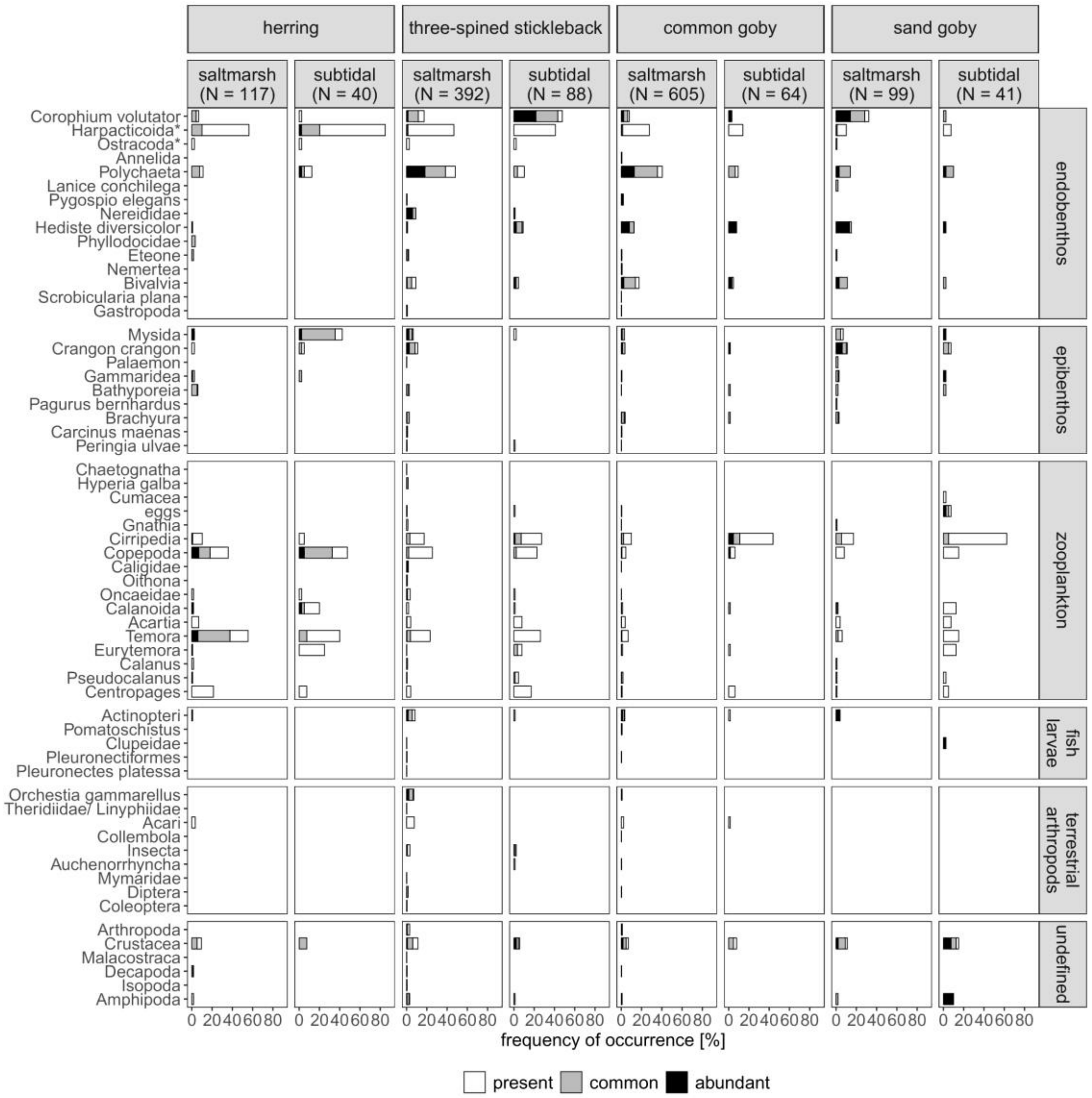


Fig. 4.2: Prey composition of the four analysed predators in the salt-marsh creeks and in the subtidal. N: number of analysed fish, including those with only mucus or undefined material in their stomach. Prey abundance classes (white = present, grey = common, black = abundant) indicate the percentage a certain prey type contributed to the total stomach content; present: < 10 % of the stomach content; common: ≥ 10 – 50 % of the stomach content; abundant: ≥ 50 % of the stomach content.

polychaete in the MEZB samples was *H. diversicolor* (Supplement B, Fig. B.3b). Bivalves were dominated by *Limecola balthica* and *Scrobicularia plana* in the salt-marsh creeks and by *Cerastroderma edule* on the tidal flat (Supplement B, Fig. B.3c).

Polychaete density was significantly lower in the creek centre than at the creek bank or halfway between both locations (W-statistic = 740.5, p-value = 3.226e-05 and W-statistic = 818.5, p-value = 6.982e-06 respectively; Supplement B, Fig. B.8). In the creek centre also the density of bivalves was significantly reduced compared to the position halfway between the creek bank and centre (W-statistic = 1096, p-value = 0.003; Supplement B, Fig. B.8). This “middle” position contained on average ca.

twice as many polychaetes and five times more bivalves than the position in the creek centre with the highest flow velocity (Supplement B, Fig. B.8).

Individual specialization on polychaete prey?

Polychaetes were the dominating prey resource in the salt-marsh creeks, both concerning its abundance and its frequency of occurrence in the stomachs. We hypothesized that fish, specialized on this prey type, may especially benefit from the

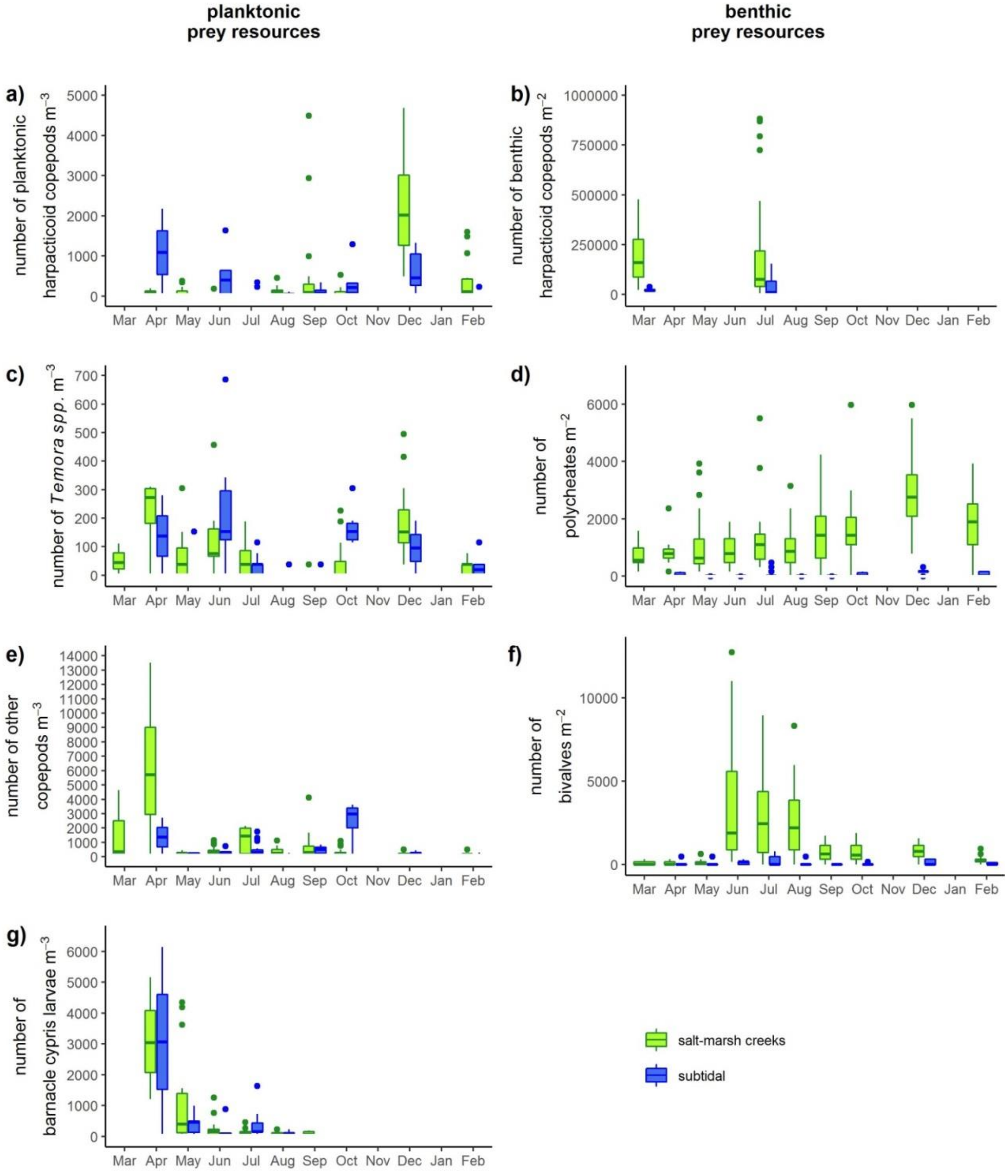


Fig. 4.3: Seasonal densities of selected planktonic and benthic prey resources for fish in the salt marsh and the adjacent subtidal (or tidal flat at *Vollerwieker Priel* and *Westerplate Nord*)

marsh creeks, because stomachs tended to be fuller and polychaetes were significantly more abundant in the salt-marsh creeks than in the subtidal (Fig. 4.1a, Fig. 4.3d). Stomach contents varied strongly between individuals of the four species, but many three-spined sticklebacks and common gobies from the salt-marsh creeks had not only high percentages of polychaetes in their stomach, but also in their guts. Moreover, a low Simpson´s Index of Diversity indicated that these individuals had specialized on using polychaetes as their main prey (Fig. 4.4). This specialization of some individuals seemed indeed to pay off, as the relative stomach content weight *S* tended to increase with increasing amounts of eaten polychaetes (Fig. 4.5). A significant positive correlation with Pearson´s *r* larger than 0.5 was found for the three-spined stickleback, the common and the sand goby in the salt-marsh creeks (Fig. 4.5). By contrast, in the subtidal less individuals were specialized on polychaete prey (Fig. 4.4). The correlations of the relative stomach content weight *S* and the amount of consumed polychaetes were also significantly positive in the subtidal (Fig. 4.5). However, these should be interpreted with caution, as they were mainly driven by very few fishes with high amounts of polychaetes in their stomachs (Fig. 4.5). In summary, among the three-spined stickleback and the common goby, about 50% of the individual fish (Fig. 4.2) were well adapted to exploit the rich benthic prey resources of the salt-marsh creeks (winners), while the other half of their conspecific were less efficient to use this abundant prey (losers).

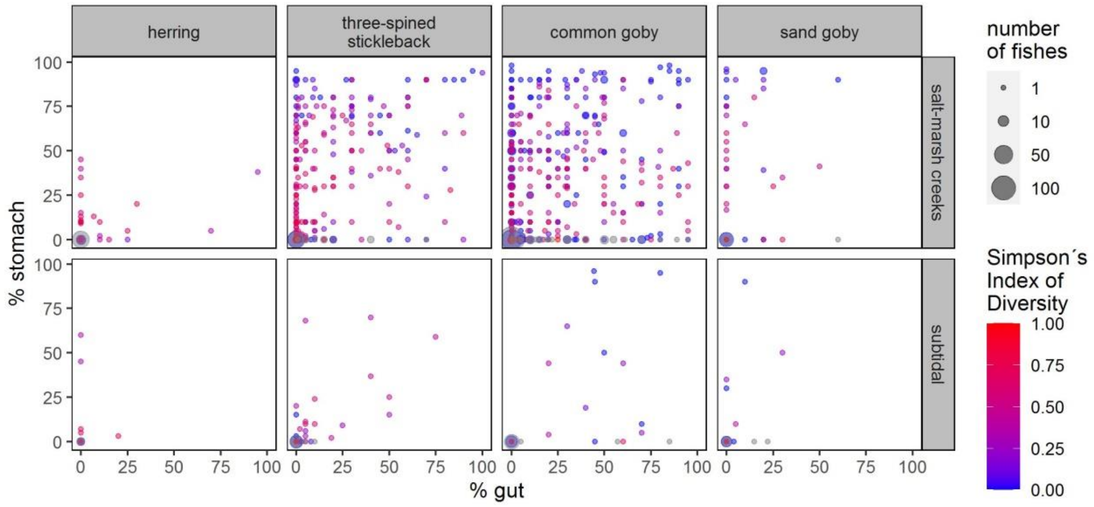


Fig. 4.4: Percentage of polychaetes in the stomach (y-axis) and in the gut (x-axis). The point size increases with the number of fishes. The colour labels the diversity of the prey in the stomachs (Simpson´s Index of Diversity), where blue indicates homogeneous and red heterogeneous stomach contents. Grey colour means that the stomach contained no identifiable prey and thus the Simpson´s Index of Diversity could not be calculated. It is assumed, that the higher the percentage of polychaetes in the stomach and in the gut and the lower the Simpson´s Index of Diversity, the more specialized is a fish on polychaetes.

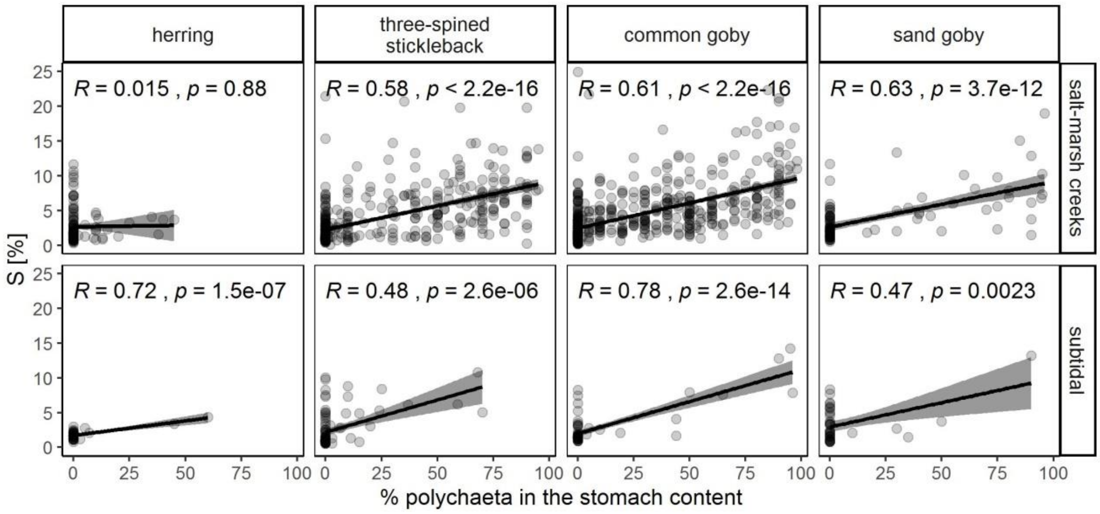


Fig. 4.5: Correlation between the relative stomach content weight *S* and the percentage of polychaetes in the stomach content for each of the four predators (rows) in the salt-marsh creeks (left) and the subtidal (right). For each panel the Pearson correlation coefficient *r* and the p-value are given. The line represents a linear regression with a 95% confidence interval.

Diet competition

The four fish species analysed share several prey resources, potentially causing inter-specific food competition. As foraging performance also varied strongly among individuals of a single species, intra-specific food competition was also considered. In order to assess the diet competition, we first quantified the extent of diet overlap and afterwards evaluated potential prey limitations based on predator and prey abundances.

Diet overlap between the four predators

The diet overlap was quantified per haul using the Schoener Index P_{jk} based on repeated calculations of random data subsets. As it was calculated per haul, and hauls with less than 5 fish per competitor were excluded, also single hauls were included in Fig. 4.6 (sample sizes of fish per comparison are given in Supplement B, Tab. B.4). The diet overlap tended to be higher in the salt-marsh creeks than in the subtidal (Fig. 4.6). The negative binomial GLMs estimated that the diet overlap within the herrings, the common gobies, and the sand gobies was 58 % (p = < $2e^{-16}$), 75 % (p = < $2e^{-16}$), and 38 % (p=0.000171), respectively, smaller in the subtidal than in the salt-marsh creeks. The diet overlap within the three-spined sticklebacks did not differ between the subtidal and the salt-marsh creeks. The intra-specific diet overlap between three-spined sticklebacks and sand gobies, between three-spined sticklebacks and herrings, and between common and sand gobies was 49 % (p = < $2e^{-16}$), 72 % (p = < $2e^{-16}$), and 72 % (p=$2.85e^{-6}$) smaller in the subtidal than in the salt-marsh creeks.

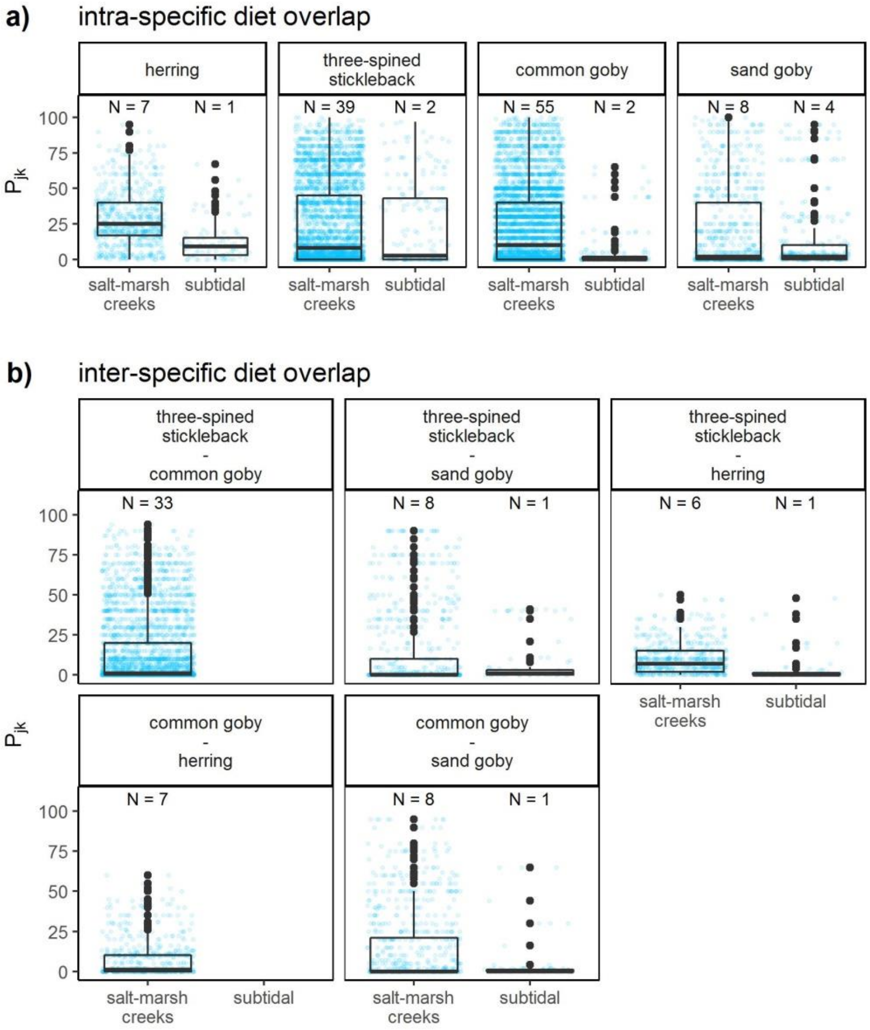


Fig. 4.6: Boxplots of the a) intra- and b) inter-specific diet overlap between the four analysed predators based on iterative calculations of the Schoener Index P_{jk} from random data subsets per haul in the salt-marsh creeks and in the subtidal. Blue points represent each single P_{jk} value of random one-to-one diet overlap comparisons of the 100 iterative calculations per haul. *N* gives the number of included hauls. The number of fish per predator combination and of each of the compared species is given in Supplement B (Tab. B.4).

Prey resource limitations

We hypothesised, that in case of prey resource limitation, the relative stomach content weight would decrease with increasing diet overlap of competitors, because less prey would be available for each of them. Therefore, the mean relative stomach content weight *S* of each predator was compared to the mean diet overlap with potential competitors per tide (Fig. 4.7). In contrast to our hypothesis, the relative stomach content weight increased with increasing diet overlap, indicating that resources were not limited (Fig. 4.7). In case of a negative slope of the regression between relative stomach content weight *S* and diet overlap P_{jk}, as for the relative stomach content weight *S* of the common goby and its diet overlap with herring (Fig. 4.7), the diet overlap was relatively low and the variance was relatively high. Thus, even this case did not support any resource limitation.

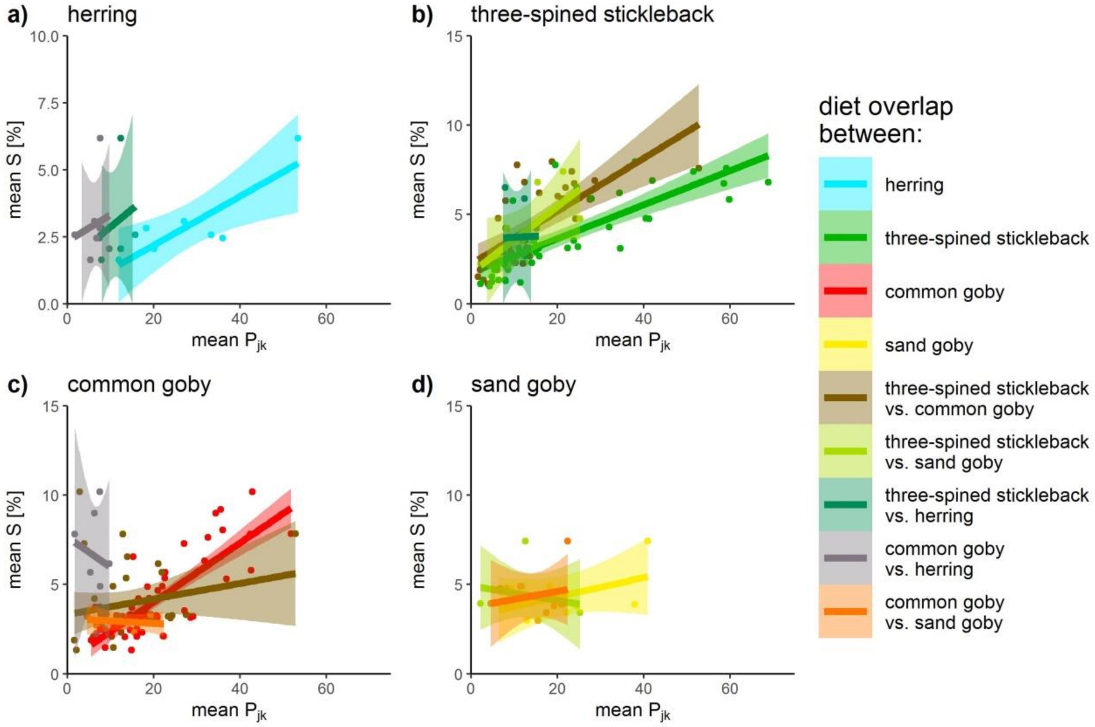


Fig. 4.7: Mean relative stomach content weight *S* of a) the herring, b) the three-spined stickleback, c) the common goby and d) the sand goby versus the mean diet overlap with potential competitors in the salt-marsh creeks. The diet overlap is based on iterative calculations of the Schoener Index P_{jk} from random data subsets per haul. Each point refers to one haul. The colors indicates to which competitor the diet overlap refers. The lines represents a linear regression with a 95 % confidence interval.

Furthermore, we hypothesized that in case of diet competition the stomachs of the four analysed predators would be less full the more potential competitors are around. The relative stomach content weight *S* tended to decrease when predator densities were unusually high (Fig. 4.8). Observations of relatively high nekton densities were, however, scarce and in 78 % - 91 % of all hauls the density of each of the four predators in the salt-marsh creeks was below 0.2 individuals per m^{-3} and thus the relative stomach content *S* was not affected by predator density.

The correlation between the density of selected prey resources (namely bivalves, polychaetes, benthic harpacticoid copepods, *Temora spp.*, other copepods, and barnacle cypris larvae) in the habitat and the percentage found in the stomachs of the four predators was analysed. A positive correlation would mean the fish would consume more if more was available and thus that the prey resource is limited at the lower densities. When the density and the abundance in the stomach do not correlate, the fishes eat probably already as much of that prey as they can handle. The percentage of *Temora spp.* and other copepods found in the stomachs of herrings correlated significantly with its density in the salt-marsh creeks (Tab. 4.2). This correlation was relatively weak for *Temora spp.* but stronger for other copepods (Pearson´s *r*: 0.3 and 0.7 respectively; Tab. 4.2). The three-spined stickleback tended to eat slightly more copepods when their densities increased, indicating that this prey resource was limited, when occurring in lower densities (Pearson´s *r*: 0.28; Tab. 4.2).

The prey consumption of the common goby and the sand goby did not positively correlate with the densities of any prey types in the salt-marsh creeks. This indicates that the selected prey resources were not limited and the two goby species could feed even at relatively low densities as much of these prey types as they were able to handle within the time frame the marsh creeks were accessible (Tab. 4.2). The same applies to the other (mainly benthic) prey types of the herring and the three-spined stickleback.

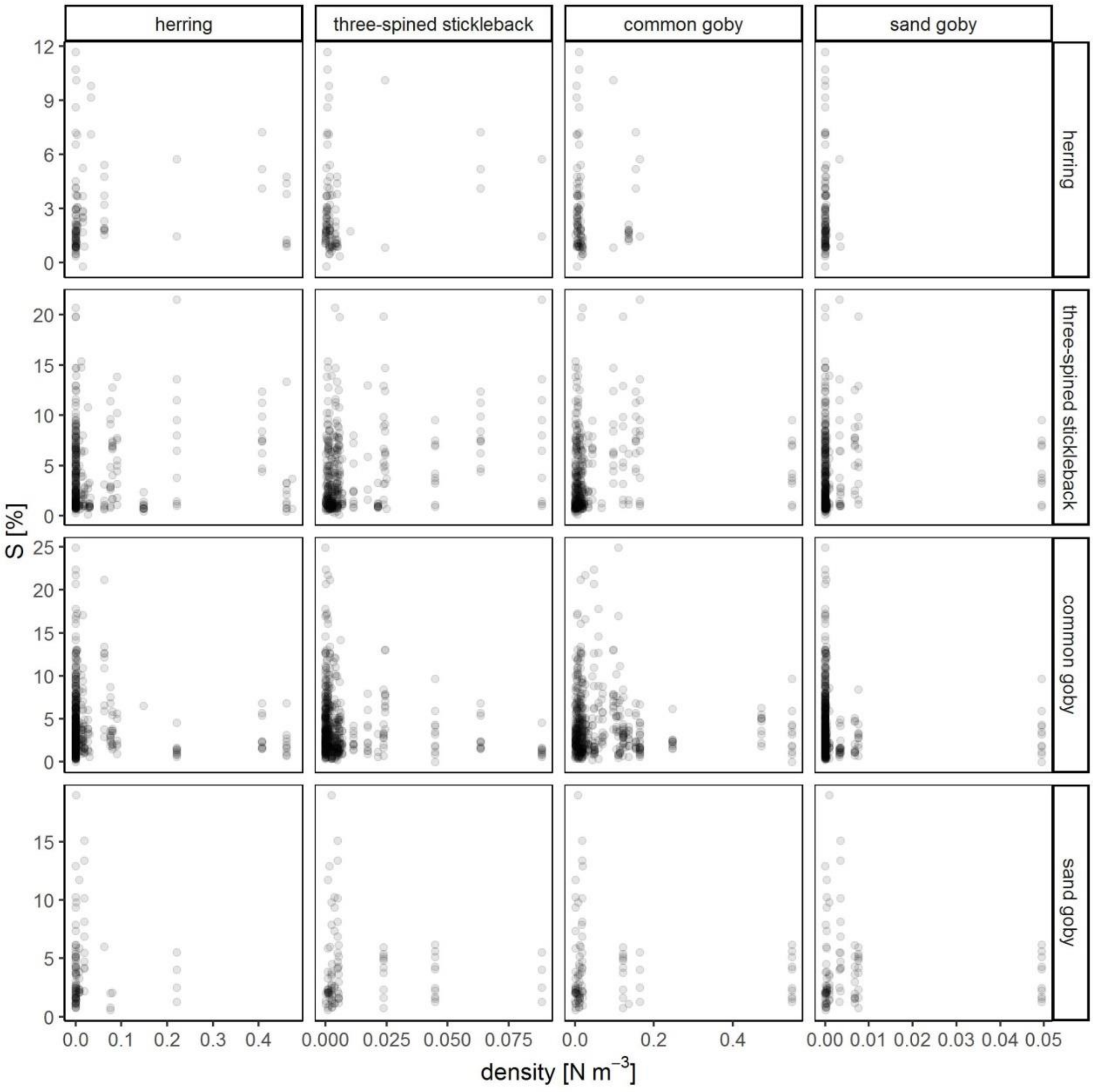


Fig. 4.8: Relative stomach content weight *S* of the four predators (in rows) versus the density of each possibly competing predator (in columns) in the salt-marsh creeks.

Tab. 4.2: Pearson correlation between the mean density of selected prey resources in the habitat and the mean percentage found in the fish stomachs. Prey density of harpacticoid copepods refers to the MEZB samples of harpacticoids. Densities of benthic prey resources were measured in numbers / m² and planktonic in numbers / m³. Significant positive correlations are printed in bold.

prey resource	**herring**		**three-spined stickleback**		**common goby**		**sand goby**	
	r	**p-value**	***r***	**p-value**	***r***	**p-value**	***r***	**p-value**
bivalves			-0.09	0.59	0.01	0.91	0.09	0.79
polychaetes	0.41	0.07	-0.06	0.41	0.10	0.08	-0.44	0.02
harpacticoid copepods			-0.17	0.30	0.00	1.00		
Temora spp.	**0.30**	**0.02**	0.19	0.08	0.09	0.57	0.21	0.70
other copepods	**0.70**	**0.00**	**0.28**	**0.00**	0.02	0.88	0.10	0.74
barnacle larvae	0.16	0.62	0.17	0.17	0.04	0.76	0.18	0.48

Whether each of the four predators would be hypothetically able to deplete each of the selected prey resources in the salt-marsh creeks, as a worst case scenario the total number of predator and prey and the possible total number consumed (based on average and maximum consumption) was calculated. When assuming that the predators would consume average amounts of the prey types, they could at maximum exploit up to 0.03 % of the bivalves, but less than 0.01 % of polychaetes and harpacticoid copepods per tide (Tab. 4.3). When assuming each predator fed the maximum ever found in a single stomach these percentage fractions consumed, still only increased to 0.12 % of bivalves, 0.21 % of polychaetes and less than 0.1 % of harpacticoid copepods within one tidal cycle (Tab. 4.3). The common goby has the potential to consume the highest proportions of these benthic prey resources (Tab. 4.3). The fraction of the zooplankton, the four predators are hypothetically able to exploit at maximum, are larger. Herring would be able to consume more than 150 % of the prey resource *Temora spp.* and more than 20 % of the other copepods and barnacle cypris larvae (Tab. 4.3). The three-spined stickleback would hypothetically be able to exploit more than 4 % of the copepods (*Temora spp.* and other copepods) and up to ca. 1.5 % of the barnacle cypris larvae in the salt-marsh creeks (Tab. 4.3). The common goby could even exploit more than 50 % of barnacle cypris larvae and other copepods than *Temora spp.*, while the sand goby could only exploit up to 0.1 % at maximum of the three planktonic prey resources (Tab. 4.3).

Although these hypothetical scenarios are highly unrealistic, because it is unlikely that each single of these rather opportunistic predators would fill its stomach exclusively with a single prey type and feeding a maximum number of it, this analysis still demonstrates, that much higher amounts of benthic prey are available in the salt-marsh creeks than could be depleted by the four analysed predators within the limited temporal accessibility of this habitat. Thus, the benthic prey resources are available on excess in the salt-marsh creeks. The zooplankton, however, which is in contrast to the benthic prey resources not stationary in the marsh creeks, can be exploited by considerable higher rates (Tab. 4.3).

Tab. 4.3: Mean and standard deviation (sd) of the percentage of hypothetically consumed versus total amounts of selected prey resources in the salt-marsh creeks per predator species, when all individuals would feed (1) as many organisms of a certain prey as they do on average or (2) as found at maximum in a single stomach.

hypothetical percentage of consumed prey resources per tide,
if all individuals of a predator species present in a creek would consume as many prey organisms as:

scenario	**found on average in a single stomach**								**the maximum found in a single stomach**							
predator	**herring**		**three-spined stickleback**		**common goby**		**sand goby**		**herring**		**three-spined stickleback**		**common goby**		**sand goby**	
prey resource	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
bivalves	-	-	0.02	0.05	0.03	0.08	0.00	0.01	-	-	0.11	0.23	0.12	0.29	0.01	0.02
polycheates	0.01	0.02	0.00	0.00	0.00	0.01	0.00	0.00	0.05	0.14	0.01	0.02	0.21	0.68	0.00	0.00
harpacticoid copepods	0.00	-	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	0.00	0.00	0.00	0.01	0.00	0.00
Temora spp.	20.79	60.43	0.22	0.41	0.24	0.79	0.00	0.00	153.32	445.71	4.06	7.72	1.66	5.57	0.01	0.01
other copepods	1.48	4.36	0.15	0.49	3.29	14.95	0.00	0.00	24.72	72.96	4.40	14.76	50.79	231.16	0.01	0.00
barnacle larvae	2.67	4.90	0.10	0.21	1.68	4.46	0.00	0.00	28.97	53.20	1.49	3.14	53.19	141.58	0.01	0.01

Discussion

Planktonic prey resources drift passively in the marsh during each tide. Thus, as expected, abundance was highly variable and no significant difference between the salt-marsh creeks and the subtidal was observed. Similarly, Valiñas et al. (2012) found no difference in the zooplankton abundance in a *Spartina* marsh and a tidal flat in Argentina. Consistently, the relative stomach contents of the planktivore herring barely differed between both habitat types. The significant positive correlation between the amount consumed and the density of copepods, especially *Temora spp.*, in the salt-marsh creeks indicated that herring would consume more zooplankton, if there would have been more available. Thus, this habitat does not provide a superabundance of planktonic prey resources. Moreover, mysids were another important prey for herring in the subtidal but not in the salt marshes. Since mysids are larger than copepods, this prey could deliver relatively more energy per handling time. In conclusion, the marsh creeks provide no advantages with regard to prey abundance for planktivore fish, such as herring. But Hibino et al. (2006) argued that in shallow waters planktivore fishes could easier locate their prey by searching only horizontally and not also vertically in the water column. Additionally, while the turbid subtidal area adjacent to the sampled marsh is appropriate for filter-feeding, the clear waters in the salt-marsh creeks may enable the visual predator herring to switch to particulate-feeding, which costs by a factor of 1.4 to 4.6 less energy – especially at the low flow velocities in the marsh creeks (Gibson and Ezzi, 1992; Robertis et al., 2003; Friese et al., 2020a; Chapter 3). Three-spined sticklebacks, and the two goby species fed also frequently zooplankton, however only low amounts and the relative stomach content weight of herring was not affected by the densities of or diet overlap with the three potential competitors. Furthermore, herring was the only planktivore species (except Nilsson´s pipefish *Syngnathus rostellatus*) entering the marsh creeks frequently and abundantly, but in comparably lower densities than in the subtidal (Friese et al., 2020b; Chapter 2). Given these points the competitive pressure for food resources is rather low for herring in the salt-marsh creeks. The temporary spatial separation to other planktivores in the subtidal also relaxes the diet competition in the offshore habitats and thus also benefits those individuals that avoid the marsh (Allen et al., 1995).

By contrast to planktivore fish, omnivores and benthivores benefit significantly from abundant benthic prey in the salt-marsh creeks. Studies on fish diets in salt marshes most frequently identified benthic invertebrates as the main prey types (Sardá et al., 1998; Valiñas et al., 2012). In European salt marshes *Hediste diversicolor*, *Corophium volutator*, mysids, and *Orchestia gammarellus* accounted for the major part of the fish diets (Cattrijsse et al., 1994; Laffaille et al., 1999; Cabral, 2000; Laffaille et al., 2001; Hampel et al., 2005; Cattrijsse and Hampel, 2006). This study from the German Wadden Sea confirmed these main fish prey species in salt marshes, however, some were only seasonally available. For instance *O. gammarellus* was only accessible during winter storm floods (Friese et al., 2018a; Chapter 5), juvenile *C. crangon* were only in summer in an ingestible size available (as they were only consumed from May to August; see Burgund, 2017 for the length frequency distribution of *C. crangon* from the same hauls as this study), and the occurrence of fish larvae of plaice (*Pleuronectes platessa*), herring (*C. harengus*) and gobies (*Pomatoschistus spp.*) in the stomachs followed their abundance in the habitat (Friese et al., 2020b; Chapter 2). In contrast to mobile planktonic prey resources, the benthic prey resources are more closely linked to the characteristics of their habitat, and thus we define them as habitat-specific prey resources.

We evaluate the feeding habitat quality of the German salt-marsh creeks for the four analysed fish species, based on this habitat-specific prey, by (1) comparing the measured prey densities with other areas, (2) discussing how their behaviour may affect their availability for small fish, (3) linking the fish diets to the prey availability and comparing it with diets reported from other habitats, (4) comparing the benefits, i. e. the dietary condition, with the literature and (5) finally evaluating the diet competition in the salt-marsh creeks.

Densities of benthic prey resources

H. diversicolor occurred with up to 5502 ind. / m² (mean: 697 ± 690 ind. / m²) in the salt-marsh creeks and up to 157 ind. / m² (mean: 25 ± 58 ind. / m²) on the tidal flat. Although literature abundance records are highly variable, they reflect the pattern of higher densities of *H. diversicolor* in muddy areas, such as salt-marsh creeks, than on sandy tidal flats. In Dutch and Belgian salt marshes densities of *H. diversicolor* ranged from ca. 3000 to 17000 ind. / m² (Heip and Herman, 1979; Hampel, 2003). Densities of *H. diversicolor* on tidal flats in the Wadden Sea region (including estuaries) remained below 1000 ind. / m² in most studies (Beukema, 1976; Ysebaert et al., 1993; del Norte-Campos, 1995; Ysebaert and Herman, 2002; Schückel et al., 2013; Sackmann, 2015); only on muddy tidal flats densities of up to 6000 ind. / m² were found (Jensen and André, 1993). Beside *H. diversicolor* and other polychaetes, the mud shrimp *C. volutator* was a favoured prey type for three-spined sticklebacks, common gobies and sand gobies partly in the marsh creeks and in the subtidal. This prey species occurred, however, rarely in the MEZB samples, either because it was not abundant in the sampling areas, or because the sampling method was inappropriate for this species, or because we missed it during the sampling periods, because it is highly mobile, and recolonizes regularly new habitats via swimming and tidal transport (Meadows and Reid, 1966; Hughes and Horsfall, 1990). Reported maximum densities of *C. volutator* in the Wadden Sea region range from 6000-400000 ind. / m² in salt marshes (Adam, 1993; Hampel, 2003) to ca. 600-40000 ind. / m² on tidal flats (Beukema, 1976; Ysebaert et al., 1993; del Norte-Campos, 1995). The migratory behavior of *C. volutator* might also explain the variability in the occurrence in the stomach contents of fish analysed in this study. Another frequently found prey category in the analysed stomachs of three-spined sticklebacks and both goby species were cropped parts of bivalvia siphons. Although these fragments could not be identified to species level, according to the species compositions in the MEZB samples, they were most likely *Limecola balthica* (formerly *Macoma balthica*), *Scrobicularia plana* or *Cerastoderma edule*. In the marsh creeks we found densities of *L. balthica*, *S. plana* or *C. edule* of on average 468 ± 1444, 65 ± 168, 27 ± 451 ind. / m² and in the subtidal 8 ± 36, 21 ± 104, 53 ± 109 ind. / m², respectively. Also in the literature mean densities of *L. balthica* are higher in the salt marshes – Hampel (2003) found 1616 ± 701 ind. / m² in a Dutch estuarine salt marsh – than on tidal flats, where mean densities range from 10 to 550 ind. / m² (Beukema, 1976; Dekker, 1989; Ysebaert et al., 1993; Reise et al., 1994; del Norte-Campos, 1995; Ysebaert and Herman, 2002; Beukema et al., 2017b, 2017a). *S. plana* is a typical species in muddy sediments (Schückel et al., 2013), thus, the higher abundance found in the muddy marsh creeks than on the sandier tidal flats (Friese et al., 2020a; Chapter 3) was expectable. However, densities comparable to those of salt marshes can be found on mudflats, e. g. Schückel and Kröncke (2013) reported densities of *S. plana* on mudflats in the Jade Bay of 263 ind. / m². Reports of *C. edule* densities in salt marshes are unkown to us, but on tidal flats densities of 34-1550 ind. / m² were reported (Beukema, 1976; Ysebaert et al., 1993; Zwarts and Wanink, 1993; Reise et al., 1994). Altogether, despite high spatiotemporal abundance variability, the densities of *H. diversicolor*, *L. baltica* and *S. plana* were high in the salt-marsh creeks compared to many offshore areas.

Prey behavior

Beside the high densities of these benthic prey species also their behaviour increases their vulnerability falling prey to small fishes. The small predators are unable to exploit infauna deep in the sediment. For instance the lugworm *Arenicola marina*, which is highly abundant on sandy tidal flats in the Wadden Sea, buries not only deeper than *H. diversicolor* but also stays in its burrows during the whole tidal cycle (Zwarts and Wanink, 1993). Only for excretion they approach the surface, but as they still stay in the sediment, only larger fish, that can penetrate into the sediment deep and fast enough, can feed on their tail tips as shown for plaice and flounder larger 10 cm (Vlas, 1979). However, the high surface detritus biomass in the salt-marsh creeks, caused by low flow velocities and high productivity, favours surface activity of the benthic fish prey, where it becomes available for the small fishes (Beukema, 1968; Taghon et al., 1980; Netto and Lana, 1997; Friese et al., 2020a; Chapter 3).

H. diversicolor can switch between multiple feeding techniques. When high amounts of organic matters are suspended in the water column, as in sandy areas with high turbulence, it remains – save from predators – in its burrows and performs suspension feeding (Esselink and Zwarts, 1989; Riisgård, 1991). Juvenile *H. diversicolor* can also perform a kind of gardening cultivating bacteria in their burrows and utilize those as food resource (Olivier et al., 1995 cited in Scraps, 2002; Lucas and Bertru, 1997). When the sediment surface offers more prey, which is the case at low flow velocities and hence in the salt-marsh creeks, they leave their burrows for deposit feeding, scavenging or active predation (Fauchald and Jumars, 1979; Reise, 1979; Esselink and Zwarts, 1989). However, at a certain predator density, olfactory cues keep them from crawling on the surface (Schaum et al., 2013). As fish and crustacean densities were lower in the marsh creeks than in the subtidal (Friese et al., 2020b; Chapter 2), this predator avoidance behaviour is most likely not triggered in the marsh creeks.

Also the clam *L. balthica* has different feeding modes, performing filter feeding at high flow velocities and surface deposit feeding at low flow velocities (Peterson and Skilleter, 1994). The largest biomass of clams is inaccessible for the small fishes utilizing the salt-marsh creeks, because of burrowing depth and protecting shells. However, when clams, such as *L. balthica*, extent their siphons to vacuum up deposited detritus or benthic diatoms on the sediment surface, the small fish can tear off the upper parts of the siphons (Peterson and Quammen, 1982; Peterson and Skilleter, 1994). This feeding strategy of fish was observed in various studies (e. g. Peterson and Quammen, 1982; Currin, 1984 cited in Currin et al., 1984; Kuipers et al., 1986; Irlandi and Mehlich, 1996). Siphons of *L. balthica* are for example a dominant component of the diets of 0-group plaice (*Pleuronectes platessa*; Vlas, 1979; Kuipers et al., 1986), which occurred abundantly in early summer in the marsh creeks (Friese et al., 2020b; Chapter 2). Siphon cropping decreases the efficiency of surface deposit feeding (Kamermans and Huitema, 1994; Peterson and Skilleter, 1994). *L. balthica* can regenerate its siphon (Trevallion, 1971), but frequent attacks shorten the siphon and increase the probability of suspension feeding, which makes the bivalve less accessible for fish. A shorter flooding period reduces probably predation pressure on *L. balthica* in salt-marsh creeks compared to the subtidal, increasing the probability of surface feeding and, hence, the accessibility for small fish.

The mud shrimp *C. volutator* is another prey species with a high surface activity, that probably increases its vulnerability to visual predators. This was hypothesized by Magnhagen and Wiederholm (1982a), who found that *C. volutator* was the predominant prey of common gobies on the Swedish west coast. *C. volutator* feeds while sitting in its burrows and scraping food from the sediment surface with its second antennae (Meadows and Reid, 1966). When feeding spots are depleted it leaves its burrows and swims to new spots, where it burrows and start feeding on the surface. But also high densities of its potential predator *H. diversolor* can force *C. volutator* to leave an area (Rönn et al., 1988). Although *H. diversicolor* might not be an important predator of *C. volutator*, it destroys their burrows and disturbs them to establish new ones (Òlafsson and Persson, 1986; Jensen and André, 1993). A contact between the two species can even trigger an immediate escape reaction of *C. volutator* (Òlafsson and Persson, 1986). As the MEZB sampling locations in the marsh contained high densities of *H. diversicolor*, this might be an explanation why we found almost no *C. volutator* there. In the stomachs of three-spined stickleback and the two goby species also fresh *C. volutator* were found indicating that this prey was consumed in the marsh creeks. However, the analysed salt-marsh creeks are geomorphologically highly diverse and there might exist patches of *H. diversicolor* as well as patches of *C. volutator*. Our MEZB sampling focused on a temporal comparability and not a full spatial coverage of the creeks. Thus, to verify whether *C. volutator* is abundant in the marsh creeks and was consumed within this habitat type, further research on such small scale patterns is needed. All three omni- and benthivore predators consumed *C. volutator* in winter and spring (December to April) but not in summer (May to October) in the salt-marshes. This could be caused by temperature dependent activity patterns. The surface activity of *H. diversicolor*, *L. balthica*, and *C. volutator* decreases with decreasing temperature (Evans, 1987). In winter, when air temperatures are cooler than water temperatures, the sediment surface warms up with the tidal flooding. *C. volutator*, burrowed on the sediment surface, may become more active to use the flooding time frame for feeding, while being undisturbed by *H. diversicolor*, which is buried deeper in the sediment and thus probably recognises the increasing temperatures later during flooding.

Beside variable activity patterns endobenthos densities on tidal flats generally peak in summer and are lowest in winter (Dales, 1951; Beukema, 1974; Zwarts and Wanink, 1993). In the salt-marsh creeks this seasonal abundance pattern did not occur, by contrast polychaete abundance and polychaete and *C. volutator* consumption by the small fishes were highest in winter. Additionally in naturally ungrazed salt-marshes terrestrial prey, namely *O. gammarellus*, adds to the diets of the small fishes (Laffaille et al., 1998; Laffaille et al., 1999; Laffaille et al., 2000b; Joyeux et al., 2017; Friese et al., 2018a; Chapter 5). Consequently, salt-marsh creeks seem to be especially valuable feeding habitats during winter. Furthermore, the benthic living harpacticoid copepods were consumed by all four predators more frequently in the cooler month from December to May but similarly in both habitat types, the salt-marsh creeks and the subtidal. We assume that this pattern is not caused by the seasonal temperature, but by the higher turbulence in those months (Friese et al., 2020a; Chapter 3), that cause the harpacticoid copepods being resuspended in the water column and mixed more than in the summer season with the zooplankton, that was as well more frequently consumed in those windy months.

Fish diets

The diets of the three-spined stickleback, the common goby and the sand goby indicate a highly opportunistic feeding strategy (Pihl, 1985; Stevens, 2006). The diets of these three predators in the marsh creeks reflected the seasonal prey availabilities depending on prey abundance, accessibility, detectability, catchability and size (Moore and Moore, 1976b, 1976a). Three-spined sticklebacks are thought to prefer planktonic food, especially in marine offshore habitats (Hislop, 1979; Allen and Wootton, 1982; Ibrahim and Huntingford, 1989b; Lefébure et al., 2014). In freshwater habitats benthic prey and aquatic insects were similarly important as planktonic prey (Ibrahim, 1988; Vorberg and Breckling, 1999). In this study their diet resembles more closely the freshwater than planktivory marine diet, since it was dominated by *H. diversicolor* in the salt marsh and in December and February additionally by the semi-terrestrial *O. gammarellus*. In the subtidal by contrast its diets were dominated by *C. volutator*. This indicates that the three-spined stickleback can adapt relatively fast to spatiotemporal differences in prey availability, and is therefore very flexible in its dietary composition and successful in exploiting temporary and seasonally changing prey resources.

The common goby fed as well predominantly on *H. diversicolor* in the salt-marsh creeks, but also fragments of bivalve siphons, and in March and April *C. volutator* occurred frequently and abundantly in the stomachs. In July and August juvenile gobies (*Pomatoschistus spp.*) populated the marsh creeks abundantly (Friese et al., 2020b; Chapter 2), and contributed to the diets of their cannibalistic adult conspecifics. In 1992 at Meldorf channel (ca. 27 km south-west of our sampling location) del Norte-Campos (1995) observed cannibalism as well, however in negligible quantities. In the analysed marsh creeks in July almost 40 % of the adults consumed juvenile gobies, and although they usually only fed one individual each, common goby density in the marsh creeks was among the highest in that month and juveniles and adults were equally abundant (Friese et al., 2020b; Chapter 2). Thus, here cannibalism could have an impact on recruitment and should be further investigated.

The diets of sand gobies in the salt-marsh creeks were similar to those of the common gobies, but it exploited higher amounts of *C. crangon*, which was also reported by del Norte-Campos (1995) and Behrends et al. (2004). From July to October the sand goby was absent in the marshes, thus in contrast to the common goby no spatiotemporal overlap with the juvenile gobies occurred and cannibalism was not observed. Few individuals fed, however, fish larvae in the marsh creeks from March till April, but this were mainly plaice larvae. Overall, the diet of the sand goby was more diverse than that of the common goby – a pattern that was also found by del Norte-Campos

(1995). Multiple studies reported diets of common goby and sand goby, but differed strongly among each other. Diets of juvenile common gobies and sand gobies of less than ca. 15-30 mm length are dominated by harpacticoid copepods, while the diets of larger gobies shift gradually towards MEZB, including amphipods (gammaridae, *C. volutator*), polychaetes (*Heteromastus filiformis, H. diversicolor*), mysids, *C. crangon*, juvenile shore crabs (*C. maenas*), bivalves (*L. balthica, C. edule*), gastropods (*Peringia ulvae*), and chironomid larvae (Magnhagen and Wiederholm, 1982a; Zander and Hartwig, 1982; del Norte-Campos and Temming, 1994; del Norte-Campos, 1995; Hampel and Cattrijsse, 2004; Leitão et al., 2006). The most important prey for common gobies were either polychaetes (this study; del Norte-Campos and Temming, 1994; Leitão et al., 2006), amphipods (Zander and Hartwig, 1982; Cattrijsse, 1994), or the isopod *Idotea chelipes* (Doornbos and Twisk, 1987). *H. diversicolor* was the preferred prey of the common goby in our study and in Magnhagen and Wiederholm (1982a), by contrast del Norte-Campos (1995) found a negative preference for this prey. The most important prey of the sand gobies were polychaetes and crustaceans, such as *C. crangon*, mysids, and *O. gammarellus* (Kühl, 1961; Evans, 1984; del Norte-Campos and Temming, 1994; Laffaille et al., 1999; Leitão et al., 2006).

Errant polychaetes, such as *H. diversicolor*, are not only more accessible for the small fishes than some sedentaria polychaetes, such as *A. marina*, they also have a higher energy content (errantia: 17.5 kJ / g dry weight, Serrano et al., 2003; sedentaria: 14.19 kJ / g dry weight, Brey et al., 1988; Schückel et al., 2010). Energy contents of bivalves (*L. balthica*, *S. plana*, *C. edule*) and *H. diversicolor* varied around 20.0-22.1 kJ / g AFDW (ash-free dry weight) and 21.8-22.3 kJ / g AFDW, respectively (Martin, 1973 cited in Goss-Custard, 1977; Chambers and Milne, 1979; Zwarts and Wanink, 1993). *C. volutator*, tended to have a lower energy content of 17.44-21.25 kJ / g AFDW (T. Wood in Goss-Custard, 1977; Boates and Smith, 1979; Chambers and Milne, 1979). Energy content of some bivalves decrease in winter and increase in summer, while *H. diversicolor* has a stable energy content year round (Zwarts and Wanink, 1993). Beside the energy content, also the prey size and thus the time and energy invested to consume a certain prey type relative to its total energy content affects the profitability of a prey (Schoener, 1971). The stomachs of the three-spined sticklebacks and the gobies were often already full when containing only one to three undigested individuals of *H. diversicolor* (depending on size), while bivalve siphons and *C. volutator* sometimes did not even fill the stomachs when up to 30 or 20 pieces were consumed, respectively. Thus, *H. diversicolor* might be a relatively profitable prey as lower foraging effort results in a relatively higher energy gain due to its larger size.

Specialization of certain individuals

We hypothesized that the continuously high densities of *H. diversicolor* together with their energy content and size, as well as their errant behaviour could tempt individual fish to specialize on this habitat-specific prey in the salt-marsh creeks (Schoener, 1971). Indeed, some individuals of the three-spined stickleback and the common gobies had not only high shares of *H. diversicolor* in their stomachs, but also in their guts together with a relatively low prey diversity indicating that these individuals fed almost exclusively on *H. diversicolor* for a relatively long time period and, hence, are possibly specialized to feed on this prey type. Milinski (1982) showed in laboratory experiments, that three-spined stickleback learn how to attack a certain prey type and stick to this prey type without deviation even when other more profitable prey types would be available. The training of a certain feeding technique increases catching success and thus maximized their energy intake per time (MacArthur and Pianka, 1966; Milinski, 1982). This specialization seemed to pay off in the salt-marsh creeks as those individuals of three-spined sticklebacks, common gobies and sand gobies that fed higher amounts of polychaetes had also fuller stomach, than their conspecifics that exploited this prey resource less successfully. Such a prey specialization can only be afforded in profitable feeding habitats, while in low quality feeding habitats fish have to take what they can get, thus developing a rather opportunistic feeding behaviour (Schoener, 1971; Piersma and van Gils, 2014). It could be hypothesized that the individuals specialized to the marsh-specific prey, *H. diversicolor*, visit the marsh creeks more frequently than their conspecifics.

Dietary condition

The dietary condition varied strongly between individuals. The amount of consumed prey depends on the boldness of the individual (Jolles et al., 2016) and on the response time an individual needs to approach a detected prey item (MacGregor et al., 2020). The foraging success of schooling three-spined sticklebacks depends on the group organization (MacGregor et al., 2020). Fast fish benefit from disordered groups via reduced competition. On the other hand, the foraging success of low performers increases in highly polarized groups via an information transfer within the group (MacGregor et al., 2020). Hence, stomach contents in highly polarized and ordered shoals, built as a predator avoidance strategy (Pitcher and Wyche, 1983; Godin, 1986), are more homogeneous than in disordered groups. The low predation pressures in the salt-marsh creeks (Friese et al., 2020b; Chapter 2) might be a reason for more heterogeneous stomach contents compared to the subtidal. However, besides being potentially caused by individual diet specialization and low predation pressure, this could also be an effect of the comparably low sample sizes from the subtidal. When sample sizes from the subtidal were similar to those of the marsh for each species and sampling period, the relative stomach content, and thus the short-term dietary condition, was significantly higher in the salt-marsh creeks. In an ad-libitum feeding experiment with the three-spined stickleback Beukema (1968) assessed a stomach content of 5 % of the wet body weight as “well-filled”. The relative stomach contents of three-spined sticklebacks in this study regularly exceeded 5 % in the marsh creeks and many had even relative stomach contents above to 10 %. For common gobies and sand gobies del Norte-Campos and Temming (1994) measured relative stomach contents of ca. 3 to 8 % and 3 to 6 %, respectively, calculated as the percentage of the content of the whole gastro-intestinal tract from the wet body weight (without the ingested food). Due to the different calculation methods a comparison is difficult here as well, but as for the three-spined stickleback, relative stomach contents of the two goby species exceed often 10 % in the salt-marsh creeks indicating a relatively high short-term condition – at least for the majority of individuals. The relative stomach content of herring was in our study in both the salt-marsh creeks and the subtidal mostly above 1 %, while from the Baltic Sea values mainly below 0.4 to 1 % were reported (Möllmann et al., 2004; Ojaveer et al., 2017). Moreover, it can be assumed that the stomach contents of all four predators are underestimated, because – due to the fishing method with fyke nets – the fish remained an unknown time period starving in the net, before the creeks ran dry and catches could be retrieved, processed and finally frozen. The reference samples from the subtidal on the other hand were collected with an active fishing method (beam trawls) allowing the fish being immediately sorted and frozen. Thus, the difference between relatively higher stomach contents in the marsh creeks compared to the adjacent subtidal areas could be more pronounced if this methodological shortcoming would be minimized, e.g. by applying active fishing methods in the marsh creeks and investigating the point in time when different fish species enter and leave the marsh creeks. Although we cannot tell whether the prey in the stomachs was indeed consumed within the salt-marshes, where the fishes were caught, our findings at least coincide with a range of studies finding fuller fish stomachs in salt-marshes than in the subtidal (Rozas and LaSalle, 1990; West and Zedler, 2000; Laffaille et al., 2001; Potthoff and Allen, 2003; Hollingsworth and Connolly, 2006) or fuller stomachs of fish leaving salt-marshes than when entering these habitats (Allen et al., 1994; Laffaille et al., 2001; Hampel and Cattrijsse, 2004; Hollingsworth and Connolly, 2006; Fonseca et al., 2011). Furthermore, the salt-marsh creeks were characterized by a lower predator abundance than the subtidal (Friese et al., 2020b; Chapter 2) and predators can hinder fish from feeding (Krause et al., 1998). Food deprivation can result in a higher relative weight loss in smaller than larger fish, as shown for the three-spined stickleback by Krause et al. (1998). In the experiments of Krause et al. (1998) small fish accepted a higher predation risk than larger fish to avoid starvation. For the same reason three-spined sticklebacks choose smaller shoal sizes when hungry (Krause, 1993). Thus, small hungry fish, for which a fulfilment of their energy demands is disproportionately more important, can especially benefit from the salt-marsh creeks with its abundant food resources and low predator and competitor density.

The long-term dietary condition (K_n and HSI) tended to be similar for all four fish species between the salt-marsh creeks and the subtidal. In those timeframes, in which it differed between the two habitats, both long-term dietary condition indices tended to be lower in the marsh than in the subtidal. This could mean, that the same population was sampled inshore and offshore, and fish from both locations migrate between similar habitats. As the marsh creeks run empty during low tide, fish migrate towards the subtidal. Thus, either the fish from the marsh visited the marsh creeks only occasionally, so that the higher relative stomach contents had only a short-term effect, or the fish from the subtidal visited the marsh creeks (or another not sampled profitable habitat) as well. A comparison of the long-term dietary condition with the literature is problematic as different studies use different calculation methods (Peig and Green, 2009; Băncilă et al., 2010; Peig and Green, 2010). One of the oldest and most commonly used indices is Fulton´s K (in which $k = 1$ and $b = 3$ in Eq. 4.3; Heincke, 1908; Ricker, 1975). However, Fulton´s K is size-dependent (Băncilă et al., 2010) and thus unsuitable when dietary conditions of fishes of different size classes are compared, as in this study, where e. g. herrings were smaller in June than in December (see also Friese et al., 2020b; Chapter 2). Furthermore, studies differ in the use of the body weight W_i; some exclude only the stomach content, so that the condition index varies with gonad maturity or gut contents, others do not define W_i at all. Although the long-term dietary condition tended to be lower (if at all) in the marsh creeks than in the subtidal a possible explanation could be found in the study of Külling and Milinski (1992). They found that three-spined sticklebacks with a good dietary condition venture closer to predators than those in a bad condition, probably because the latter have less energy reserves to escape in case of an attack (Külling and Milinski, 1992). Thus, fishes with a relatively low dietary condition could possibly be more obliged to leave the predator-rich subtidal with the rising flood finding their way to the predator-poor salt-marsh creeks at the upper edge of the intertidal zone (Friese et al., 2020b; Chapter 2).

Diet competition

The intra- and inter-specific diet overlap tended to be higher in the salt-marshes than in the subtidal due to the predominance of polychaetes and frequently occurring harpacticoid copepods in the stomachs. Since Wadden Sea salt-marsh creeks are a relatively extreme environment (Friese et al., 2020a; Chapter 3), they only accommodate few prey species in high abundances. Thus, the rather opportunistic predators shared more likely the same prey resources. By contrast, fish from the subtidal may have migrated between different habitat patches with different prey resources, and hence have a higher probability for more diverse diets. Despite the relatively high diet overlap, we found no indications for diet competition. We hypothesized, that in case of resource competition, (1) the relative stomach content weight would decrease with increasing diet overlap with potential competitors, (2) the relative stomach content weight would decrease with increasing predator density, and (3) the proportion of a prey type in the stomachs would increase with prey density indicating limited availability at low densities.

First, the diet overlap with potential competitors did not limit the food consumption of each. On the contrary, the relative stomach content weight increased with increasing diet overlap, possibly because fuller stomachs tend to contain more different prey types. Second, the predator density was – except a few hauls – low and did not affect the relative stomach content weight. Third, herrings and three-spined sticklebacks increased their consumption of planktonic prey, particularly copepods, with increasing prey density, indicating that planktonic prey was limited during some sampling periods. By contrast, benthic prey densities and proportions in the stomachs did not correlate, indicating that benthic prey was not limited. Summarizing the results, diet competition in the salt-marsh creeks is low, especially for the marsh-specific benthic prey resources. However, planktonic prey resources, which can be exploited during the whole tidal cycle and in various habitats, can be limited seasonally with an increased potential for competition.

The potential competition between the common goby and the sand goby has been repeatedly examined. Pihl (1985) measured a high diet overlap between the two species concluding a high diet competition among them, but did not estimate predator and prey abundances. Edlund and Magnhagen (1981) concluded by contrast, that the two species avoid small scale competition by food segregation, but that the common goby was suppressed by the sand goby. To avoid its competitor the common goby was forced to occupy shallower areas (Magnhagen and Wiederholm, 1982b). Our study indicates that the relation of competitive strength is reversed in the shallow salt-marsh creeks. Here by contrast to the common goby, the sand goby seems less efficient in exploiting the most profitable prey resource, *H. diversicolor*, visiting this habitat less frequent and less abundant, and thus retreats to the subtidal.

Prey limitation is usually analysed via the exploitation efficiency, that is the food consumption divided by the prey production (Tableau et al., 2019). In this study a calculation of prey production using production/biomass ratios (P/B ratios) from the literature was not applicable, because – due to logistic and financial limitations – prey biomass could not be measured and prey densities could not be converted into biomass as sizes differed considerably during seasons (pers. observation). For an analysis of potential prey limitation, we calculated a hypothetical worst case scenario assuming that each predator would only consume one prey type and then computing the percentage fraction consumed within each tide. This methodology is not suitable to quantify prey limitation, but to test the hypothesis that prey availability is limited. In case the fish could only consume minor fractions of the prey resources in the salt-marsh creeks, despite the hypothetical scenario of a maximum predation pressure, a prey limitation would be highly unlikely. From the total prey abundances in the creeks on average 0.24 % of the bivalves, 0.27 % of the polychaetes and negligible fractions of the harpacticoid copepods could be possibly exploited per tide by the four predators under the worst case scenario. Planktonic prey, such as *Temora spp.*, other copepods and barnacle cypris larvae could be exploited by much higher fractions ranging from 1 to 231 % of the total abundance in the marsh creeks per tide. This indicates that a prey resource limitation of benthic prey is less likely than of planktonic prey, but to classify, whether the consumed fractions of the prey resources in the creeks per tide are low or high, P/B ratios of the prey types must be considered. Although P/B ratios differ with body mass, longevity, location, and temperature (Banse and Mosher, 1980), values from the literature can help to assess whether prey resources in the salt-marsh creeks are limited in relation to the consumed fractions. Annual P/B ratios of the most common North Sea copepods range from 2.5 to 14 (Fransz et al., 1991), meaning that the biomass is replaces 2.5 to 14 times per year, i. e. every 26th - 146th day. Thus, the consumption of copepods by the four analysed predators could exceed the production, potentially leading to prey limitation and competition. Annual P/B ratios of bivalves and polychaetes were lower, e. g. 0.75 for *S. plana* (Banse and Mosher, 1980), 2.07 for *L. balthica* (Chambers and Milne, 1975b), and 3.0 for *H. diversicolor* (Chambers and Milne, 1975a), meaning that the biomass of bivalves (*S. plana*, *L. balthica*) and polychaetes (*H. diversicolor*) is replaces every 176th – 487th day and 122nd day. Ignoring production, exploiting 100 % of the bivalve and polycheate resources in the salt-marsh creeks would take the four predators 416 tides (ca. 207 days) and 370 tides (ca. 185 days), respectively. As the biomass of bivalves and polychaetes is replaced within this time frame, even when assuming a maximum predation pressure, the four predators would not be able to deplete the bivalves and polychaetes in the marsh creeks.

Indeed, benthic prey resources are probably even more unlimited, because the hypothetical scenario most likely overestimates predation pressure. Predation of the small fish on bivalves is non-lethal as they mainly crop the siphons, which can be regenerated (Trevallion, 1971), thus they unlikely affect the bivalve population sizes. Although not all potential competitors using the same prey resources could be included in the analysis, e. g. other fish species, crustaceans, such as *C. crangon*, and wading birds, the salt marshes offer also many more prey resources, such as *C. volutator*, fish larvae, mysids, *C. crangon* and *O. gammarellus*, that were not included in the hypothetical scenario. As fish use also these other prey resources and not all individuals are able to fill their stomachs up to the maximum, diet competition is likely more relaxed. During low tide wading birds could feed on the same benthic prey resources in the salt-marsh creeks as used by fish. However, we observed their footprints only rarely in the marsh creeks. Salt-marsh creeks could possibly be dangerous feeding grounds for wading birds, because the marsh edge reduces the bird´s view to a few meters. Thus, it might notice mammalian and avian predators relatively late compared to the tidal flats, where they are save from mammalian predators and can detect avian predators from hundreds of meters (Piersma et al., 1993). Hence, also competition with wading birds is probably of minor importance, though further investigations would be necessary to assess bird foraging in salt-marsh creeks. To sum up the diet competition analysis, fish visiting German Wadden Sea salt marshes could not control the habitat-specific benthic prey due to the limited access time and the unlimited prey availability.

Compared to the subtidal, prey availability was rather high, predator density rather low, and predator body size rather small, meaning that they could only ingest small amounts of prey – and finally the access time was limited by the tides. However, also the Wadden Sea tidal flats can provide excess food availability (Reise, 1979; Zander and Hartwig, 1982). Supply of excess amounts of food in salt marshes was also described by Kneib and Stiven (1982), Kneib (1982a, 1986), and Hampel et al. (2005), while on the other side, Vince et al. (1976) and Sardá et al. (1998) reported that nekton had the ability to control the abundances of their prey in salt marshes. As predator and prey densities vary spatiotemporally, also the feeding habitat quality of a specific habitat type, such as salt marshes, can differ between geographical regions. Therefore, it was important to analyse the feeding habitat quality of Wadden Sea salt marshes, that differ in their geomorphology, flooding dynamics, vegetation, and nekton and its prey, from well-studied salt marshes in the US (Cattrijsse and Hampel, 2006). But even within the salt-marsh creeks, the rich food availability and low competition is not equally distributed. The species composition of the benthic infauna appeared homogenous, but the local abundance varied within the small-scale topographic differences of the creeks. In the creek centre, where flow velocities are highest, and on the upper creek banks, where submergence time is shortest, MEZB densities were lower than on the creek slopes, which also account for the largest area shares. Hampel et al. (2009) found small-scale differences in the benthic macrofauna communities and abundances between marshes and among different creek sizes. In the confined salt-marsh creeks the well-known tidal zonation of benthic infauna distribution patterns (Kneib, 1984; Ysebaert et al., 2003; Schückel et al., 2013) is squeezed into a few meters. Thus, salt marshes consist of a mosaic of multiple microhabitats providing differing conditions. Further research on these small-scale habitat patterns within the salt marshes could provide valuable information for restoration projects.

Conclusion

The findings of this study demonstrate, that the bare and unvegetated salt-marsh creeks are a valuable feeding habitat for small fish, predominantly because the high benthos density, particularly *H. diversicolor*, relaxes the diet competition between fish. Salt marshes are part of the habitat mosaic of the seascape (Nagelkerken et al., 2015) and thus the good feeding conditions in the analysed salt-marsh creeks can also relax diet competition in adjacent habitats via spatial segregation (this study, Friese et al., 2018a, 2020a; Chapter 3 and 5). When the creeks run dry during low tide the small fish have to migrate back to the subtidal, where the probability of predator encounter is increased. However, as they have already satisfied their nutritional demands in the marsh creeks, they can be more cautious on avoiding and escaping predators in the subtidal, hence, benefiting from the temporal use of the marsh creeks during the whole tidal cycle. Our results indicate that for three-spined sticklebacks and common gobies the high densities of *H. diversicolor* in the marsh creeks could be an attraction. It is still unknown whether fish visit the same Wadden Sea salt-marsh creeks repeatedly and actively decide to enter the marsh creeks. But they can learn how and where they get successfully food (Milinski, 1982; Ioannou et al., 2015), remember profitable habitats (Green et al., 2012) and orientate in space. Although the tidal cycle limits the temporal accessibility of the salt-marsh creeks, this limited temporal accessibility limits also the prey exploitation and hence promotes high prey densities. Therefore, the limited temporal accessibility could be simultaneously a key factor for the high quality as feeding habitats for fish. This study could reveal that the salt-marsh creeks offer unlimited benthic prey resources for small fishes. Large areas of this feeding habitat for fish were lost in the past due to coastal protection measures. Protecting and promoting the development of larger salt-marsh areas with accessible and regularly flooded creeks would not only benefit the coastal protection as wave height is reduced with increasing marsh width (van Loon-Steensma, 2015) but also the nektonic fauna via an increased foraging habitat area and a longer accessibility time. These features of salt marshes could be enhanced by restoring the marsh creeks towards large, long, and deep creeks that are easily accessible for fish coming from the subtidal.

5

Grazing management affects fish diets in a Wadden Sea salt marsh

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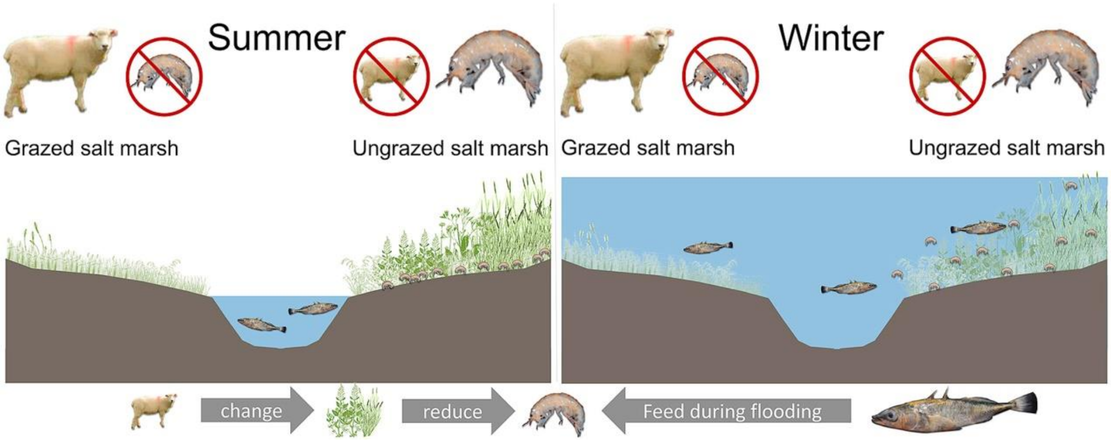


Abstract

Salt marshes provide favourable feeding conditions for fish thanks to a variety of food sources including terrestrial prey, which can be negatively affected by livestock grazing. We evaluated the seasonal effect of sheep grazing on fish diets in a Wadden Sea salt marsh. Consumed quantities and frequencies of terrestrial prey differed between predators. While terrestrial prey was unimportant for herring and sand goby, common goby and three-spined sticklebacks consumed it immediately during winter, when it became available through marsh flooding. In contrast to the relative stomach content weights, the stomachs content compositions differed between grazing treatments. Sticklebacks consumed terrestrial prey more often and in higher amounts in the ungrazed than in the grazed marsh. Using random forest models, the importance of grazing management for fish compared to other influencing factors was analysed based on sticklebacks. Its most important terrestrial prey was the energy-rich and probably easy to catch amphipod *Orchestia gammarellus*. Both the ratio of fishes feeding on *O. gammarellus* and the consumed amount of Orchestia depend mainly on the accessibility, determined by the flooding height and duration. The abundance of *O. gammarellus* was the second most important factor determining its consumed amounts. *O. gammarellus* densities are significantly reduced by sheep grazing. Therefore, sheep grazing has a negative impact on fish feeding opportunities in winter, when marine prey on the tidal flats is scarce. To improve the feeding habitat value of Wadden Sea salt marshes for fish it is advisable to keep lower elevated marshes with large creeks ungrazed.

Introduction

At the interface between land and sea in temperate areas, intertidal salt marshes represent an extreme and challenging but also very productive environment for many organisms, including fish (Lefeuvre et al., 2000; Beck et al., 2003). With the incoming tide fish enter the marsh to feed and to find temporary shelter from predators within the complex salt marsh structures (Boesch and Turner, 1984). This utilization pattern has been observed in marshes around the globe, with good feeding conditions being the prime benefit (e.g. Allen et al., 1994; West and Zedler, 2000; Hollingsworth and Connolly, 2006; Fonseca et al., 2011). In open coastal marine areas fish can feed on other fish, zooplankton and benthos. These prey sources are also available in salt marshes, where terrestrial invertebrates add to the prey spectrum available to the fish, when the vegetated marsh surface is flooded during winter storm floods or the terrestrial organisms accidently fall into the creeks (Laffaille et al., 2000b; Whitley and Bollens, 2014).

The availability of prey, like e.g. terrestrial prey in salt marshes, depends on (1) its catchability, (2) its accessibility and (3) its local abundance. Analogously to the concept of “catchability” in fishery biology (Arreguín-Sánchez, 1996), we define “catchability” as the ability of the predator to detect, to catch, to ingest and to digest the prey. This ability depends on the morphology, physiology and behaviour of both prey and predator and is therefore species dependent. While the catchability of terrestrial prey is species-specific and the accessibility depends on the water levels, the abundance of terrestrial invertebrates is closely linked with livestock grazing (Meyer et al., 1995; Laffaille et al., 2000b; van Klink et al., 2013).

Coastal areas in general and salt marshes in particular are subject to a wide variety of anthropogenic stressors (Green and Short, 2003; Lotze et al., 2005; Gedan et al., 2009). The salt marshes in the Wadden Sea along the Dutch, German and Danish North Sea coast rank among the most severely modified marsh systems worldwide (Essex County Council, 2010). Land reclamations along the entire Wadden Sea coast lasting for centuries have left only a narrow band of salt marshes which are cut off from the hinterland by dikes (Airoldi and Beck, 2007; Esselink et al., 2009; Gedan et al., 2009). In the Middle Ages salt-marsh creeks were dredged and straightened for quick drainage of the dike foot, while the vegetated marsh surface was used for livestock grazing since the Neolithic (Bakels and Zeiler, 2005, cited by Esselink et al., 2009; Knottnerus, 2005). With the establishment of the Wadden Sea National Parks, dredging was reduced and livestock grazing decreased in the German marshes (Bakker et al., 2003; Stock, 2003). The consequences of livestock grazing on e.g. sedimentation (Andresen et al., 1990; Nolte et al., 2013), plants (Andresen et al., 1990; Kiehl et al., 1996; Kleyer et al., 2003), arthropods (Andresen et al., 1990; Meyer et al., 1995; Rickert et al., 2012; van Klink et al., 2013) and birds (van der Graaf et al., 2002; Bos et al., 2005; Erb, 2012; Mandema et al., 2013) have been well studied, while research on its effects on fish is rare. Juvenile sea basses (*Dicentrarchus labrax*) in Northern France had emptier stomachs in sheep-grazed than in ungrazed marshes due to grazing effects on their main prey, the semi-terrestrial amphipod *Orchestia gammarellus (Orchestia* hereafter). By contrast in salt marshes in Western France, the diets of sea basses were unaffected by grazing, although *Orchestia* abundance was reduced in the grazed marsh as well (Joyeux et al., 2017).

Of all European salt marshes 20 % are located in the Wadden Sea area (Doody, 2008). It is virtually unknown if and which fish occur the German Wadden Sea salt marshes and, at the European scale, how valuable tidal marshes are for fish (Cattrijsse and Hampel, 2006). To fill this gap, we investigated the value of intertidal salt-marsh creeks in the Schleswig-Holstein Wadden Sea, Northern Germany, as feeding habitat for fish. According to our concept of prey availability, we hypothesized that different fish species found in the creeks would differ in their use of terrestrial prey with respect to season and grazing treatment (grazed or ungrazed).

Material and Methods

Study area

Samples were collected in salt marshes at Ehstensieler Plate in Schleswig-Holstein, Germany, ca. 9.5 km west of the mouth of the river Eider (Fig. 5.1). With a salinity range of 25.8-39.1 and a mean tidal range of 3 m (BSH, 2014), conditions are quasi-marine rather than estuarine. Four intertidal creeks were sampled, two of which drain an intensely sheep-grazed marsh (*G1* and *G2*), the other two drain an ungrazed marsh (*U1* and *U2*). The creeks *G1*, *G2*, *U1* and *U2* were 520 m, 803 m 858 m and 11190 m long with watersheds of 0.067 km², 0.093 km², 0.117 km² and 1.066 km², respectively (Fig. 5.1, Tab. 5.2). Watershed area was calculated using *r.watershed* in GRASS GIS 7.2.0, with a threshold of 1000. The creeks are flooded for approximately 6h per tide and empty completely during low tide. The vegetated marsh surface is only flooded during storm floods. The geographical and morphological differences between the salt marsh creeks can influence species distribution and interactions (Allen et al., 2007; Jin et al., 2014). We used a combined approach of prey abundance measurements, stomach-content analyses and modelling of the importance of multiple influencing factors to address the site-specific differences between grazing treatments.

Sampling and sample processing

Fishing

Monthly sampling took place from March 2015 to February 2016, except in November 2015 and January 2016, when sampling was impossible due to storm and ice, respectively. Following Dänhardt et al. (2011a), campaigns were scheduled around spring tide when water levels and intertidal range were highest. Fish were caught using fine-meshed (6 mm) fyke nets of 1.5 m (*G2* and *U2*) and 1.0 m (*G1* and *U1*) height, depending on creek size (Supplement C, Fig. C.1). At low tide, the fykes were placed mid-creek near the creek mouth covering less than half of the creek width. This way fish could enter with the incoming tide and were caught with the outgoing tide. Fykes were emptied at low water. During spring tide, low water was in the morning and in the evening, yielding clearly separated day and night catches, allowing addressing diurnal differences in habitat use and feeding dynamics. Catches were sorted by species, weighed to the nearest g, measured to the mm standard length below, and frozen at -20 °C immediately afterwards.

Stomach-content analyses

In the laboratory, stomach contents were examined of fish species frequent and abundant enough to ensure a sufficient sample size across seasons. These were three-spined stickleback (*Gasterosteus aculeatus*, stickleback hereafter), herring (*Clupea*

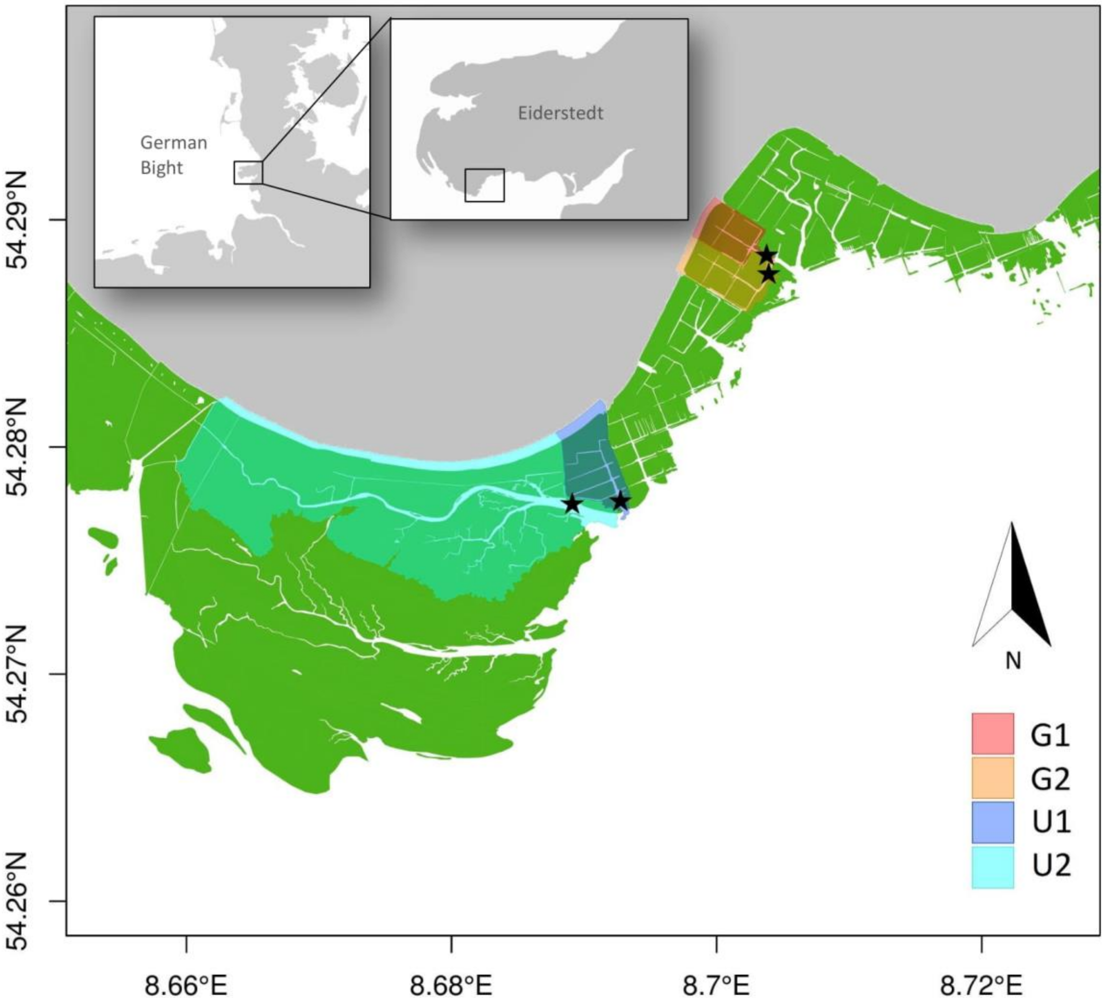


Fig. 5.1: Location of the analysed salt marsh with spatial extent of the watersheds of each of the four marsh creeks in the grazed (red = G1, orange = G2) and the ungrazed (dark blue = U1, light blue = U2) marsh. The positions of the fyke nets are indicated as black stars.

harengus) and common goby (*Pomatoschistus microps*). Although less abundant, sand gobies (*Pomatoschistus minutus*) were also considered for comparison with the common goby. Despite its abundance, Nilsson´s pipefish (*Sygnathus rostellatus*) was neglected for stomach analyses, because, due to its morphology the standard dissection procedure was not applicable, which would result in an incomparable relative stomach-content weight (see below). When possible, a random subsample of 10 individuals per haul and species with similar size ranges was selected from the four fish species for analysis (Supplement C, Tab. C.1).

After slow defrosting on ice, individual fishes were re-weighed to the nearest mg, re-measured to the mm standard length below and dissected using precision tweezers, microscopy scissors and scalpels. Gutted fish and stomachs were immediately weighed. Prey digestion progresses with intestine transit time. Increased digestion biases stomach fullness estimates and reduce prey identification accuracy. Therefore only the stomachs and not intestines were utilized for further analyses. The gastrointestinal tract of gobies is not divided by a sphincter into stomach and gut (Andersen, 1984), though it builds two loops (Jaroszewska et al., 2008). The first loop functions as a bottleneck – almost similar like a sphincter. Hence, we defined the anterior intestine from the oesogaster to the first loop as the stomach. Stomach content was calculated as the wet weight difference between full and empty stomach. Prey items were identified to lowest possible taxonomic level. The volume percentage composition of prey items was visually estimated as most of the prey items were too small or too digested to be weighed. Percentage composition of prey items was converted into prey weight using the weight of the total stomach content.

Prey density

The abundance of terrestrial invertebrates as potential fish prey was estimated using pitfall traps, which were set up in transects of five per creek close and parallel to the creek edge. Although pitfall traps measure activity rather than absolute abundance, they were shown to reliably approximate abundance per area (Mantzouki et al., 2012).

Traps were filled with a saturated salt solution (300 g sea salt/ L fresh water) and placed for three days in the marsh. After collection samples were preserved in 4 % borax-buffered formaldehyde fresh water solution until identified and counted in the laboratory. We classified the caught organisms to the same taxonomic levels like the terrestrial prey items identified in the fish stomachs, ranging from species to class. Although salt solution is a poor preservative (Aristophanous, 2010), it was chosen due to its harmlessness to the environment in case of flooding. We assume that this uncommon preservative did not affect the results, because its preservation qualities were sufficient to match up to the digested prey items in the fish stomachs, and because sea salt occurs naturally in the salt-marsh environment and is therefore – in contrast to e.g. formaldehyde – unlikely to act as an attractant or repellent to certain arthropods, ensuring a randomized sampling of all species. Densities of terrestrial arthropods were likely underestimated in March, May, December and February, when some pitfall traps were flooded. Flooding terminates the trapping and can even flush organisms out of the trap. As flooded samples still give us information about the minimum abundance, we did not exclude them.

The abundance of macroendozoobenthos was estimated in each creek with five replicates of randomly selected benthos cores (20 cm deep, Ø 9 cm) located approximately in the middle between the waterside and the line of maximum flow velocity. Samples were sieved in the field on a 500 µm mesh and taxonomically classified with the unaided eye, because this was sufficient to identify the benthos organisms to the same taxonomic level like the ones found in the fish stomachs. The number of individuals was counted or visually estimated, when numbers exceeded ca. 50 individuals or samples contained amounts of litter, that hampered accurate counting.

A detailed taxonomic identification of rarely occurring prey species, especially of those that were not found in the fish stomachs, was considered redundant for our research questions. With regard to the stomach contents, we limited our results to the most important prey types for fish, which are *Orchestia* as terrestrial prey and polychaetes as endobenthic prey.

Data analyses

Cumulated tidal flooding volume

The size and duration of habitat available to the fish was estimated using a cumulated tidal flooding volume index (CTFV) per creek and tidal cycle. The CTFV is defined as the sum of the water volume within the watershed of each creek (Fig. 5.1) per 30 min time step. These were derived from site-specific water levels and digital elevation model (DEM) based on aerial laser scanning (courtesy of *Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein*). The DEM resolution is 1 m² and elevation accuracy is 15 cm. Water levels were logged every 5 minutes in each creek close to the fyke positions (Cera-Divers D1702 combined with a Baro-Diver D1500, Schlumberger Water Services).

Fishing effort

Absolute fish numbers per haul were standardized to water volume. Runoff water volume per 30 min time step was calculated between high tide and the time catches were retrieved by using the site-specific water levels and the DEM (see 2.3.1. Cumulated tidal flooding volume). The fished portion of the flooded creek profile area per time step was identified using water levels, fyke opening width and the creek profile, which was measured with a laser distance meter (Leica DISTO^{TM} X310). The fished profile area percentage share was used to calculate the fished percentage of the runoff water volume per time step. The fished water volumes run off during each time step were then summed up, yielding the fished water volume per haul used to express catch per unit effort (CPUE) as the number of fish per m³ water volume filtered by the fykes.

Stomach contents

To approximate short-term dietary condition (a. k. a. nutritional condition or body condition), we used (1) the ratio between the weights of the stomach content and gutted body weight of the whole fish (Hyslop, 1980; Dänhardt et al., 2007; Pasquaud et al., 2007; Berg et al., 2011), per prey type as well as the entire stomach content, and (2) the relative share of empty stomachs. To check for differences in those dietary condition indices between grazed and ungrazed marshes as well as between day and night, we performed Wilcoxon rank sum tests with continuity correction, because data were not normally distributed. The dependence of the number of fishes with or without terrestrial prey on the grazing treatment, was checked using the Pearson's Chi-squared test with Yates' continuity correction based on a 2 x 2 contingency table.

Fishes with empty stomachs or those containing mucus only were included in all presence-absence analyses, because an empty stomach also verifies the absence of a certain prey. In quantitative prey composition analyses we excluded those empty stomachs, because they do not deliver relevant information in that context (stickleback: 25, 6.3 %; common goby: 117, 19.3 %; sand goby: 13, 13.0 %; herring: 75, 35.9 %).

Following Costello (1990), the integrated representation of frequency and quantity of consumed prey types was calculated from the frequency of occurrence (Hynes, 1950; Hyslop, 1980) and the biomass share of each prey type, the latter being given by

$$\%\,biomass_i = \frac{\sum S_i}{\sum S_t} \times 100 \qquad \text{(Eq. 5.1)}$$

where S_i = relative weight of prey i and S_t = total relative stomach-content weight of all fishes from the haul (Amundsen et al., 1996). The seasonal importance of different prey types for the stickleback was visualized by means of Costello plots (Costello, 1990) including modifications by Amundsen et al. (1996), where S_t was restricted to those fishes with prey i in their stomachs. The modified Costello plots show, how many fishes (x-axis) eat how much of a certain prey type (y-axis).

Prey density

Differences in prey abundances between the grazed and the ungrazed marsh were visualized using boxplots and analysed using Wilcoxon rank sum tests with continuity correction. Seasonal differences in prey abundances were analysed using Kruskal-Wallis rank sum test and Dunn´s Post-hoc test with the Benjamini-Hochberg adjustment, which was performed with the R-package ‘dunn.test’ version 1.3.5 (Dinno, 2017).

Statistical approach to quantify the importance of the grazing effect

Stickleback occurred frequently and abundantly year around, consumed the highest amounts of terrestrial prey and would, thus, be suitable for investigating and quantifying grazing effects on prey availability for fish. Therefore, we chose this species as a model organism. On the prey side, we restricted our analyses to adult *Orchestia*, which was the dominant terrestrial prey for the stickleback both in frequency of occurrence and in the biomass amounts in the stomachs.

A random forest (RF) classification model based on presence-absence of *Orchestia* in the stickleback stomachs was used to analyse under which conditions stickleback consume *Orchestia*. In a second step, a RF regression model was used to identify factors determining the amount of *Orchestia* consumed by stickleback.

RF models have several advantages over other methods. They are nonparametric, they can deal with both small sample sizes and large numbers of predictor variables (Cutler et al., 2007) and they do not overfit the data (Breiman, 2001).

Both models were started with all available predictor variables: (1) grazing treatment (grazed vs. ungrazed), (2) creek (G1, G2, U1, U2), (3) month, (4) day / night, (5) air temperature, (6) cloudiness, (7) precipitation, (8) sun shine hours, (8) humidity, (9) wind velocity, (10) wind direction, (11) cumulated tidal flooding volume (CTFV) and (12) mean *Orchestia* abundance per pitfall trap (caught numbers within three days). The predictor variable (13) standard length was only used in the RF classification model, that was based on individual fishes. Hourly open access meteorological data were provided by the Climate Data Center of Deutscher Wetterdienst (access date: 25.08.2016). Quality proofed historical data of the weather station “Sankt Peter Ording” (station-ID: 4393) were chosen. The weather station is located at 54°19'40.44" N and 8°36'10.80" E and is at 7.9 km distance from the sampling area. Over each fishing time period precipitation height and sun shine duration were summed and air temperature, cloudiness, humidity, wind velocity and direction were averaged. Further details on measurement methods and devices are given in the online descriptions (Deutscher Wetterdienst).

For the RF classification model, each of the 394 stickleback stomachs (including empty stomachs) was assigned presence or absence of *Orchestia*. The full RF classification was based on 1500 decision trees with a subset of 3 variables at each split. Creek, month, wind velocity and the CTFV index were most important for presence or absence of *Orchestia* in stickleback stomachs and resulted in an optimal model fit with lowest number of variables (Murphy et al., 2010). Thus, they were selected for the final model using a seed value of 1234. The final classification model was performed with 1000 trees and a subset of 2 variables per split. Cross validation was performed with 99 iterations.

For the RF regression model, stomach-content data (excluding empty stomachs) were aggregated per haul containing at least five sticklebacks (40 hauls, including 349 sticklebacks) to control for zero inflation and because predictors were also only at haul level. Percentage biomass of consumed *Orchestia* per haul was used as response variable (Eq. 5.1). The full regression model with 5000 trees and 4 variables at each split yielded mean *Orchestia* abundance, the CTFV index, month, and wind velocity as predictors to be used in the final model, for which 1000 trees were sufficient with a subset of 2 variables per split. Like in the RF classification model a seed value of 1234 was used.

Data processing

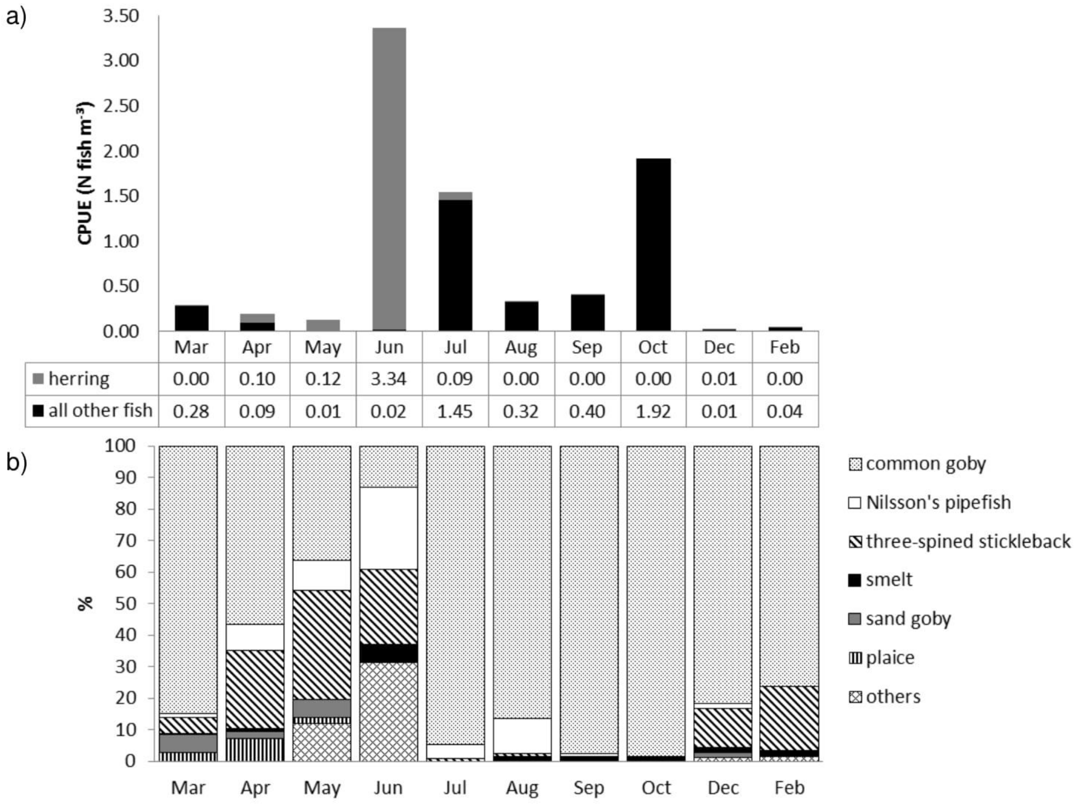
The data were analysed in R version 3.4.1 (R Core Team, 2017). The map (Fig. 5.1) was processed using shapefiles of the salt marsh mapping in 2012 by the Trilateral Monitoring and Assessment Programme (TMAP) (courtesy of *Landesbetrieb für*

Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein) and the R packages ‘maps’ version 3.2.0 (Becker and Wilks, 2017), ‘mapdata’ version 2.2-6 (Becker and Wilks, 2016) and ‘rgdal’ version 1.2-8 (Bivand et al., 2017). Fig. 5.2 and Fig. 5.3 were prepared using Microsoft Excel 2010. Fig. 5.4 and Fig. 5.5 were prepared using the R package ‘ggplot2’ version 2.2.1 (Wickham, 2009). The 3D plot (Fig. 5.6) was generated using the R package ‘plot3D’ version 1.1.1 (Soetaert, 2017). The RF models were performed using the R package ‘randomForest’ version 4.6-12 (Liaw and Wiener, 2002), which was also used to plot the variable importance (Fig. 5.7). For model selection and validation we used the R package ‘rfUtilities’ version 2.1-0 from Evans and Murphy (2017) containing methods based on i.a. Murphy et al. (2010) and Evans et al. (2011). To evaluate the regression model fit *rfUtilities::rf.regression.fit()* (Evans et al., 2011) was used. P-values were generated using the function *rfUtilities::rf.significance()* (Evans et al., 2011). A visual comparison between the actual data and the RF model predictions as well as a visual interpretation of predictor effects was done using the R package ‘ggplot2’ version 2.2.1 (Wickham, 2009) especially with LOESS smoothing (Fig. 5.8).

Results

In spring and summer but not in fall and winter, herring was by far the most abundant fish species found in the marsh creeks (Fig. 5.2). Other than herring, common gobies outnumbered all other fish species throughout the season, except in May and June, when stickleback, Nilsson’s pipefish and, in sum, other fish species became increasingly dominant (Fig. 5.2). Sticklebacks were found in high and rising numbers in March to June and December to February, whereas Nilsson`s pipefish immigrated to the marsh in April and departed in September (Fig. 5.2). Smelt were regularly present, but in order of magnitude lower numbers than the aforementioned species (Fig. 5.2). In contrast to the common goby the sand goby was rarely found in the salt-marsh creeks and was completely absent from July to October (Fig. 5.2). Plaice larvae were observed in high densities from March until May 2015. However, due the mesh size of 6 mm this size class was most likely not caught quantitatively (Fig. 5.2).

Given the dominance patterns described above, we analysed stomach contents of stickleback, common goby, sand goby and herring. While there were marked differences in the relative frequency of occurrence and biomass of terrestrial prey in the stomachs of these four species, a consistent seasonal pattern became apparent, showing that terrestrial prey was mainly consumed during winter and, to a lesser extent, in spring (Fig. 5.3).



	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Dec	Feb
■ herring	0.00	0.10	0.12	3.34	0.09	0.00	0.00	0.00	0.01	0.00
■ all other fish	0.28	0.09	0.01	0.02	1.45	0.32	0.40	1.92	0.01	0.04

Fig. 5.2: Fish abundances within all quantitative hauls (71 out of 80 hauls). a) Seasonal fish abundance as catch per unit effort (CPUE) showing herring abundance (grey) and all other fish species (black) separately; b) Seasonal trajectory of relative catch composition based on monthly averages of CPUE excluding herring. Herring CPUE is presented separately in a) to avoid masking of other data by the seasonally high herring abundances. Species with an average share less than 0.2 % were summarized as “others”, comprising plaice (*Pleuronectes platessa*, 47.36 %), sprat (*Sprattus sprattus*, 24.19 %), nine-spined stickleback (*Pungitius pungitius*, 11.59 %), common sole (*Solea solea*, 5.60 %), flounder (*Platichthys flesus*, 4.14 %), shorthorn sculpin (*Myoxocephalus scorpius*, 2.67 %), thick-lipped mullet (*Chelon labrosus*, 1.73 %), European anchovy (*Engraulis encrasicolus*, 1.01 %), Garfish (*Belone belone*, 0,85 %), eelpout (*Zoarces viviparus*, 0.41 %), sandeel (*Ammodytes spec*., 0.41 %), European perch (*Perca fluviatilis*, 0.04 %).

Three-spined stickleback

Terrestrial prey was most frequent and most abundant in the stomachs of sticklebacks compared to the other fish species (Fig. 5.3). Sticklebacks consumed terrestrial prey significantly more often ($X^2 = 4.822$, df = 1, p-value = 0.028) and in higher amounts (W = 14828, p-value = 0.004) in the ungrazed marsh than in the sheep-grazed marsh. This difference was caused by *Orchestia* (numbers of fishes with vs. without *Orchestia* in the stomachs: $X^2 = 8.328$, df = 1, p-value = 0.004; amount of *Orchestia* in the stomachs: W = 15206, p-value = 0.001), making up 87.2 % of the sticklebacks terrestrial prey. The remaining terrestrial diet fractions (insects: 10.6 %, mites: 1.0 %, isopods: 0.6 %, and spiders: 0.5 %) did not differ between the grazed and the ungrazed salt marsh (numbers of fishes with vs. without other terrestrial prey, excluding *Orchestia*, in the stomachs: $X^2 = 0.552$, df = 1, p-value = 0.457; amount of other terrestrial prey, excluding *Orchestia*, in the stomachs W = 16150, p-value = 0.179). There were no diurnal differences of *Orchestia* shares (W = 17116, p-value = 0.799), but the other types of terrestrial prey were consumed significantly more during daytime (W = 18062, p-value = 0.043). Regardless of month, more than 50 % of the sticklebacks consumed polychaetes at relative shares of more than 50 % (Fig. 5.4). In winter, *Orchestia* became almost as important as the polychaetes, but only in the ungrazed marsh (Fig. 5.4). Other terrestrial prey items occurred in the stomachs more frequently than *Orchestia*, but with hardly any measurable effect on relative stomach weight (Fig. 5.4). Although the most utilized prey, the polychaetes were available in all analysed salt-marsh creeks year round (Fig. 5.5b), the stickleback immediately consumed *Orchestia* as soon as it became available as prey.

There was neither an inter-site (grazed vs. ungrazed) difference in stomach weight relative to gutted body weight (W = 16708.5, p-value = 0.496) nor in the relative share of empty stomachs (W = 255.5, p-value = 0.078). But the relative stomach content weight tended to be higher in winter and spring than in the warmer months (Supplement C, Tab. C.1).

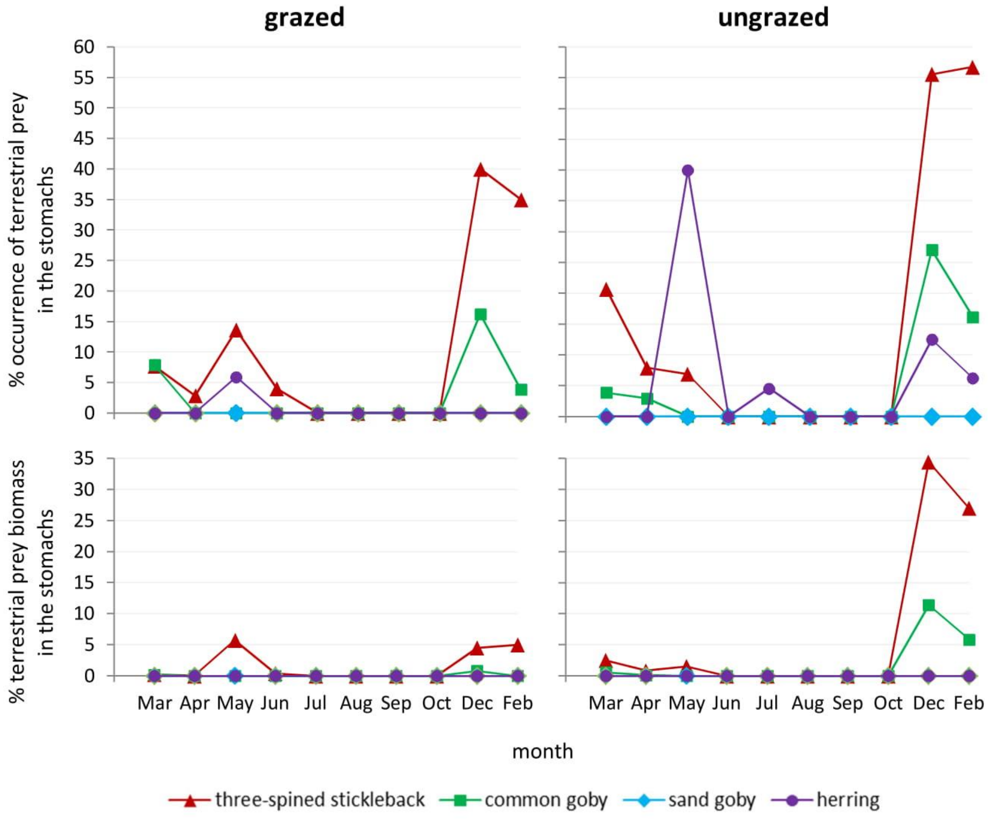


Fig. 5.3: Seasonal percentage occurrence and percentage biomass of terrestrial prey in the fish stomachs per salt marsh grazing treatment for four selected predators

Common goby

Like sticklebacks, common gobies fed on terrestrial prey mainly during the winter months, but less frequently and in lower amounts than the sticklebacks. The tendency of more terrestrial prey in the stomachs of common gobies caught in the ungrazed site than in the grazed site (Fig. 5.3) could not be confirmed statistically (number of fishes with terrestrial prey: $X^2 = 0.349$, df = 1, p-value = 0.555; relative terrestrial prey weight: W = 29005.5, p-value = 0.410). With more than three quarters, *Orchestia* (75.7 %), and almost another quarter, insects (22.0 %), were the dominant terrestrial prey by biomass consumed by the common goby, while mites (1.7 %) and collembolans (0.5 %) were only rarely found. The common gobies consumed their prime terrestrial prey, *Orchestia*, mainly during night (W = 28371, p-value = 0.018), whereas feeding on other terrestrial prey was equally distributed between day and night (W = 29639, p-value = 0.228). Both the relative stomach content and the share of empty stomachs were similar in the grazed and ungrazed salt marsh (W = 31228, p-value = 0.901 and W = 311, p-value = 0.122, respectively).

Sand goby

The sand goby was less abundant in the analysed salt-marsh creeks than its close relative the common goby (Fig. 5.2). Despite the similarities between the two goby species, the sand goby did not eat any terrestrial prey (Fig. 5.3). Consequently, the grazing treatment affected neither the relative stomach weight (W = 827, p-value = 0.996) nor the percentage of empty stomachs (W = 12, p-value = 0.808).

Herring

Atlantic herring, a pelagic planktivore, only rarely fed on terrestrial prey. When it did, it tended to be in the ungrazed marsh (Fig. 5.3), but the feeding incidence did not differ significantly between the grazed and ungrazed marsh ($X^2 = 1.162$, df = 1, p-value = 0.281). The amount of terrestrial prey did also not differ between sites (W = 1837.5, p-value = 0.056). Terrestrial items were fed on only during daytime and consisted almost exclusively of mites. Collembolans and insects were also found in the herring stomachs, but in amounts too small to be reliably quantified. Sheep grazing had no effect on the relative stomach weight (W = 2243, p-value = 0.122) or the share of empty stomachs (W = 28, p-value = 0.679) of herring.

Effect of sheep grazing on potential fish prey abundances

Year around, the grazed salt marsh provided significantly less *Orchestia* (W = 1181, p-value < 0.0005) and other terrestrial invertebrates (W = 4012, p-value = 0.023) than the ungrazed marsh (Fig. 5.5a). The most important fish prey (Fig. 5.4), the polychaetes, were significantly less abundant in the grazed salt marsh than in the ungrazed salt marsh (Fig. 5.5b; W = 3867.5, p-value = 0.003). However, abundance patterns of the polychaetes were variable over seasons and no stable differences between the grazing treatments were visible (Fig. 5.5b). In both grazing treatments the abundance of polychaetes increased significantly in winter, December and February, compared to spring and summer, March to May and June to July (Fig. 5.5b; Tab. 5.1).

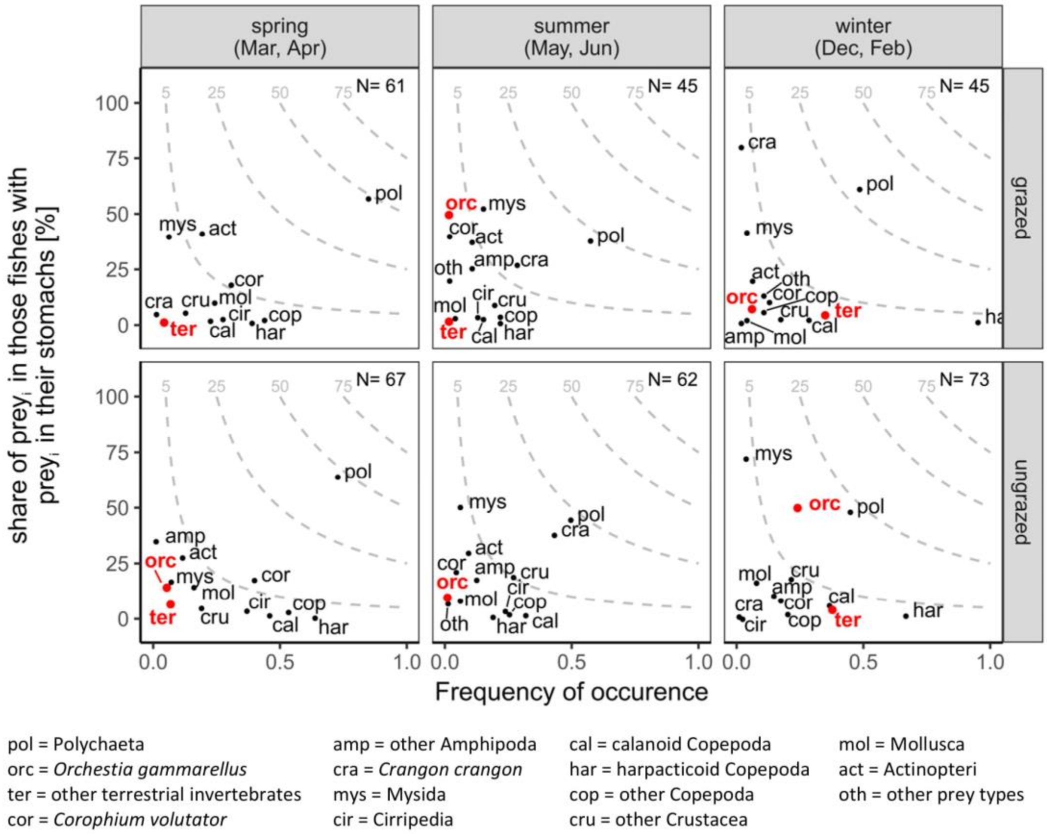


Fig. 5.4: Seasonal importance of different prey types for three-spined stickleback in grazed and ungrazed salt marshes, shown by a Costello plot modified according to Amundsen et al. (1996). Each point reflects one prey type (abbreviations given below the plot). The combination of the frequency of occurrence of a prey type in the stomach (x-axis) and the relative share of that prey type within the stomachs of those fishes that ate that prey type (y-axis), gives an overview of the importance of each prey type. Prey types close to the axis are either rarely eaten (close to the y-axis) or only consumed in small amounts, when they were eaten (close to the x-axis). The closer a prey item is at the upper right corner of the plot, the more important it is for the predator. The importance of a prey type can therefore be quantified by the area enclosed by the co-ordinates of the two axes. The sum of those areas for all prey types, will equal the total area of the plot. The percentage of this area is indicated by the isolines (of 5, 25, 50 and 75 % of the total area of the plot; coloured in grey) to help assessing the importance of a prey item.

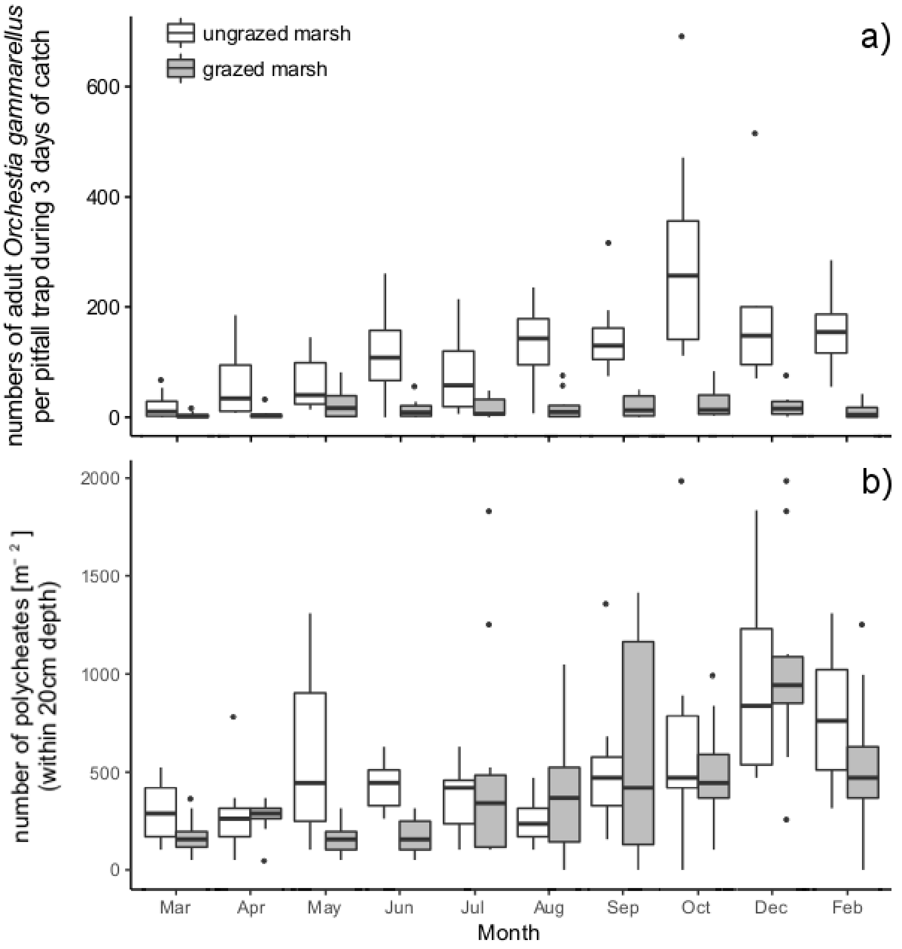


Fig. 5.5: Prey abundances in the sheep-grazed and in the ungrazed salt marsh during the sampling period (10 samples per boxplot). a) adult *Orchestia gammarellus* (abundances underestimated in March, May, December and February due to flooding of the pitfall traps), b) polychaetes

Tab. 5.1: Effect of seasonality on polychaete abundances. Results of Kruskal-Wallis rank sum test and Dunn´s Post-hoc test using the Benjamini-Hochberg adjustment. Spring = March to May (N = 30), summer = June to August (N = 30), autumn = September and October (N = 20), winter = December and February (N = 20).

grazing treatment	**ungrazed marsh** Kruskal-Wallis chi-squared = 27.6174 df = 3, p-value < 0.0005			**grazed marsh** Kruskal-Wallis chi-squared = 26.2701 df = 3, p-value < 0.0005		
season	autumn	spring	summer	autumn	spring	summer
spring	2.251 p = 0.0244*			2.988 p = 0.0028*		
summer	2.186 p = 0.0216*	-0.074 p = 0.4707		1.949 p = 0.0385	-1.162 p = 0.1226	
winter	-2.143 p = 0.0192*	-4.599 p < 0.0005*	-4.534 p < 0.0005*	-1.598 p = 0.0660	-4.739 p < 0.0005*	-3.700 p = 0.0003*

*indicates significance if p ≤ 0.025

Importance of sheep grazing for the diet of three-spined stickleback

To discover possible pathways how livestock grazing would affect prey availability for fishes in salt marshes, we simplified our model system by focusing our analyses on stickleback and its main terrestrial prey *Orchestia*.

When a high CTFV index coincided with high mean *Orchestia* abundances in the marsh, *Orchestia* tended to occur more frequently (Fig. 5.6a) and in higher amounts (Fig. 5.6b) in the stomachs of sticklebacks. The importance of these two variables, the CTFV index and the *Orchestia* abundance was confirmed by the RF model results. Concerning the share of individual sticklebacks that consumed *Orchestia*, the RF classification model selected the CTFV index as the most important influencing factor (Fig. 5.7a). The probability of *Orchestia* consumption seemed to increase with a CTFV index threshold of ca. 500000 m³ (Fig. 5.8a). The model also reflected the seasonal patterns with an increased probability of *Orchestia* consumption during winter months and high wind velocities (Fig. 5.8a). Creek was also an important factor as the probability of a fish consuming *Orchestia* was highest in the largest creek *U2* in the ungrazed marsh (Fig. 5.8a, Tab. 5.2). Compared to the covariates explaining the accessibility (CTFV, month, wind velocity and creek), the *Orchestia* abundance was of minor importance for the presence or absence of *Orchestia* in the stomachs and was therefore excluded from the final model by the algorithm. The final RF classification model was significant with a p-value of 0. It correctly predicted 94.3 %

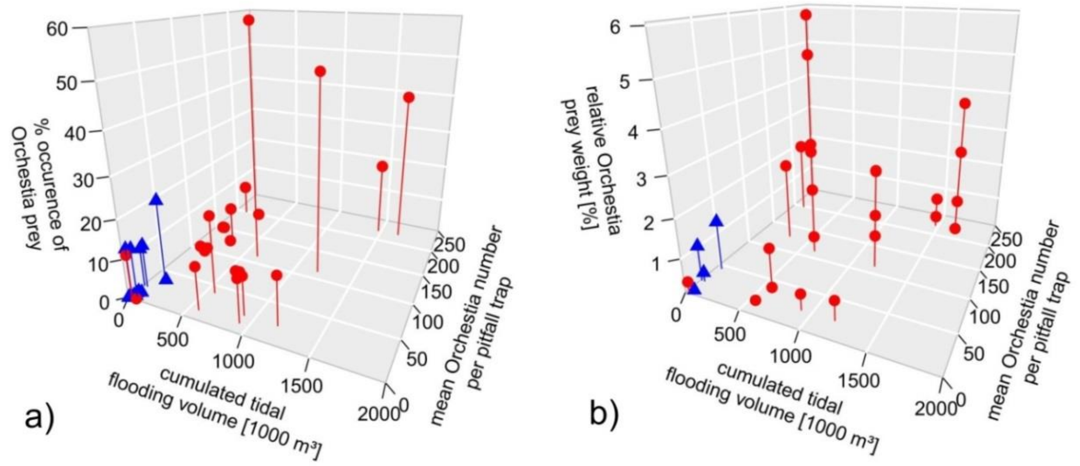


Fig. 5.6: Frequency of occurrence of *Orchestia gammarellus* (abbreviated as *Orchestia*) in the stomachs of three-spined sticklebacks per haul (N = 40, including only those hauls with at least 5 sticklebacks), b) relative prey weight of *Orchestia* per individual fish (including only those fishes that ate *Orchestia*, N = 28 of 394 analysed fishes) and per salt marsh (red dot = ungrazed; blue triangle = sheep-grazed) in dependence of the accessibility (defined by the flooding volume) and the prey abundance (defined by the mean number of *Orchestia* per pitfall trap)

of *Orchestia* abundances in the stomachs, but misclassified 40 % of the *Orchestia* absences. Furthermore, it performed clearly better than an indiscriminate model (see true skill statistic, Matthews correlation coefficient, accuracy, F-score, and area under the ROC curve in Tab. 5.3).

Like in the first model, the CTFV index was the most important predictor in the final RF regression model (Fig. 5.7b). However, a close second came the *Orchestia* density (Fig. 5.7b), which had the second strongest positive influence on the quantity of consumed *Orchestia* after the CTFV index (Fig. 5.8b). Additionally wind velocity and month were important predictors for the amount of consumed *Orchestia* by sticklebacks, while the different creeks were unimportant and therefore excluded from the final model. The final RF regression model was significant with a p-value of 0.03. It performed slightly poorer than the classification model (see e.g. Cohen´s f^2, explained variance and R^2 in Tab. 5.3), but the model predictions showed a high similarity to the original data (Fig. 5.8b).

The two RF models revealed that the share of fish feeding on *Orchestia* and the consumed quantity depend mainly on the flooding strength. However, the amount of consumed *Orchestia* was also strongly determined by the abundance of this prey. As the abundance of *Orchestia* is significantly reduced in grazed salt marshes (Fig. 5.5a), sheep grazing also affects the fish diet. In summary, the availability of *Orchestia* for the fish depends on its abundance, which is determined by the sheep grazing, and on its accessibility, which is determined by the water levels.

Tab. 5.2: Geomorphological characteristics of the analysed salt marsh creeks

grazing treatment	**creek**	**creek length [m]**	**creek width at fyke net position [m]**	**max. depth [m above MHT***	**watershed area [km²]**
sheep-grazed	G1	520	10.04	0.50	0.067
	G2	803	10.62	0.28	0.093
ungrazed	U1	858	13.87	0.08	0.117
	U2	1119	42.43	0.12	1.066

*MHT = mean high tide

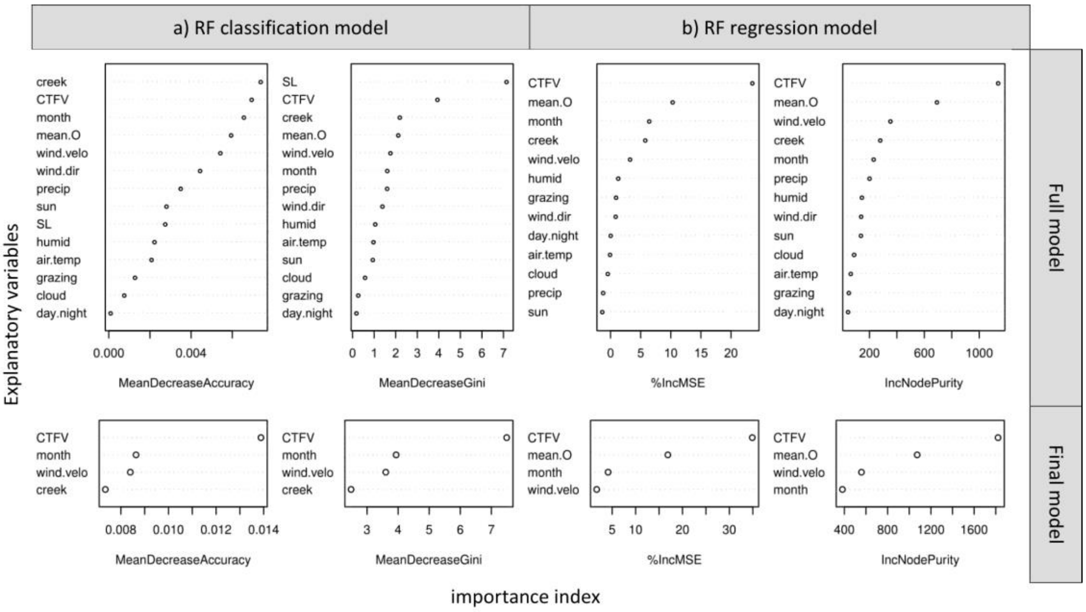


Fig. 5.7: Unscaled importance of explanatory variables in the full and final models for a) the random forest classification model and b) the random forest regression model. I. Variables (y-axis): grazing = grazed / ungrazed salt marsh, creek, month, day.night = day / night, air.temp = air temperature, cloud = cloudiness, precip = precipitation, sun = sun shine hours, humid = humidity, wind.velo = wind velocity, wind.dir = wind direction, CTFV = cumulated tidal flooding volume, mean.O = mean Orchestia abundance per pitfall trap, SL = standard length of the fish. II. Importance indices (x-axis): the larger the importance index, the more important is the specific variable. “MeanDecreaseAccuracy” and “%IncMSE” measure the prediction error of the out-of-bag data, when the features of the concerning variable are permuted, as mean decrease in prediction accuracy and percentage increase in mean squared error for the classification and regression model, respectively. “MeanDecreaseGini” and “IncNodePurity” describe the quality of a variable to split the data by measuring the node impurity decrease and the purity increase for the classification and regression model, respectively. All importance indices are calculated as means over all randomized trees in the forest.

Tab. 5.3: Random forest model summaries

RF classification model	
p-value	0
accuracy [%]	93.4
F-score	0.97
area under the ROC curve	0.89
sensitivity (the percentage of presences correctly classified)	0.943
specificity (the percentage of absences correctly classified)	0.6
true skill statistic	0.54
Matthews correlation coefficient	0.33
Cohen`s Kappa value	0.29
RF regression model	
p-value	0.03
Mean of squared residuals	87.335
% Variance explained	20.22
Fit Mean squared error	88.533
root-mean-square error	9.345
Cohen’s f2	0.2
R^2	0.167

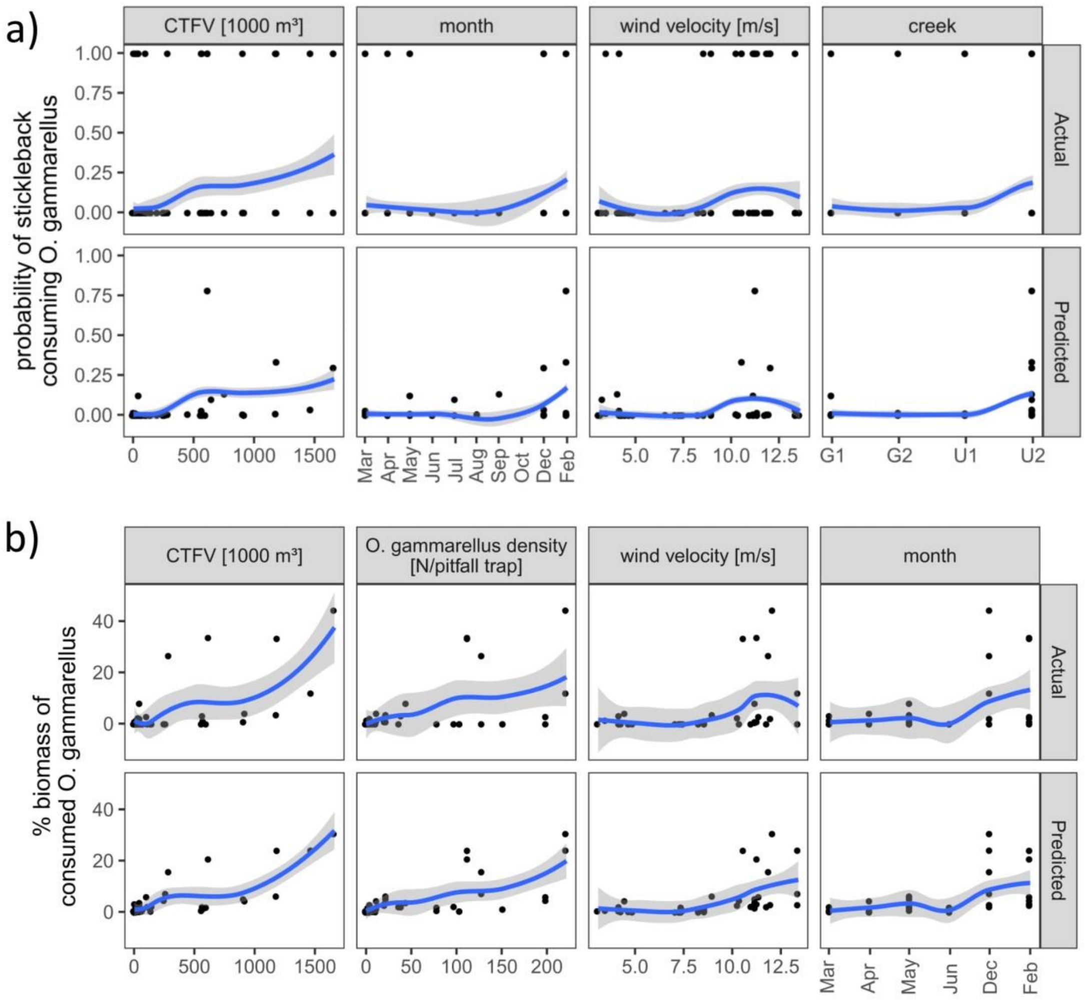


Fig. 5.8: Actual and predicted data a) from the final RF classification model and b) the final RF regression model for each predictor variable of the respective model: cumulated tidal flooding volume (CTFV), wind velocity, month, salt-marsh creek and *Orchestia gammarellus* density

Discussion

Our results confirmed the hypothesis that diets of fish species found in intertidal marsh creeks, that differ in sheep grazing stress, differ in the relative share of terrestrial prey. As revealed by the random forest models the proportions of consumption frequency and the amounts of terrestrial prey in stickleback stomachs increased in winter and decreased with grazing pressure. This indicates that marsh management can affect fish dietary conditions by modifying terrestrial biomass production, a mechanism that becomes particularly relevant during the winter months, when offshore marine biomass density in the Wadden Sea is low (Beukema, 1974; Kuipers and Dapper, 1981; del Norte-Campos, 1995; Krause et al., 2003).

Of all fish species found in the creeks, sticklebacks consumed terrestrial prey most frequently and in highest amounts. The frequency and amounts of consumed terrestrial prey by stickleback responded immediately and strongly positive to the availability of *Orchestia*. Sticklebacks bony armour shields them against injuries by terrestrial vegetation during storm flood events allowing them to access vegetated marsh surfaces. The ability to immediately adapt their foraging strategy to the availability of terrestrial prey on vegetated marsh surfaces, makes the sticklebacks successful predators in the salt marsh environment.

The benthivorous common gobies also tended to feed on terrestrial prey with similar spatiotemporal patterns like the sticklebacks, but less frequent and in smaller quantities. Its close relative, however, the sand goby, completely ignored terrestrial prey items, even though it temporarily also appeared in the marsh creeks. Sand gobies and common gobies are very similar, but they appear to avoid direct competition by spatial segregation of their preferred habitat along a depth gradient with gradually increasing grain size (Fonds, 1973; Edlund and Magnhagen, 1981; del Norte-Campos, 1995). Along this gradient, common gobies occupy the shallowest areas with high mud contents, including salt-marsh creeks and oyster reefs (Tulp et al 2017), whereas sand gobies distribute themselves over sandier grounds (Fonds, 1973; del Norte-Campos, 1995). Thus, common gobies might be more familiar with terrestrial prey than sand gobies. A similar contrast has been observed between sand gobies and Lozano’s goby (*Pomatoschistus lozanoi*), feeding almost exclusively on *Orchestia* and mysids, respectively, in a marsh in Northern France (Laffaille et al., 1999). This example shows how flexible gobies are in using their environment and how similar species behave to avoid competition for the same prey types.

In herring, no preference of terrestrial prey became evident. Instead, they occasionally fed on mites, which resembles mesozooplankton, the herring’s preferred prey (Dickey-Collas et al., 2015). Mites were frequently found in herring stomachs, yet only in small numbers, suggesting they were consumed accidentally. Without an apparent trophic benefit, it remains unknown why the herring enter the shallow marsh creeks, frequently and sometimes in huge numbers (this study, and A. Dänhardt, unpublished). Having one of the most sensitive skins among the fish community in the Wadden Sea, herring should avoid shallow, structurally rich habitats where they risk injuring their fragile mucous layer and scales (Suuronen et al., 1996).

We conclude that omnivorous and robust predators, such as sticklebacks, are likely to profit from terrestrial prey made available in the salt marshes (Whitley and Bollens, 2014), while benthivores such as the common gobies are capable of using terrestrial prey, but less frequent and in smaller quantities and perhaps less targeted than the stickleback. Sensitive planktivores such as herring do not seem to have an immediate trophic benefit from entering the marsh creeks.

For stickleback and common goby the most important terrestrial prey species was the supralitoral beachhopper *Orchestia*. It was also found in the stomachs of sea bass (*Dicentrarchus labrax*), flounder (*Platichthys flesus*), and other gobies (*P. minutus* and *P. lazanoi*) in French and Dutch salt marshes (Laffaille et al., 1998; Laffaille et al., 1999; Laffaille et al., 2000b; Laffaille et al., 2001; Hampel, 2003; Hampel et al., 2005; Laffaille et al., 2005). In French salt marshes *Orchestia* was even the most important terrestrial prey for juvenile sea bass and the loss of *Orchestia* in sheep-grazed marshes resulted in reduced stomach content weights of sea basses (Laffaille et al., 2000b). In contrast to Laffaille et al. (2000b), the lack of differences in relative stomach weight and in the share of empty stomachs between the grazed and ungrazed site in our analysed marshes indicates that stickleback were able to find enough polychaetes to compensate for terrestrial prey missing in the grazed marsh. However, although polychaetes were abundantly available year round – especially in winter – in the marsh creeks, a quarter of the sticklebacks in the ungrazed marshes fed on *Orchestia* at relative shares of 50 % once made available by storm floods. Therefore *Orchestia* might be the preferred prey type.

Orchestia contains more energy per gramm dry weight than e. g. polychaetes (Brey et al., 1988; Maier, 2014a), and it is relatively large, making it a very profitable prey item (Gill and Hart, 1994). An amphipod closely related to *Orchestia*, *Platorchestia platensis,* displays increased activity during flooding events, resulting in an increased mortality due to predation (Rüppell, 1967). Instead of becoming more active, most other terrestrial arthropods such as insects, spiders, mites or collembolans clamp on the vegetation, bury in the sediment or migrate to higher elevated areas during flooding events (Foster and Treherne, 1976; Irmler et al., 2002; Pétillon et al., 2008; Pétillon et al., 2009). Higher activity during flooding may thus increase vulnerability of *Orchestia* to be eaten by fish compared to hidden or fled other terrestrial arthropods, offering an explanation of why many fish species exploit *Orchestia* in salt marshes (Laffaille et al., 1999; Laffaille et al., 2000b; Hampel, 2003; Hampel et al., 2005). The behaviour of leaving sheltered vegetation may increases the foraging success of fish and may also benefit their energy budget by reduced foraging effort.

Although *Orchestia* was present in the marsh in comparable numbers during the whole year, stickleback fed on this prey type during the winter months only. Flooding of the marsh surface during winter storm surges resulted in the prey becoming accessible to the predator. Spring tides and storm floods with a high water volume and long duration (represented by the CTFV index) resulted in an increased number of stickleback feeding on *Orchestia*. In combination with a high *Orchestia* abundance in the ungrazed marsh, flooding also resulted in an increased amount of this prey in their stomachs. Flooding height and duration depends on wind direction and strength, the lunar cycle, and the marsh elevation and topography (Rozas, 1995). As the exploitation of terrestrial prey was limited to flooding events, our results suggest, that this food source is otherwise unavailable to the fish lurking in the creeks. In turn, habitat quality of salt marshes for fish and crustaceans increased when the vegetated marsh surface was flooded (Rozas and LaSalle, 1990; Javonillo et al., 1997; Potthoff and Allen, 2003).

Sticklebacks consumed most terrestrial prey in the creek with the longest shoreline (*U2*) draining an ungrazed marsh, obviously supporting the interaction between the terrestrial and the marine system. The analysed creeks in the ungrazed marsh were deeper, wider and thus inundated longer than the creeks in the grazed marsh. These site-specific differences of inundation patterns are also part of the CTFV index as the flooding volume and duration increases with creek depth and length and the watershed size. The random forest models revealed, that the CTFV index - and hence the accessibility of the prey - is more important for the exploitation of *Orchestia* than its abundance. Also for other animals in other habitats prey accessibility is more crucial for foraging success than prey density (fish: Main, 1985, Diggins et al., 1979; seabirds: Boyd et al., 2017, Dänhardt and Becker, 2011a; mammals: Hopcraft et al., 2005, Mitani et al., 2004). As terrestrial prey become available especially during winter, when other prey types in the Wadden Sea decrease (Zwarts and Wanink, 1993), fish can benefit from the accessibility to energy-rich terrestrial prey sources, like *Orchestia* (Brey et al., 1988; Maier, 2014a).

Orchestia is abundant in ungrazed old marshes (Bakker, 2014) and those in the latest successional stages (Schrama et al. (2015) with densities at mean high tide level of up to 3690 individuals m^{-2} (Dias and Sprung (2003). *Orchestia* is mainly found and consumed by fish in vegetation consisting of *Atriplex portulacoides* and *Elymus athericus* (Laffaille et al., 1999; Laffaille et al., 2000b; Laffaille et al., 2001; Laffaille et al., 2005). Both plant species produce high amounts of organic matter (Lefeuvre et al., 2000) which is beneficial for the litter-feeding *Orchestia* (Creach et al., 1997). *A. portulacoides* is the preferred habitat of *Orchestia* (Laffaille et al., 2005) and due to lower stem densities during flooding probably a better foraging habitat for fish than *E. athericus* (Gotceitas and Colgan, 1980; Savino and Stein, 1989b, 1989a; Gotceitas, 1990). *A. portulacoides* grows in the lower marsh and is more frequently flooded than *E. athericus* in the upper marsh (Esselink et al., 2009), suggesting that marshes with large patches of *A. portulacoides* are most valuable for fish, as they maximize both abundance and accessibility of *Orchestia*.

Livestock grazing changes the plant communities of a marsh and has especially a negative influence on *A. portulacoides* and *E. athericus* (Bos et al., 2002). By reducing plant detritus, grazing and mowing adversely affects the abundance of the detritus feeder *Orchestia* (Andresen et al., 1990; Meyer et al., 1995; Laffaille et al., 2000b; Joyeux et al., 2017). One could speculate that the lower vegetation canopy height in the grazed marsh (Andresen et al., 1990) would increase the foraging success of fish (Savino and Stein, 1989a) and thus reduce *Orchestia* abundance in the grazed marsh. However, we are confident to discard this idea of a top-down control considering the limited temporal access of fish, the fish density in the marsh and their consumption rates, and that they consume *Orchestia* in winter, when its mortality is generally low (Dias and Sprung, 2003).

Although the varying geomorphological characteristics of the sampling sites affect the flooding dynamics and therefore the accessibility of the sticklebacks to their main terrestrial prey *Orchestia*, the RF regression model revealed that the site-specific geomorphological differences (predictor: creek) are rather unimportant for the consumed amounts of *Orchestia* by sticklebacks compared to the flooding (predictor: CTFV). Beside accessibility, the consumed amounts of *Orchestia* depend on the abundance of *Orchestia, which* is limited by sheep grazing (Andresen et al., 1990; Meyer et al., 1995). Therefore we conclude, that fish diets are seasonally affected by sheep grazing and that it is not just an artefact from the different sampling sites.

Sticklebacks, although they find sufficient amounts of prey also in creeks draining grazed marshes, benefit from ungrazed marshes with higher abundances of *Orchestia*, which can keep a positive energy budget during food shortage in winter. Beside terrestrial prey, salt-marsh creeks in the upper intertidal area offer a variety of benthic prey (Hampel et al., 2005; Schückel et al., 2013). Several attributes define how marsh creeks should be structured to provide rich feeding habitat for fish such as three-spined stickleback. They should run through ungrazed marshes, providing favourable conditions for *Orchestia* by allowing plant detritus to accumulate. The creeks should be deep, wide and meandering to increase the length of the shoreline. In addition, frequent flooding should be allowed to occur, since the fish can only reach terrestrial prey when the marsh surface is flooded.

These benefits from the fish perspective need, of course, to be balanced with other stakes and conservation objectives. Ungrazed salt marshes tend to become monocultures of *E. athericus* in the higher marsh (Esselink et al., 2009), whereas grazed marshes can increase the plant diversity and offer breeding space, e. g. for waders such as redshank *Tringa totanus* or oystercatcher *Haematopus ostralegus* (Valle and Scarton, 1996; Mandema et al., 2015). Developing a mosaic of moderately grazed and ungrazed salt marshes with deep-lying marshes, long, deep and wide creeks, and long shorelines kept ungrazed may be feasible to address fish in the conservation agenda along the Wadden Sea coasts.

6

Discussion

General Discussion

Fishes and crustaceans interact with the habitats they use and via migration they contribute to the connectivity of habitats within the habitat mosaic, the seascape (Nagelkerken et al., 2015). This connectivity expands in the salt marshes – at least up to the dikes – towards the terrestrial ecosystem. Salt marshes are part of an ecoscape, that merges the marine seascape and the terrestrial landscape (Kneib, 2002). Fishes and crustaceans are affected, on the one hand, by their environment, and on the other hand, they can cause changes in the environment they use. In US salt marshes mummichogs (*Fundulus heteroclitus*) can control abundances of their invertebrate prey (Vince et al., 1976; Kneib, 1986; Sardá et al., 1998) and crab burrows can cause marsh erosion and die-offs (Bertness and Coverdale, 2013; Crotty et al., 2017; Raposa et al., 2019). Furthermore, nekton using salt marshes – in particular when consuming terrestrial arthropods – can export the marsh production to the subtidal food webs via faeces or when eaten by predators. Export rates may, however, vary locally (Odum, 1980; Lefeuvre et al., 1999; Cattrijsse and Hampel, 2006). But salt marshes can also be valuable nurseries for juvenile fish contributing to adult stock size – sometimes having even effects on fishery yields (Turner, 1977; Boesch and Turner, 1984; Orth and van Montfrans, 1990; Minello and Webb, 1997; Rozas et al., 2005; Minello et al., 2012). Worldwide, salt marshes have proven important or even essential for a wide variety of marine nekton (Weinstein, 1979; Laffaille et al., 2001; Paterson and Whitfield, 2003; Mazumder et al., 2011). Due to their high structural diversity and their position at shallow coasts, salt marshes provide shelter from predators for small nekton (Weinstein, 1979; Cattrijsse et al., 1997; Halpin, 2000; Minello et al., 2003). As a consequence of nutrient runoff from land and high light intensity, they are also relatively productive, providing abundant food resources (Chapman, 1977; Boesch and Turner, 1984; Lefeuvre et al., 2000).

Wadden Sea salt marshes, however, differ from many other marshes as they are severely modified by humans since centuries (Knottnerus, 2005; Airoldi and Beck, 2007; Gedan et al., 2009). Although the Wadden Sea is nowadays listed as World Heritage and protected as a National Park, nekton was not yet included in the salt-marsh management, because information about the interaction of this species group with the salt-marsh environment was lacking. Knowledge of species abundance patterns and their drivers is important to understand ecological processes, which is a prerequisite for a successful ecosystem management (Sheaves, 2016). Therefore, this study aimed to fill this gap of knowledge by analysing the nekton community of this habitat and whether the use of this habitat is advantageous, e. g. via food and shelter, or disadvantageous for nekton, e. g. via low oxygen levels or too high temperatures.

The approach of this empirical study was to investigate temporarily resolved species-habitat interactions. We investigated which species and size classes use the Wadden

Sea salt marshes, whether they entered the habitat randomly or by habitat selection (Chapter 2), which biotic and abiotic conditions they experience in this habitat (Chapter 3 to 5), whether they profit energetically from using the salt marshes (Chapter 3 to 4), and whether they are affected by sheep grazing (Chapter 5).

The quality of Wadden Sea salt marshes as nekton habitats

In **Chapter 2** spatiotemporal habitat utilization patterns were analysed to answer which nekton species use the salt marshes and whether the utilization patterns were driven by preference, avoidance or coincidence. The Wadden Sea salt marshes are inhabited by small-sized species-poor nekton community dominated by common shore crab (*Carcinus maenas*), brown shrimp (*Crangon crangon*), three-spined stickleback (*Gasterosteus aculeatus*), common goby (*Pomatoschistus microps*), Nilsson´s pipefish (*Syngnathus rostellatus*), herring (*Clupea harengus*) and smelt (*Osmerus eperlanus*). Nekton densities in the marsh creeks tended to be low compared to densities reported from other Wadden Sea areas (Berghahn, 1984; Hinz, 1989; Breckling and Neudecker, 1994; del Norte-Campos, 1995; Breckling, 1999; Vorberg and Breckling, 1999). The low biodiversity seems to be typical for salt marshes (Sogard and Able, 1991; Cattrijsse, 1994; Visintainer et al., 2006), but the species composition, differed from other European salt marshes (Laffaille et al., 2000a; Mathieson et al., 2000; Hampel, 2003). Depletion patterns during repetitive samplings and the frequency and abundance of the above mentioned species suggest, they selected to enter this habitat. Other species, such as e. g. whiting (*Merlangius merlangus*), were never caught in the salt marshes but in the subtidal, indicating avoidance of the shallow marsh creeks, and yet others occurred only occasionally in the marsh creeks, indicating a coincidental habitat use. The narrow size composition and absence of large piscivore fish coincides with studies of other salt marshes worldwide (Cain and Dean, 1976; Weinstein, 1979; Gewant and Bollens, 2012; Jin et al., 2014). The fishes and crustaceans of the dominant species were adults of small-sized species or juveniles. Especially a seasonal sequence of larval occurrence of plaice (*Pleuronectes platessa*), herring, and goby (*Pomatoschistus sp.*) indicated this habitat may also serve as a nursery, as many other salt marshes worldwide (Weinstein, 1979; Rogers et al., 1984; Minello et al., 2003; Whitfield, 2017). However, the abundance of small-sized species, such as common gobies and three-spined sticklebacks, implies that rather body size than life stage structures nekton occurrence in this habitat type. In conclusion, compared to the subtidal, predation pressure in the salt-marsh creeks can be assumed low for small nekton, due to the absence of large aquatic predators and probably unfavourable foraging conditions for birds (Whitfield and Blaber, 1979; Kneib, 1982b; Manderson et al., 2004).

The avoidance of the salt-marsh creeks by large predators, the low biodiversity and density could be caused by the extreme abiotic conditions in this habitat. The abiotic conditions were examined in **Chapter 3**. Water temperatures in the shallow water bodies of the salt-marsh creeks adapted rapidly to air temperatures resulting in a thermally more extreme environment than in the deeper subtidal. Despite temporary high summer temperatures, the oxygen concentrations remained within the physiological tolerance windows of the marsh-using nekton – obviously due to tidal mixing and primary production. Large nekton tends to be less tolerant towards high temperatures and low oxygen levels (van Donk and de Wilde, 1981; Björnsson et al., 2001; Handeland et al., 2008; Pörtner and Farrell, 2008; Otto and Zahn, 2008; Elshout et al., 2013). Small nekton, especially juveniles, can benefit from warmer temperatures in combination with sufficient oxygen and food supply, via accelerated growth rates (Houde, 1989; Munk, 1993; Attrill and Power, 2002; Pörtner, 2002; Attrill and Power, 2004). The weather-depended temperatures in the marsh creeks can be unpredictable, potentially transforming the habitat to an ecological trap. When temperatures exceed the tolerance window of an organism forcing it to leave the marsh creeks ahead of the ebb flow, it has to pay high energetic costs for additional swimming effort and an increased basal metabolism. While the hydrological parameters in the salt-marsh creeks are highly dynamic, the hydrodynamic parameters are more constant, and thus had a higher power to explain species distribution patterns. Located close to mean high water level and sheltered from wind and waves by the vegetated marsh, the salt-marsh creeks are characterized by low flow velocities, low turbidity and fine sediments. This environment will likely energetically benefit small fishes and crustaceans by increasing visual prey detection, increasing their swimming performance, and decreasing energy investments, hence, finally increasing their foraging success. Larger fish have a higher swimming power and benefit less from low flow velocities than small fish (Bainbridge, 1958; Schmidt-Nielsen, 1972). In the low tide surf zone higher turbidity and coarser sediments were measured. This deeper area is inhabited by larger nekton and used by small nekton emigrating from the salt marsh during low tide. Small nekton can hide during low tide in the turbid surf zone to avoid its predators and forage during high tide in the clear salt-marsh waters. We conclude that salt marshes seem to be beneficial at low risks for small nekton and risky at low benefits for large nekton.

Foraging opportunities for herring, three-spined stickleback, common goby and sand goby in salt-marsh creeks were assessed in **Chapter 4**. The stomachs tended to be fuller in the salt marsh than in the subtidal. However, the higher food intake in the salt marshes was not reflected in the long-term dietary body condition, either because the individuals visited the marsh creeks infrequently or the same populations were sampled in the marsh and in the subtidal. The diet composition of the planktivore herring in the salt marsh resembled that from the subtidal. Consistently, the abundance and density of zooplankton did not differ among the two habitats. The other omnivore and benthivore fish species consumed more polychaetes, especially the common ragworm *Hediste diversicolor*, in the salt marsh than in the subtidal. In contrast to the planktonic prey resources, the benthic prey resources, especially *H. diversicolor*, occurred in higher densities in the salt-marsh creeks. Despite a relatively high diet overlap in the salt-marsh creeks, the densities of this prey were – relative to the low predator densities – high enough to relax diet competition. Thus, the results of Chapter 4 imply that the Wadden Sea salt marshes – although fish are mostly restricted to the marsh creeks – are valuable feeding habitats. Cattrijsse and Hampel (2006) argued that the bare, unvegetated salt-marsh creeks are not different from the tidal flats. Our results revealed that they are different. Shallow tidal flats can be indeed hydrologically as extreme as the salt-marsh creeks (Berghahn, 1984), but they are not as much sheltered from wind and waves (Friese et al., 2020a; Chapter 3). In the salt-marsh creeks fine sediments can settle down, resulting in a higher softness and penetrability than in wave exposed areas with sandy sediments (Johnstone and Norris, 2000; Valiñas et al., 2012). This enhances the ability of small fishes and crustaceans to forage in the surface sediments, reflected in the higher stomach contents we found in the muddy salt-marsh creeks. These fine sediments are also denser, thus anoxic in the deeper layers, and accumulate organic detritus and benthic algae on the surface layers. The sediment surface layers of muddy substrates are inhabited by e. g. harpacticoid copepods or the mud shrimp *Corophium volutator*. Even those macrobenthic species, that can inhabit the deeper anoxic zone by building a protective layer, are attracted by the surface. In clear waters, as in the salt-marsh creeks, surface deposit feeding is more profitable than filter feeding (Esselink and Zwarts, 1989). This stimulates surface activities of the benthic infauna, such as *H. diversicolor* or the bivalve *Limecola balthica* (Taghon et al., 1980; Peterson and Skilleter, 1994), and increases its accessibility to small fishes. By contrast in sandy substrates, sediment erosion and overlay disturbs frequently the surface layers and stimulates the benthic infauna to recede into the deeper layers (Zwarts and Wanink, 1993), where it is inaccessible for small fishes. Small juvenile fish eat more in relation to their body weight than large adult fish, they have less energy reserves, and thus sufficient food resources are more important for them as for larger adult fish (Cushing, 1975). Therefore, in relation to the potential risks (Friese et al., 2020a; Chapter 3) small fish have higher potential benefits from using the salt-marsh creeks than adults would have. In conclusion, although the vegetated marsh surface is rarely accessible, the salt-marsh creeks are valuable feeding habitats for fish due to low diet competition and abundant and accessible benthic prey resources.

The importance of the accessibility of prey resources became also apparent in **Chapter 5**. This chapter investigated the importance of terrestrial prey resources, which were assumed one of the benefits salt marshes can provide for fish (Laffaille et al., 2000b; Whitley and Bollens, 2014). We hypothesised that the consumption of terrestrial prey differs between fish species, seasons and the grazing treatment of the salt marsh. Livestock grazing can change the vegetation and consequently the terrestrial arthropod communities (Meyer et al., 1995; van Klink et al., 2013). Indeed, livestock grazing by sheep narrowed the diet of fishes in the Wadden Sea salt marshes during winter. However, this anthropogenic impact affected only the three-spined stickleback and the common goby and not the herring and sand goby. On the one hand, livestock grazing decreased the abundance of the most important terrestrial prey, *Orchestia gammarellus*, significantly, probably due to decreasing plant detritus in the marsh. On the other hand, the accessibility to terrestrial prey was limited to winter storm floods. Hence, the negative effect of sheep grazing was only a temporary phenomenon during winter season. *O. gammarellus* is an energy-rich and probably an easy to catch prey – in case it behaves similar as its close relative, *Platorchestia platensis*, which emerges from the vegetation during flooding and swims agitated through the water column in search of flotsam to clamp on and to drift towards the coast (Rüppell, 1967). Low energetic costs and high energetic benefits of foraging on *O. gammarellus* in the salt marshes during a time period, when other marine prey becomes scarce (Zwarts and Wanink, 1993), can benefit the three-spined stickleback and the common goby. In the absence of *O. gammarellus* – in the grazed salt marsh – they found still similar amounts of other prey resources, especially *H. diversicolor*. While *H. diversicolor* was the preferred prey year round and also available during winter in the marsh, three-spined sticklebacks and common gobies switched their diets towards *O. gammarellus* as soon as this prey became available indicating that it is even preferred over *H. diversicolor*. Compared to the first study concerning the effect of sheep grazing on fish diets (Laffaille et al., 2000b), our results showed that the importance of this anthropogenic impact depends on various factors, namely the flooding height and the predator fish species. We conclude, that sheep grazing of salt marshes affects fish diets negatively, but as only certain fish species are affected and due to the limited temporal impact and the availability of other than terrestrial prey, even grazed Wadden Sea salt marshes can be valuable feeding grounds for fish.

In **summary**, the results of this thesis indicate, that, the Wadden Sea salt marshes provide profitable conditions for small fishes and crustaceans, although the marshes are anthropogenically modified and the vegetated marsh surface is rarely accessible. But salt-marsh creeks are also a potential trap; they provide only a single exit to enter and leave the habitat. Only a few small-sized species were tolerant enough taking the risks, such as high temperature or getting trapped in small pools during low tide. However, those individuals using the salt marshes find shelter from predators and profitable feeding conditions via clear waters and low flow velocities, high prey densities and low competition pressure. During winter, when marine prey is scarce, some species, such as the three-spined stickleback and the common goby, can additionally exploit terrestrial arthropods, such as *O. gammarellus*, from the flooded marsh surface. Although no long-term nutritional benefit was found in this study, the combination of low predation disturbance, high food availability, low diet competition, relatively low energetic costs for catching prey, seasonally higher temperatures and sufficient oxygen supply, promote a faster growth of nekton using the salt marshes. Summarizing the results of the thesis, the Wadden Sea salt-marsh creeks combine two valuable habitat properties for small nekton: high food availability and low predation pressure. Animals are attracted by habitats of high prey resources and so are their predators – leading to a trade-off between risking predation mortality and satisfying energetic demands. In salt-marsh creeks, however, the extreme abiotic conditions seem to favour small nekton and their prey, but to exclude their predators.

Salt marsh microhabitats

Salt marshes are dynamic ecotones of a variety of microhabitats, such as the different zones on the vegetated marsh surface, different creek sections of variable structural complexity and flow dynamics, different geomorphological shapes of the marsh edge and salt marsh pools and ponds (Chapter 1). Knowledge of how these small scale units affect nekton can provide valuable information on which features should be considered in salt-marsh restoration projects.

The results of the macroendozoobenthos distribution within the salt-marsh creek cross-section indicates that creeks with a U-shaped cross-section might be more valuable for fish than V-shaped creeks, because in the former a larger area is longer inundated and thus available as foraging ground. In the creek centre, we observed increased deposition of broken fragments of mussel shells compared to the areas closer to the creek bank. This is probably caused by higher flow velocities in the creek centre and might also explain the lower densities of polychaetes and bivalves there. Thus, this narrow strip, where also at low tide a small rivulet (ca. 0.5-1.5 m width and ca. 2-20 cm deep in the sampling area, depending on creek size) keeps flowing, might be a less profitable feeding habitat than the lateral creek slopes, which have a lower flow velocity and higher densities of polychaetes and bivalves. The higher elevated creek banks are flooded less frequently, offering less benthic food and a shorter access time. In U-shaped creeks the higher elevated creek banks cover a smaller area and provide a longer access time relative to the foraging area than V-shaped creeks.

Whether the marsh edge is connected to the aquatic system via shallow or steep slopes can affect nekton abundance and density (La Peyre and Birdsong, 2008). La Peyre and Birdsong (2008) observed a higher species richness but lower densities in salt-marsh edge microhabitats with steeper than with shallower slopes in a salt marsh in Louisiana, USA. They hypothesized that the larger irregularity on steep slopes provides more diverse ecological niches and, hence, potentially explains the larger species richness. In Wadden Sea salt marshes such small scale habitat utilization patterns are still unknown, but naturally meandering creeks with alternating shallow slip-off slops and steep cut banks would increase habitat complexity and are thus probably of higher quality for nekton (Mattila, 1992; Almany, 2004) than artificial straight salt-marsh creeks, which dominate along the Wadden Sea coast.

The geomorphological shape of salt marshes and thus the compilation of microhabitats within the marsh is affected by multiple processes interacting differently over different time scales. For example, in a nine-year nutrient-enrichment experiment in a cordgrass-dominated salt marsh in Massachusetts, USA, eutrophication caused on the short term an increased production of benthic algae and invertebrates and finally an increase in fish abundance, in particular the mummichog (Nelson et al., 2019). However, on the long-term the eutrophication destabilized the creek banks via i. a. a reduction in below-ground biomass of the cordgrass (*Spartina spp.*) and an increased water content of the soil (Deegan et al., 2012). As a consequence creek banks collapsed into the salt-marsh creeks causing not only an annual loss of 0.2 m^3 of marsh within each meter along the creek channel edges (Deegan et al., 2012), but also a decoupling of the food webs of the terrestrial parts of the marsh and the aquatic creek (Nelson et al., 2019). The steep marsh cliffs reduced the accessibility of fish to terrestrial invertebrates and the cracks and crevices, in which predators, such as the American eel (*Anguilla rostrata*), can hide, hindered the small fish to enter the high-marsh habitats (Nelson et al., 2019). Finally, the loss of terrestrial invertebrate food reduced the growth rates and the abundance (biomass and density) of the small fishes (Nelson et al., 2019). In summary, the nutrient-enrichment experiment in the USA demonstrates that ecosystem processes that initially affect the terrestrial part of the salt marsh can also affect the nekton in the marine part and that they may cause different consequences in the long-term than in the short-term (Deegan et al., 2012; Nelson et al., 2019). Although the cordgrass marsh of this long-term experiment differs significantly from the Wadden Sea salt marshes (Cattrijsse and Hampel, 2006), some similarities can be observed: (1) in Wadden Sea salt marshes creek slopes, especially in the high-marsh areas, are steep, (2) the terrestrial and marine food webs are mostly decoupled and fish can use the terrestrial invertebrates only during winter storm floods (Friese et al., 2018a, 2020c; Chapter 4 and 5), (3) terrestrial invertebrates, in particular *O. gammarellus*, was a favoured prey, when accessible (Friese et al., 2018a; Chapter 5), (4) large areas of the German Wadden Sea salt marshes are used for livestock grazing (Esselink et al., 2017), that fertilizes the marsh with sheep and cattle faeces, and (5) the soil pores of the grazed salt marshes are less connected resulting in a higher water content (Keshta et al., 2020). However, whether belowground biomass, that stabilizes the soil, is higher or lower in grazed than in ungrazed Wadden Sea salt marshes is still unclear (Elschot et al., 2015; Müller et al., 2017) and erosion along the creek edges not a major concern (Esselink et al., 2017). Still, the Wadden Sea salt marshes have higher similarity to the eutrophication-induced altered geomorphology of the marshes in the experiment than to the unaffected control sites of the experiment. This raises the question, whether the habitat quality for nekton and the connection of the terrestrial and marine food web are already decreased compared to a Wadden Sea salt marsh that is less affected by anthropogenic impacts.

Beside the above mentioned small-scale vertical differences within the creek´s cross-section, habitat quality and function varies probably also in a horizontal dimension. Abiotic habitat characteristics (flooding duration, depth, flow conditions, temperature, etc.) change within salt-marsh creek system along a sea-land gradient. Landward low-order creeks are flooded shortest but provide the highest structural complexity with overgrowing vegetation than seaward high-order creeks. In US marshes nekton abundances were higher in narrow and shallow low-order than in wider and deeper high-order creeks (Weinstein, 1979; Rozas and Odum, 1987c; McIvor and Rozas, 1996). However, in Chinese and German salt marshes the opposite pattern, i. e. higher abundances in high-order than in low-order salt-marsh creeks, was observed (Jin et al., 2010; Dänhardt et al., 2011a).

Marsh microhabitats that are inundated during the whole tidal cycle, such as the small rivulets in the creek centre or salt-marsh pools, may serve as predator refuges for fish larvae even during low tide (MacKenzie and Dionne, 2008; Rieucau et al., 2015; Allen et al., 2017). In the salt marsh near St. Peter-Ording, we observed abundant plaice larvae during low tide in the rivulets and juvenile gobies and sticklebacks in marsh pools (Friese et al., 2020b; Chapter 2). In the UK, salt-marsh pools are also used by juvenile sand gobies, mullets (*Chelon spp.*), and flatfishes, such as plaice (Healey, 1972; Frid, 1988; Frid and James, 1989). Frid (1988) reported that sand gobies even spent the whole summer in pools on the salt-marsh surface. In a salt marsh in the St. Lawrence estuary, Canada, also adult sticklebacks (*Gasterosteus wheatlandi*, *G. aculeatus*, *Pungitius pungitius*) inhabited the marsh pools (Walsh and FitzGerald, 1984). In the Wadden Sea some pools are only connected to the marine tidal system during winter storm floods; others are connected via small ditches during spring tides. Opportunities to access and escape this environment are limited and the pools can become traps with various potential threats. Oxygen shortage might occur more often, especially during night (Koop-Jakobsen and Gutbrod, 2017; R. Klinger, pers. comm.), and salinity and temperature may vary stronger in marsh pools than in the creeks as tidal mixing is largely missing (Frid, 1988; Cattrijsse et al., 1997; Hunter et al., 2009). Furthermore prey availability and refuge from foraging birds is limited in the enclosed pools (Rieucau et al., 2015), though predation mortality on mummichogs in a high marsh pool, USA, was low in a predator exclusion experiment (Kneib, 1982b). Continuously inundated areas in the salt marshes could provide some benefits as spawning and nursery habitats, e. g. common gobies may use these areas for spawning (K. Heubel, pers. comm.). Male common gobies prepare a nest under an empty shell or something similar (Healey, 1972), and court the females with acoustic and visual traits. Noise, e. g. from marine traffic, disturbs the acoustic courtship (Jong et al., 2018). Anthropogenic noise pollution is probably lower in the remote located salt-marsh creeks than in the open waters. Additionally, the salt-marsh creeks were less turbid, thus also visual courtship is possibly more successful than in the turbid subtidal (Friese et al., 2020a; Chapter 3). Also the relatively warmer summer temperatures in the salt-marsh creeks and pools can increase the spawning success. Common gobies spawn from April to September (Jones and Miller, 1966; Healey, 1972; Fonds and Buurt, 1974), and the juveniles (0+ age group) occurred from June to October in the marsh creeks (Friese et al., 2020b; Chapter 2; Supplement A, Fig. A.3). From June to September water temperatures in the salt-marsh creeks ranged on average around ca. 15-20 °C (Friese et al., 2020a; Chapter 3), just the temperature range of highest goby egg survival (Fonds and Buurt, 1974). The egg development accelerates exponentially with increasing temperatures; in laboratory experiments the time till hatching decreased from 26 days at 10 °C to only 4 days at 25 °C (Fonds and Buurt, 1974). Especially during the summer season, water temperatures are higher in the shallow salt marshes than in the subtidal, thus eggs will develop faster, parental care of the males will be reduced and the fish could reproduce more often over one breeding season (Blom et al., 2019; Friese et al., 2020a; Chapter 3). In conclusion, common gobies could increase their reproductive rate, when selecting the salt marshes as spawning habitats, where they may have a higher mating success (due to lower noise pollution and turbidity) and a faster egg development (due to higher temperatures), while at the same time being relatively save from predators (Friese et al., 2020b; Chapter 2).

Connectivity within the seascape

The role of the salt-marsh-specific nekton in the Wadden Sea ecosystem

The salt marshes are connected with other habitats in the seascape via the tidal flows and currents but also via migratory animals, for example fishes and crustaceans. The nekton that visited the salt marshes were predominantly small-sized, including adults, but also juveniles and larvae, some of which were – when fully grown – important for the commercial fishery, such as brown shrimp, plaice, and herring (Friese et al., 2020b; Chapter 2). The small-sized nekton, whether larva, juvenile or adult, can fill important positions as mesopredators, that transfer nutrients from the lower to the higher trophic levels, in the coastal food web (Fox, 1972; Pockberger et al., 2014; Bergström et al., 2015). The small-sized nekton consumes planktonic and benthic food in the shallow coastal areas, such as the salt-marsh creeks, and migrate back into the subtidal at low tide, where they are eventually eaten by predators, such as larger fish (Ntiba and Harding, 1993; Vorberg and Breckling, 1999; Pockberger et al., 2014), birds (Dänhardt et al., 2011b; Dänhardt and Becker, 2011b; Jouta et al., 2018), or seals (Hall et al., 1998). The common goby is supposed to be a keystone species in the shallow waters of the Wadden Sea and similarly the three-spined stickleback was shown to reshape the food web via top-down and bottom-up effects in the Baltic (Bergström et al., 2015). The North Sea ecosystem is driven by both, top-down and bottom-up processes (Lynam et al., 2017) and thus wasp-waist interactions are supposed important (Fauchald et al., 2011). The intermediate trophic level in wasp-waist ecosystems is usually filled by small planktivore and pelagic schooling fishes, e. g. herring (Bakun, 2006). However, the shallower the waters the more is the productivity of planktonic prey resources outpaced by that of benthic resources. Thus, here small benthivore fish and crustaceans, such as brown shrimp, common goby and three-spined stickleback, may fill this central food web position.

Outwelling hypothesis

Salt marshes are among the most productive systems worldwide (Kneib, 1997a). The outwelling of particulate organic matter (POM) from salt marshes could possibly also fuel larger areas of the coastal ecosystem (outwelling hypothesis; Turner et al., 1979b, 1979a; Kneib, 1997a; Sheaves et al., 2015). Fish visit the highly productive salt marshes during high tide for feeding (e. g. Rozas and LaSalle, 1990; Hollingsworth and Connolly, 2006; Platell and Freewater, 2009; Friese et al., 2018a, 2020c; Chapter 4 and 5) and thus they may function as biotic vectors transporting POM to the adjacent habitats (Weisberg and Lotrich, 1982; Laffaille et al., 1998; Lefeuvre et al., 1999). In the Bay of Mont Saint-Michel, France, fish exported more than 12 kg POM (dry weight) per year and hectare from the salt marshes towards the coastal area (Laffaille et al., 1998; Lefeuvre et al., 1999). Compared to the amounts of POM exported via the tidal currents, i. e. via abiotic vectors, the export via fishes seemed to be subordinated, accounting for 0-10 % of the outwelling POM (Laffaille et al., 1998; Lefeuvre et al., 1999). However, the POM exported via fish is faster integrated into the food web, e. g. when the fish are eaten offshore by predators or scavengers, thus turnover rates are probably higher (Lefeuvre et al., 1999). The outwelling of marsh production into the marine food web increases with increasing salt marsh flooding frequency, height and duration (Baker et al., 2013). In North American salt marshes, where the vegetated marsh surface is regularly flooded, the tides can export almost half of the production (Teal, 1962), while in the Wadden Sea salt marshes, where the tidal current remains predominantly within the unvegetated marsh creeks, only up to 14 % of the production is exported or POM is mainly imported not exported (Wolff et al., 1979; Dankers et al., 1984; Bouchard et al., 1998). Thus, in the higher elevated Wadden Sea salt marshes, organic matter fluxes via the trophic cascades including nekton as biotic vectors (Fig. 6.1) could be relatively more important. Estimations of Cattrijsse et al. (1997) showed, that if all juvenile brown shrimps inhabiting a 27 km² tidal marsh in the Westerschelde Estuary in 1990 would have grown to commercial size (ca. 50 mm total length, Temming and Damm, 2002), their biomass would be almost equal to the total yield of the Belgian brown shrimp fishery of that year. The organic matter export of coastal to offshore habitats via nekton depends also on the migration behaviour of nekton (Currin, 1984). Resident species tend to enter the salt marshes earlier during the flood tide than transient species, and leave the habitat later with the receding tide (Kneib, 2002). Thus, they could possibly ingest more food and consequently export higher amounts of organic matter to the subtidal. However, the home range of resident nekton species is smaller and transient species as well as some juvenile life stages, that emigrate from the salt marshes, can disperse the productivity of the marsh to larger areas in the seascape or even into other ecosystems (Currin, 1984; Kneib, 2002). Whether the organic matter import or export predominates, and thus whether the coastal system can benefit from the high productivity of the salt marshes, depends on multiple biotic and abiotic factors (Fig. 6.1). Therefore, the organic matter fluxes are subject to strong spatiotemporal variations and the role of salt marshes in the organic matter fluxes in ecoscapes must be investigated regionally and over longer time scales.

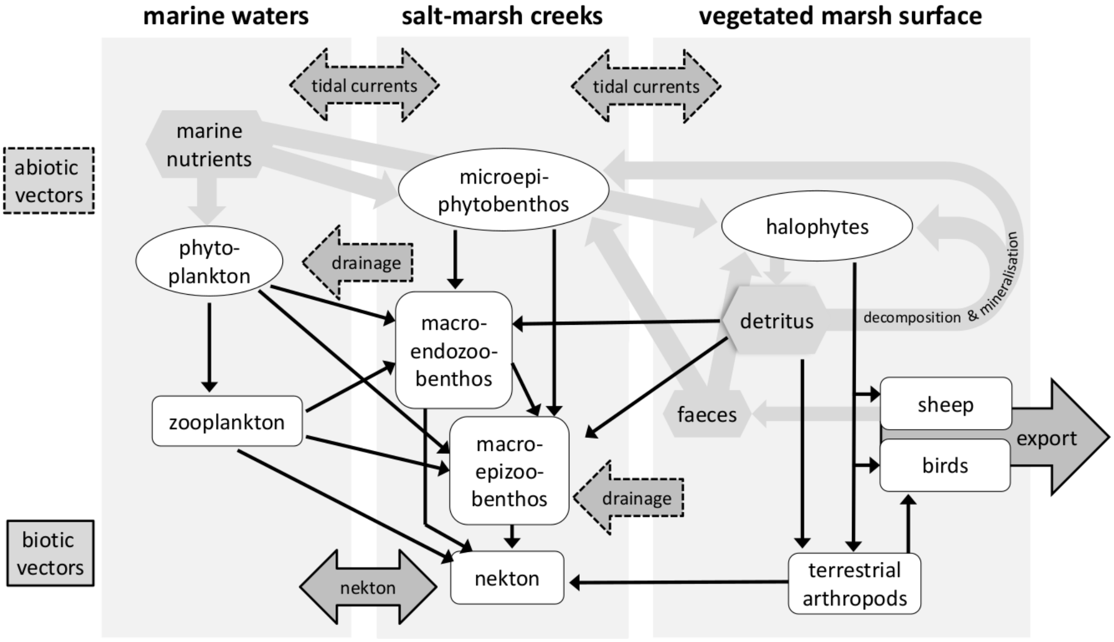


Fig. 6.1: Possible pathways of organic matter fluxes towards fish in the Wadden Sea salt-marsh creeks originating from the adjacent marine waters and the vegetated marsh surface. Black arrows indicate organic matter fluxes via consumption, grey arrows indicate nutrient fluxes.

Salt marshes as sedimentation areas in the coastal ecosystem

Finding pelagic schooling fish, like hering and smelt, in shallow marsh creeks was surprising as they usually prefer deeper water layers (Dänhardt and Becker, 2011a) and as they have a relatively sensitive skin, and physical contacts can cause scale loss and injuries with potential lethal effects (Suuronen et al., 1993; Suuronen et al., 1996). Compared to the omni- and benthivore fishes, the salt-marsh creeks also offer no additional food resources for the planktivore herring (Friese et al., 2018a, 2020c; Chapter 4 and 5). However, the low flow velocity and low turbidity may be an attractive habitat feature in salt-marsh creeks for herrings and other nekton species, as it improves their foraging skills (Moore and Moore, 1976b; Robertis et al., 2003; Tudorache et al., 2012; Guthrie, 2014). Laur et al. (2014) argued that fish larvae, particularly goby larvae that are only 2.5-3.0 mm large at hatching (Fonds, 1970), are especially sensitive to physical contacts with suspended sediments, because sand grains could damage their epidermis, which consists of only a few cell layers (O´Connell, 1981; Boehlert, 1984). Thus, specifically very small larvae, such as goby larvae, can benefit from the low flow velocities, low amount of suspended particles, and fine-grained sediments in the salt-marsh creeks.

Sedimentation areas, such as salt marshes, where suspended sediments can settle down, affect not only those animals that use these habitats, but can also affect the water turbidity of the large-scale coastal ecosystem. A loss of muddy areas, i. e. sedimentation areas, dredging of the seabed, sand extraction, as well as deepening rivers that pour into the Wadden Sea, caused sediments to remain longer in the water column and thus increase the turbidity of the Wadden Sea (Jonge et al., 1993; Wilhelmsen and Dittmann, 2004). An increased turbidity reduces the photosynthesis capacity of phytoplankton and microepiphytobenthos (Jonge et al., 1993) and the foraging success of common terns (Baptist and Leopold, 2010). Laur et al. (2014) hypothesised, that the decrease in the abundance of goby larvae (*Pomatoschistus spp.*) in the last 50 years might be related to increased water turbidity. Salt marshes could contribute in reducing the turbidity in the Wadden Sea, while at the same time accumulating sediment, which benefits coastal protection.

Limitations of the study

Nekton size classes

The aim of this thesis was to evaluate the habitat value for a broad variety of nekton species and life stages. Thus, the findings are not sufficient to, assess the nursery value of the salt marshes, because the applied mesh size of the fishing gear was not adjusted to catch larvae and – depending on size and net clogging – larvae abundance was probably underestimated. Still, a variety of larvae and juveniles were caught, such as plaice, herrings, gobies, brown shrimps, and shore crabs, raising the question whether the salt marshes serve as nurseries for them. Cattrijsse et al. (1997) observed that postlarval brown shrimps used an estuarine marsh in the Westerschelde for up to three weeks as a nursery, but the nursery value varied interannually and the importance for the adult stock remained unclear.

Temporal habitat utilization

The applied fishing gear affects not only the body sizes caught, but also catch amounts and species composition. Habitat comparisons require usually different methods due to different physical characteristics of the habitats and therefore different efficiency of gears (Blaber et al., 1989; Eggleston and Dahlgren, 2001; Gillanders et al., 2003; Lechêne et al., 2018). Hence, comparing nekton communities in different habitats comes with methodological difficulties. Passive gears, such as fyke nets, are highly efficient in shallow, confined and moving waterbodies, such as salt-marsh creeks (Hinz, 1989; Mazumder et al., 2005). In deeper subtidal areas, however, fyke nets are less efficient and catchability of different species may vary from shallow and confined waters. Trawl nets, which are a standard fishing gear in deeper areas, cannot be applied in the small, shallow and uneven salt-marsh creeks (Cattrijsse and Hampel, 2006). Therefore, comparisons of nekton densities in the salt marsh and in other habitats of the seascape must be interpreted with caution. The catchability of fyke nets in salt marshes depends on the species-specific residence time and the time of leaving the habitat. Resident species stayed longer in flooded North American marsh areas than transient species due to their longer travel distance and a lower tolerance to the risk of stranding (Allen et al., 2017; Kneib, 1995; Kneib and Wagner, 1994). The lower the water levels the less water ran past the fyke nets and the less likely organisms were missed to be caught. Thus, catchability may vary among resident and transient species and the point in time they leave the salt-marsh creeks. In contrast to American marshes, the Wadden Sea salt-marsh creeks and the offshore tidal flats run almost completely empty, so that the majority of nekton has to travel the same distance to the subtidal to bridge low tide. During spring tide the inundation time of the salt-marsh creeks, the interaction between the terrestrial and marine systems, the habitat availability and the potential residence time is maximized (Kneib, 2002), which is why sampling was conducted at spring tide. However, species compositions, abundance, and diets may vary at neap tide (Hampel and Cattrijsse, 2004). Furthermore, spring tides coincided with low tides in the mornings and evenings resulting in clearly separated day and night catches. Habitat utilization patterns are likely to vary from our results, when e. g. tides with high tide at dusk and dawn are analysed. Thus, further investigations on these species-specific small-scale residence times and feeding ecology are important to quantify temporal habitat utilization and, hence, to progress in understanding the habitat quality of the Wadden Sea salt marshes for each of the seven characteristic species of this habitat (Friese et al., 2020b; Chapter 2).

Future perspectives

Potential future changes in the salt marsh habitat

Various threats, such as pollution and sea-level rise, may affect salt marshes increasingly in the future, and thus possibly change the habitat quality for nekton.

As salt marshes are sedimentation areas, they are predestined to accumulate drifting plastic waste (pers. observation). The specific situation of macro- and microplastics and other anthropogenic litter in the Wadden Sea salt marshes is largely unknown and was not even addressed in the last Wadden Sea quality status report (Esselink et al., 2017; Fleet et al., 2017). Especially microplastics, which also act as carriers for toxic chemicals, can be mistaken as prey by fish, such as herring (Hermsen et al., 2017). In laboratory experiments Oliveira et al. (2013) found neurotoxic effects of microplastics and the chemical pyrene on juvenile (0+ age group) common gobies. Common gobies – including juvenile life stages – are a characteristic species of salt marshes and are thus especially threatened. Thus, plastic pollution can decrease the habitat quality of Wadden Sea salt marshes for nekton and research efforts to scale the impact are of urgent need.

The summer temperatures are already extreme in the salt-marsh creeks and the worldwide temperature increase predicted by climate models would transfer faster to the water temperature in the shallow salt-marsh creeks than in deeper coastal areas (Oczkowski et al., 2015). Hence, in the future also the oxygen concentrations in the salt-marsh creeks and pools may drop. Indeed, the oxygen concentrations are nowadays sufficient for the nekton (Friese et al., 2020a; Chapter 3), and the salt-marsh-specific nekton community is relatively robust towards high temperatures, but at too high temperatures and too low oxygen levels the salt-marsh creeks could become temporarily uninhabitable (Pörtner and Knust, 2007). Moreover, laboratory experiments showed that the three-spined stickleback did not adapt its temperature preference despite a multigenerational exposure to increased ambient temperatures (Pilakouta et al., 2019). Rising temperatures in combination with the current salt-marsh management that promotes an increase of water-logging to increase plant diversity could cause an increased abundance of mosquitos, which inhabit salt-marsh pools during larval development (Lühken et al., 2009). In recent years – possibly as a consequence of several consecutive warm years – invasive mosquito species emerged in Germany, some of which are vectors of disease agents (Kampen et al., 2017). Since the Early Middle Ages the Wadden Sea was a malaria-stricken region with outbreaks coinciding with high summer temperatures (Knottnerus, 2002). In the 1950s malaria finally disappeared as a consequence of a change of the lifestyle of the coastal population and the drainage of the coastal areas, including the salt marshes, during the last centuries (Knottnerus, 2002). Nowadays, a return of malaria in Northern Europe is highly improbable (Knottnerus, 2002), but the combination of invasive mosquito species, rising temperatures and an increasing water-logging requires an adapted salt-marsh management in the future. Diseases transmitted by mosquitoes could possibly also be a threat for breeding birds (Lühken et al., 2017). In many US salt marshes drainage ditches were used for mosquito control (Gedan et al., 2009). However, on the other side, some breeding birds use mosquito larvae from salt-marsh pools as food resources (Clarke et al., 1984). A reduction of these microhabitats and food resources decreased the breeding habitat quality of intensively drained salt marshes for birds (Clarke et al., 1984). Fish could possibly control mosquito densities in salt-marsh pools, when the pools are connected with the tidal system to allow fish to enter and leave this microhabitat (Harrington, Jr. and Harrington, 1961; Morton et al., 1987; Morton et al., 1988; Hulsman et al., 1989).

The predicted temperature increase will entail a sea-level rise. The sea-level rise would cause more frequent salt marsh flooding and thus increase the habitat accessibility, which is nowadays a major constraint of the utilization of salt marshes by nekton as concluded from this thesis. Although, nekton will benefit from sea-level rise on the short term, on the long term it could result in erosion and thus in salt marsh area loss. In case the sediment accretion rates cannot keep pace with the sea-level rise, the regularly flooded pioneer zone, including patches of *Spartina spp.*, which is valued as fish nursery in the USA, would diminish first as it is squeezed within the mud flats and the marsh cliffs, that break off during the higher storm floods (Esselink et al., 2017). Sediment accretion rates differ between the different salt marsh zones and between different salt marsh types, they are higher in the mainland salt marshes than in the back-barrier island marshes (Butzeck et al., 2015; Esselink et al., 2017). Thus, the modelled sea-level rise will have probably a more negative effect on the spatial extent of back-barrier salt marshes than on the mainland salt marshes (Butzeck et al., 2015) and might turn high marsh areas into low marshes (Butzeck et al., 2015). Such changes in flooding dynamics would have major effects on the long-term habitat availability and accessibility for nekton.

Under a rising ocean scenario the importance of salt marshes for coastal protection will increase. The importance of salt marshes for fish and crustaceans will also increase with increasing flooding frequencies and thus an increased accessibility. Although, salt marsh nekton habitats cover only small areas today, the importance of these areas in relation to other habitats could increase with increasing flooding. Moreover, the importance of salt marsh habitats for the salt-marsh specific nekton might increase, when the quality of other habitats in the seascape used by these species decreases. For example, when the Sylt Outer Reef (Natura 2000 site) becomes a zero use zone (EU-proposal of Germany; Sell et al., 2011), the Dutch shrimper will likely shift their fishing effort towards the coast of Schleswig-Holstein, increasing the competition in the areas off the islands and likely tempting the German fishers to shift their efforts further into the Wadden Sea (T. Schulze, pers. comm.). Thus, under this scenario the fishing effort of the brown shrimp fishery in the Wadden Sea would increase. Gobies, sticklebacks, juvenile herring and flatfish, and undersized brown shrimp – the typical species and life stages of the salt marshes – are regularly caught and discarded in the brown shrimp fishery, and hence, for these species and life stages refuge areas that cannot be used by commercial fisheries, such as salt marshes, may become increasingly important as nursery, feeding, and refuge habitats.

Future research needs

This thesis was the first comprehensive study evaluating the habitat quality of marine Wadden Sea salt marshes for nekton and a variety of ecosystem processes and links between the marine and terrestrial systems could not be addressed within this study.

First of all, the value of salt-marsh pools as fish nurseries should be investigated, because these microhabitats were identified as important nekton habitats and nurseries in many other salt marshes (MacKenzie and Dionne, 2008; Hunter et al., 2009; Allen et al., 2017). Also in the German salt-marsh pools, we observed juvenile fish, but these habitats are rare in the man-made marshes. Whether the marsh pools are also used as spawning habitats, and which characteristics (e. g. size, depth, connectivity) are needed by the fish larvae and juveniles, is important for considering these microhabitats in future management decisions.

Next, research on the importance of the vegetation for nekton would be needed, because modifying vegetation patterns, mostly via livestock grazing, is one of the most important management tools in Wadden Sea salt marshes (Nolte, 2014). Grazing, reduces the abundance of the two plant species *Atriplex portulacoides* und *E. atherica* in salt marshes, thus causing a habitat loss for the amphipod *O. gammarellus*, which prefers these two plant species (Laffaille et al., 1999; Laffaille et al., 2000b; Laffaille et al., 2001; Laffaille et al., 2005). As *O. gammarellus* is the favourite terrestrial invertebrate prey of fish, livestock grazing finally affects fish diets negatively (Laffaille et al., 2000b; Friese et al., 2018a; Chapter 5). However, it is still unclear whether fish and maybe also crustaceans enter the vegetated salt-marsh surface during storm flood events, as they do in North American salt marshes (Kneib, 1987; Rozas and LaSalle, 1990; West and Zedler, 2000; MacKenzie and Dionne, 2008). If they enter the salt marsh vegetation, the accessibility of the area could depend on the plant community, as the stem density and thus interstices differ. Salt marshes, where fish frequently enter the vegetated surface are mostly dominated by *Spartina spp.*, which has a rather low stem density compared to those plants dominating European salt marshes, particularly *E. atherica*. Thus, the habitat quality of a flooded salt-marsh surface might depend on the distribution of vegetation patches. To find out whether fish enter the vegetated salt marsh for foraging or whether they remain in the salt-marsh creeks and consume the prey that is washed out with the tide, the vegetated salt marsh must be sampled. A comprehensive review on catch methods to sample fish on the surface of salt marshes was recently published by Harrison-Day et al. (2020). A promising approach to sample particularly the vegetated surface of the German Wadden Sea salt marshes would be a flume weir (Kneib, 1991).

Additionally, studies evaluating the predation pressure on nekton in salt-marsh creeks and pools by birds are needed to validate the refuge hypothesis, that nekton in salt marshes are not only save from aquatic predators (Friese et al., 2020b; Chapter 2), but also from avian predators. We hypothesized that the confined and relatively shortly flooded salt-marsh creeks are an unfavourable feeding habitat for birds (Friese et al., 2020b; Chapter 2). To my knowledge, only Enners et al. (2019) reported that birds, particularly pied avocets (*Recurvirostra avosetta*), feed on fish in intertidal creeks in the lower salt marsh. To estimate predation mortality further studies on bird´s foraging habits in salt marshes are needed.

Previous studies highlighted that salt marshes can contribute substantially to commercial fishery by serving as nurseries for exploited species (Rozas and Hackney, Courtney, T., 1983; Boesch and Turner, 1984; Minello et al., 2012). The most relevant fishery in the Wadden Sea targets brown shrimp. Cattrijsse et al. (1997) reported that brown shrimp used an estuarine tidal marsh in the Westerschelde as nursery, that provided food and shelter from predators. In the marine salt marshes, investigated in this thesis, brown shrimp was the second most frequently and abundantly caught species following the common shore crab, which however is attracted by the fyke nets. The majority of brown shrimps in the salt marsh were below consumption size (< 50 mm total length; Temming and Damm, 2002; Burgund, 2017). This correlates with previous studies that report that larger brown shrimp live mainly in deeper areas, while juveniles inhabited the shallow tidal flats during flood tide (Janssen and Kuipers, 1980; Boddeke et al., 1986; Saathoff, 2018). Brown shrimp is not only an important fishery species, it is also one of the most abundant epibenthic species in the Wadden Sea and serves during all life stages as prey for a variety of predators, e. g.

gadoid fish (Kühl, 1961; Moore and Moore, 1976b, 1976a; Tiews, 1978; Redant, 1980; Jansen, 2002). Thus, the role of salt-marshes within the life cycles of brown shrimp, which prey resources they use there and whether using salt marshes has a positive or negative effect on their condition would be worth investigating.

Finally, also the connectivity of the microhabitats within the salt marshes and between different habitats in the coastal seascape demand further investigations. Fish feed within the salt marshes (Friese et al., 2018a, 2020c; Chapter 4 and 5) and thus benefit from the high productivity of these habitats (Chapman, 1977). Through which pathways nutrients from the three kinds of primary producers (terrestrial halophytes, microepiphytobenthos and phytoplankton) are transferred to the higher trophic levels, i. e. the fish, is still unknown (Fig. 6.1), but could be revealed via stable isotope analysis (Friese et al., unpublished). To understand organic matter fluxes and ecosystem processes, we need further research on the home ranges of the salt-marsh-specific nekton community and their migration routes, e. g. whether they use predominantly intertidal creeks for migrations. These migration patterns could be analysed via mark-recapture experiments (Teo and Able, 2003), stable isotope analysis (Green et al., 2012), or otolith microchemistry (Arai et al., 2003).

This study analysed seasonal and diurnal habitat utilization patterns to take account for the temporal variations in species-habitat interactions. However, interannually and tidally resolved data were not within the scope of this study. Due to the highly variable conditions, predominantly short-living species, such as gobies and sticklebacks, or only certain life stages inhabit the salt marshes. Thus, abundances can vary significantly between years, because the influence of new cohorts on the population size increases with decreasing life span or because only a single cohort inhabits the salt marshes as in the case of larvae and juveniles. Multi-annual presence-absence data were used to define frequent and abundant species that are typical for the Wadden Sea salt marshes. However, these data were not sufficient to analyse interannual abundance variabilities. A tidal resolution covering spring and neap tides or species-habitat-interactions covering the course of the tide could not be obtained during this study. Albeit, the lunar and tidal cycle are important factors structuring animal occurrence demanding further investigations (Boswell et al., 2019; Nemerson and Able, 2020).

The importance of small-scale and long-term research

This PhD project highlighted that salt marshes are highly diverse habitats for nekton. Habitat characteristics and consequently ecosystem processes seemed to become increasingly structurally complex towards the coast. While (1) subtidal areas provide comparably homogenous temperature conditions, currents and sediment characteristics that change over hundreds of meter, (2) tidal flats have less stable temperatures, but currents and sediment characteristics still change on a relatively large scale, and finally (3) salt-marsh creeks have strongly varying temperatures and flow and sediment characteristics changing within centimetres. Small-scale variability of ecosystem processes and function might be especially important at ecotones, where two different ecosystems interact. For example encounter rates between fish larvae and zooplankton are strongly influenced by small-scale turbulence within tidal fronts (MacKenzie and Leggett, 1991).

Although marine ecosystems are more than terrestrial systems affected by large scale and even global processes, the importance of small-scale research should not be underestimated – especially in shallow coastal systems. Small-scale local events can have an impact on large scales, e. g. Temming et al. (2007) reported that whiting (*Merlangius merlangus*) consumed a local aggregation of over 50 million juvenile cod (*Gadus morhua*) within 5 days. They concluded, that a large portion of predation mortality of juvenile cod is likely driven by such small-scale effects, which might possibly affect large scale population dynamics (Temming et al., 2007). Thus, local and small-scale research can help to understand ecosystem processes. When these abiotic and biotic interactions are proper understood locally, this knowledge can be transferred to other areas with similar features. Worldwide studies on nekton in salt marshes benefited from the huge research efforts in this topic in US salt marshes (e.g. various studies by R. T. Kneib in the Sapelo Island salt marshes mainly since the 1980s). Having decades of multidisciplinary research (including e. g. geology, plant ecology, behavioural ecology, physiology, etc.) within one salt marsh (like the Sapelo Island marshes, Pomeroy and Wiegert, 1981) can enhance our knowledge and understanding of species interactions, abiotic effects, carbon and nutrient fluxes and finally ecosystem services – not only for humans but also for certain organism groups, like fish.

Especially in coastal systems spatiotemporal dynamics are more complex and field work is more challenging than offshore. At least in Germany – most research projects are planned on a time frame of 3-4 years and staff at marine research institutes often change at similar time spans. Thus, some elaborate or protracted experiments (e. g. mark-recapture experiments to evaluate habitat connectivity and migration routes) are rarely performed. With changing staff after research project, know-how on specific methodologies is likely to get lost and equipment is unlikely to be refined over years. For instance, stomach content analyses improve substantially with experience (Hyslop, 1980) and especially with the knowledge of potential prey species in the specific sampling area. As stomach contents are sometimes only fragments of the prey with differing digestion degrees, being familiar with the shape and texture of the fresh prey species and how colours, shape and texture change during digestion can remarkably improve the data quality. Furthermore, coastal research often demands other sampling methods than used standardly on research vessels. The equipment is often self-made and needs to be developed in accordance with the specific characteristics of the habitats and research questions in focus. Even within certain habitat types, e. g. salt-marsh creeks or oyster reefs, methodologies might have to be adapted to local conditions. For example, although fyke nets are suitable fishing gears for fish sampling in salt-marsh creeks (Mazumder et al., 2005), they were not applicable at Hamburger Hallig (see map, Chapter 3), because the creeks were too muddy to work inside, and on the island Neuwerk (see map, Chapter 3), where due to tidal flood gates the flow velocity in the salt-marsh creeks was too high for applying fyke nets. Thus, site-specific knowledge can be essential for successful data collection.

Low-budget research projects, like INTERFACE, would benefit from field laboratories established for decades to analyse multiple aspects of an ecosystem in a specific area (e. g. Marine Institute on Sapelo Island, USA, or Alfred Wegener Institute on Sylt, Germany). Such long-term field stations cannot only provide high quality technical opportunities, which allow also analysis that demand short travel distances between field and laboratory, but can also provide site-specific know-how, when operated at least partly by long-term staff. Altogether coastal research could be more cost-efficient and productive, when close-to-coast facilities, like field laboratories, are established and maintained over decades.

Management implications

Management measures need to reconcile the multiple ecosystem services of salt marshes (Chapter 1). Transferring the findings of this study into management implications will focus on fishes and crustaceans, however, possible consequences of recommended management measures on other ecosystem components will be discussed as well.

The findings of this thesis indicate that the accessibility, the habitat size and the inundation time are the major limits in the habitat quality of salt marshes for nekton (see also Minello and Webb, 1997). According to archaeological studies, anthropogenic modifications of the coastline decreased the habitat size of salt marshes (Probst, 1996; Lotze et al., 2005; Airoldi and Beck, 2007; Esselink et al., 2009; Gedan et al., 2009). Additionally, sheep grazing can negatively affect the fish diets by reducing the abundance of terrestrial prey resources (Friese et al., 2018a; Chapter 5). Thus, management measures, that aim to improve the habitat quality of Wadden Sea salt marshes for nekton, should increase the spatiotemporal accessibility of the salt marshes.

Fishes and crustaceans can only use the flooded parts of the salt marshes, i. e. the intertidal creeks and pools. Longer, deeper and wider salt-marsh creeks keep more water during a longer time than smaller creeks, thus complex wide networks of ramified meandering salt-marsh creeks are likely more beneficial for nekton than the short, straight, and rectangular creeks system dominating in German Wadden Sea salt marshes (Fig. 6.2a and b). In this rectangular well-drained pattern of creeks, the marsh surface tends to be even and in the marsh creeks the water runs off uniformly. Thus, no surface depressions can evolve, neither on the vegetated marsh nor in the creeks, thus low-tide nekton habitats in the salt marshes, i. e. pools (Allen et al., 2017), are rare. Such an evenly distributed drainage comes with several problems, for example the high marsh tends to become monocultures of *E. atherica*, reducing the breeding habitat quality of the salt marshes for some birds (Esselink et al., 2009). When the water runs off evenly over the tidal flat instead of flowing together into increasingly large intertidal creeks (Fig. 6.2b), the salt-marsh creeks become later accessible during the tidal cycle and the nekton will less likely find their way into the salt-marsh creeks (Dänhardt et al., 2011a).

Meandering creeks, especially when they run partly parallel to the coastline, will provide a larger nekton habitat in relation to the salt-marsh area, than straight creeks that run orthogonal to the coastline. Although the drainage ditches are not maintained since decades, they persist till today. In Lower Saxony, clay extraction sites in *E. atherica* monocultures in the high salt marsh were used to led the marsh evolve newly with a natural drainage system (Esselink et al., 2017). However, the new establishment of vegetation within the clay pits can take several decades (Esselink et al., 2017). Another management measure applied in Lower Saxony and the Netherlands is the removal of top-soil to fill up parts of the drainage system and restore the salt-marsh creeks (Esselink et al., 2017). Designing new tidal creek systems with excavating machines would not only be expensive but also damage parts of the salt marshes. Another more cost-efficient and more eco-friendly option to promote meandering salt-marsh creeks would be the installation of alternating groynes. Groynes can redirect the tidal currents towards the opposite creek bank, and thus promote an oscillating current line, that results in cut banks and slip-off slopes (Eberstaller-Fleischandert and Eberstaller, 2014). In the lee of the groynes most likely potholes would evolve and these could serve as low tide refuge and nurseries for nekton (Allen et al., 2017). Thus, alternating groynes at the creek banks could not only increase the habitat diversity but also the similarity to natural salt-marsh creek systems. Natural salt marshes tend to keep more water during low tide in their creeks (indicated by the dark areas in the satellite pictures in Fig. 6.2c and d). The meanders cause a structurally more diverse creek bed in which depressions can evolve, and which then can be used by nekton during the whole tidal cycle. All measures to restore the drainage system will be time consuming as either, in the case of an installation of groynes, the creeks will need several decades to change their pathways, or in case of construction measures with excavating machines the soils and vegetation would take decades to recover.

But an establishment of complex meandering creeks systems will come with a variety of benefits for the salt-marsh system, because it will also increase the topographic variability of the salt marshes. During flooding events, sediment is predominantly

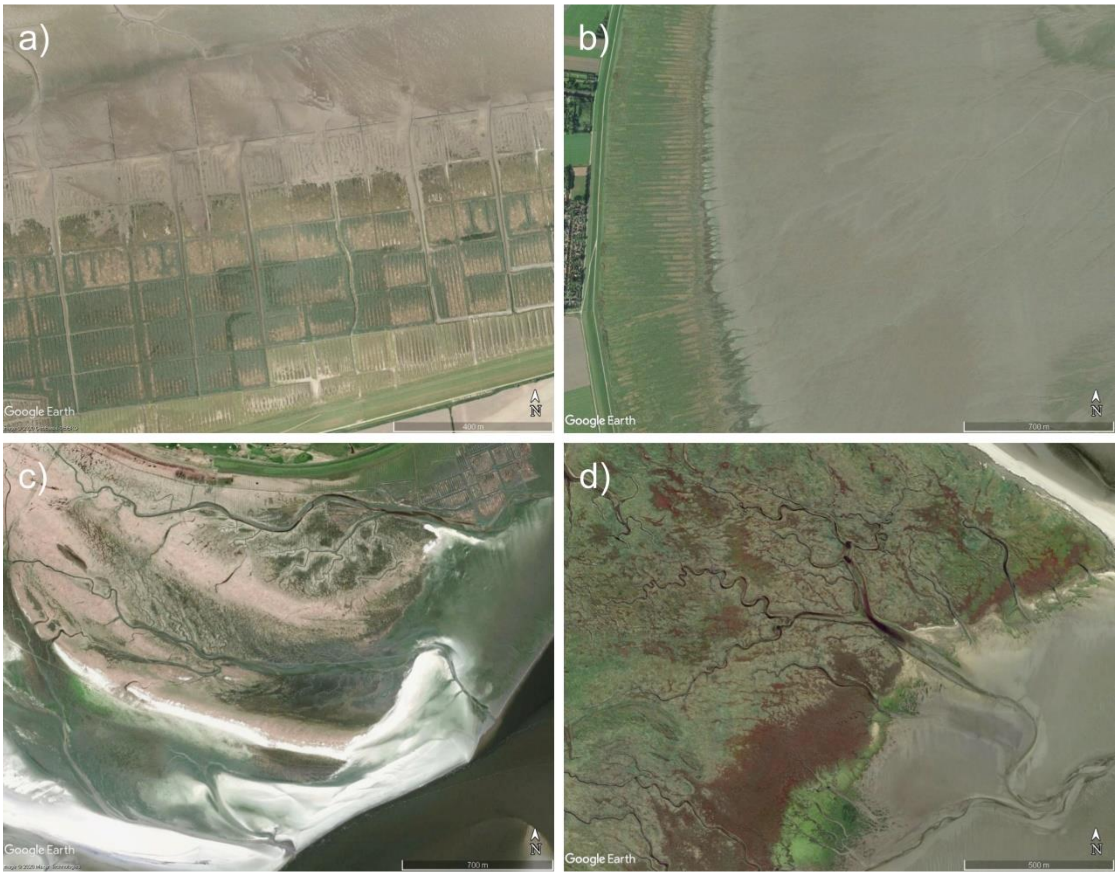


Fig. 6.2: Examples of salt marshes in the German Wadden Sea, a) a typical mainland salt marsh at Norderheverkoog, b) a salt marsh in the Jade Bay near Wilhelmshaven, c) St. Peter-Ording, the largest naturally developed mainland salt marsh in the German Wadden Sea, d) an island salt marsh on the uninhabited island Mellum.

deposited at the marsh edges towards the sea and along the creeks, resulting in a higher elevation on the marsh edge and a lower in the inner marsh (Bartholdy et al., 2010; Groot et al., 2011; Nolte, 2014). The more large and small creeks permeate the marsh, the more “hills” and “valleys” will develop. This can (1) increase plant diversity, and thus promote breeding habitats for various bird species (Esselink et al., 2017), (2) increase the marsh accretion rates, and thus increase the resilience of salt marshes to sea-level rise, and (3) increase the probability of the development of salt-marsh pools, which could be valuable fish nurseries (MacKenzie and Dionne, 2008; Rieucau et al., 2015; Allen et al., 2017). A more diverse topography may also benefit the coastal protection value of the salt marshes as storm tides are slowed down more, when hills and valleys have to be crossed. In this context, meandering creeks and creeks that run parallel to the coastline can also slow down the waves during storm flood events, as the water has to overcome the variable topography of the salt marsh, instead of being directed straight towards the dike, via the straight creeks, that dominate many Wadden Sea salt marshes today. Thus, complex meandering creek systems might be hydrologically equally or even more effective to reduce the wave power compared to the wave attenuation by the salt-marsh plants (Franziska

Rupprecht, 2015). Complex salt-marsh creek systems and large creeks running parallel to the coastline could also benefit breeding birds, because they decrease the accessibility of the breeding areas for mammalian nest predators, such as the red fox (*Vulpes vulpes*). At Westerhever, Schleswig-Holstein, two large salt-marsh creeks are planned to be filled with sediment in order to facilitate water-logging, to increase biodiversity, particularly of plants and birds, and to decrease habitat suitability for the red fox, and thus protect the birds. But it was not considered, that such management measures will destruct a rare nekton habitat and thus decrease also species and habitat diversity. Filling small ditches, that are rarely used by nekton (Dänhardt et al., 2011a), can be beneficial to increase water-logging and re-establish a natural creek system (Esselink et al., 2017). Larger salt-marsh creeks, however, are a valuable nekton habitat, as shown in this thesis, and should be protected or restored. Some parts of older ditches in the high marsh evolved to salt-marsh pools that are connected during spring tides via the ditch with the salt-marsh creeks and are used as nurseries by gobies and three-spined stickleback (pers. observation). When filling small ditches, it is important not to cut the connections of the salt-marsh pools with the tidal zone. In salt marshes that lack larger creeks and are exclusively drained by small ditches (Fig. 6.2b), it could be worthwhile to fill some ditches in order to facilitate the others to merge into a larger stream, that connects the salt marsh with the subtidal. Such a larger stream would also be deeper and thus longer inundated and improve the accessibility of the salt marsh for nekton.

Promoting a spatial increase of salt marshes would not only benefit coastal protection (van Loon-Steensma, 2015) and bird breeding, but also increase the area and inundation time of salt-marsh nekton habitats. In the past, brushwood groynes were installed seawards to accelerate sedimentation and thus the salt-marsh development. These groynes were arranged in a rectangular pattern as they were designed to enhance accretion and allow for dyke drainage, but not for large meandering and ramified creek systems. As they are still in the deeper sediment layers of the man-made salt marshes, they sometimes hamper till today the development of naturally-shaped creeks. Hence, potential future plans of installing brushwood groynes to accelerate salt-marsh development should already plan for a naturally creek system and arrange the groynes in a non-rectangular way that conducts the water into meandering currents.

Accessibility of salt marshes for nekton can also be increased by removing barriers, such as summer polders. Removing summer polders increases the saltwater influence on the marsh, which makes the marsh not only more accessible for nekton, especially when creeks are available, but also enhances sediment accretion (Saiberling and Stock, 2009) and changes the arthropod community, particularly causing an increase in the abundance of *O. gammarellus*, the preferred terrestrial prey of three-spined sticklebacks (Götting, 2001; Friese et al., 2018a; Chapter 5). Another kind of barriers that may hamper but not inhibit nekton access to salt-marsh creeks can be found on the islands in the Wadden Sea. On the island *Neuwerk*, the salt-marsh is surrounded by a summer polder that includes tidal gates (1.5 m width), which are permanently open and allow the tide to flow in and out the salt-marsh creek (ca. 20 m width), but can be closed at storm floods. However, these tidal gates are a bottleneck during the tidal flow and cause the flow velocity increasing substantially during flood and ebb tide. The small nekton may still be flushed in and out more or less passively, but the findings of this thesis indicate that the low flow velocity is a key advantage of salt-marsh creeks for small nekton. In case the salt-marsh-specific nekton uses flow velocity as an environmental cue to evaluate habitat quality and to direct their migratory movements, the altered flow dynamics at the tidal gate would keep them from entering the salt marsh. Additionally, the sudden acceleration trough the bottleneck could cause physiological stress and possibly minor injuries, which would reduce the habitat quality of the salt-marsh creeks behind the barrier. Due to coastal protection the summer polder cannot be removed here, but the bottleneck could be removed by installing a wider tidal gate (optimally as wide as the creek) that allows the tidal current to flow gently in and out. On the island *Spiekeroog* the entrance of the salt-marsh creek *Weekschloot* was separated from the deep harbour basin by a small wall, to prevent the sediment from being washed out and the creek from deepening unnaturally. With the rising tide fishes and crustaceans have to wait until the water level is high enough to pass this wall. Still, we found an abundant and diverse nekton community in the marsh creeks behind this wall (Dänhardt and Hufnagl, unpublished data; Friese et al., 2020b; Chapter 2), but a comparison with the neighboured salt-marsh creeks without such a barrier, *Steenschloot* and *Schillschloot*, would be needed to evaluate whether the wall affects the nekton negatively. Although the impact of this structure is unknown, a wall, such as at *Weekschloot*, would probably affect nekton less when it would be constructed as a sloped bank instead of a vertical wall.

In summary, many possible management measures that would benefit the nekton, would also benefit the breeding birds and the coastal protection – or at least would not interfere with each other. However, there is a major conflict of interests with the livestock grazing. For fish and crustaceans a structurally complex salt marsh with many different-sized creeks and connected pools would be favourable, while for sheep and cattle small-scale grazing patches and a maze of creeks and ponds and uneven swamp-like soils would be unfavourable or would even keep the ungulates from using that marsh areas. Livestock can drown in the creeks and ditches of the salt marsh (Esselink et al., 2017; pers. observation), and thus the shepherds welcome the backfilling of ditches, that is conducted to control *E. atherica* vegetation, but can decrease nekton habitats. Furthermore, sheep grazing reduces plant detritus and thus the abundance of *O. gammarellus*, which contributes to the winter diets of three-spined sticklebacks and common gobies (Friese et al., 2018a; Chapter 5). As a compromise lower elevated and thus more frequently inundated salt-marsh areas could remain ungrazed, while the higher elevated areas that are rarely available for nekton can serve for livestock grazing. In many salt marshes sheep do not use the whole marsh up to the seaward edge but remain mostly closer to the dike. Thus, the difference in winter fish diets between grazed and ungrazed salt marshes might be less pronounced in other locations than in the salt marshes studied by Friese et al. (2018a), in which the whole area of the grazed marsh was intensively grazed by sheep. More than from transforming grazed to ungrazed salt-marsh areas, fish would probably benefit from a larger salt-marsh-to-creek-interface, thus longer creek banks, that allow for a larger interaction between the marine and the terrestrial system. In relation to the salt-marsh area a larger salt-marsh-to-creek-interface could be achieved by promoting a complex meandering creek system.

Salt-marsh restoration projects have likely a positive cost-benefit-ratio and nekton habitats in salt marshes can recover within one to two decades (Creighton et al., 2019; Duarte et al., 2020). However, whether restored salt marshes have a comparable habitat quality for nekton as natural salt marshes depends on the applied management measures and on the monitoring time frame. Thus, studies on salt-marsh restoration projects are contradictory, either finding restored marshes compared to natural marshes equally valuable (Gray et al., 2002; Teo and Able, 2003; Scholle et al., 2017), or less valuable (Allen et al., 1994; Minello and Webb, 1997; Minello, 2000). Although, many small-scale processes between the microhabitats of the Wadden Sea salt marshes and their effects on nekton are still unknown, restoring man-made marshes towards a similar morphology and hydrology as can be found in natural marshes (Fig. 6.2c and d) is a promising start (Peterson and Turner, 1994). Furthermore, not only the salt marshes but also connected habitats and ecological processes must be protected for a successful habitat conservation (Levin and Stunz, 2005). Conservation and potentially restoration of salt marshes with regularly inundated areas, such as pools and naturally meandering creeks, and access pathways to other habitats in the seascape will conserve habitat and species diversity and thus the ecosystem resilience towards potential future disturbances.

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Supplement A

Tab. A.1: Overview of used *R* packages

Usage	***R* package**	**Version**	**Reference**
Data handling	*data.table*	*1.12.0*	Dowle and Srinivasan (2019)
	dplyr	*0.7.8*	Wickham et al. (2018)
	lubridate	*1.7.4*	Grolemund and Wickham (2011)
	measurements	*1.3.0*	Birk (2018)
	OpenMx	*2.13.2*	Boker et al. (2019); Hunter (2018); Neale et al. (2016); Pritikin et al. (2015)
	plyr	*1.8.4*	Wickham (2011)
	readxl	*1.2.0*	Wickham and Bryan (2018)
	reshape2	*1.4.3*	Wickham (2007)
	stringr	*1.3.1*	Wickham (2018b)
Plotting	*cowplot*	*0.9.4*	Wilke (2019)
	ggplot2	*3.1.0*	Wickham (2016)
	ggrepel	*0.8.0*	Slowikowski (2018)
	ggsignif	*0.4.0*	Ahlmann-Eltze (2017)
Spatial mapping	*broom*	*0.5.1*	Robinson and Hayes (2018)
	geosphere	*1.5-7*	Hijmans (2017)
	ggmap	*2.7.904*	Kahle and Wickham (2013)
	ggsn	*0.4.0*	Santos Baquero (2017)
	maptools	*0.9-4*	Bivand and Lewin-Koh (2018)
	proj4	*1.0-8*	Urbanek (2012)
	raster	*2.8-4*	Hijmans (2018)
	rgdal	*1.3-6*	Bivand et al. (2018)
	rgeos	*0.4-2*	Bivand and Rundel (2018)
	scales	*1.0.0*	Wickham (2018a)
	sp	*1.3-1*	Bivand et al. (2013); Pebesma and Bivand (2005)
Statistical analyses	*car*	3*.0-2*	Fox and Weisberg (2019)
	vegan	*2.5-3*	Oksanen et al. (2019)

Tab. A.2: Excluded fyke net hauls for quantitative analyses of the field campaign in St. Peter-Ording in 2015-2016

year	**month**	**daytime**	**creek**
2015	May	night	G1, G2, U1
	June	day	U2
	December	night	G2
2016	February	day	G2
		night	G2, U2

Tab. A.3: Seasonal and diurnal mean density of the most common nekton species in the salt-marsh creeks. As not the whole water volume of the flooded marsh creeks were fished, the minimum density (“min”) and the maximum density (max) are given. min: number of individuals caught per 1000 m², assuming no nekton organisms passed the net uncaught. Max: number of individuals caught per 1000 m², assuming the unfished runoff water contained the same density of organisms as the fished runoff water.

mean density (± sd)	***Carcinus maenas***		***Clupea harengus***		***Crangon crangon***		***Gasterosteus aculeatus***		***Osmerus eperlanus***		***Palaemon sp.***		***Pomatoschistus microps***		***Pomatoschistus minutus***		***Syngnathus rostellatus***	
ind. per area (1000 m²)	min	max	min	max	min	max	min	max	min	max	min	max	min	max	min	max	min	max
day																		
Mar	0.1 (± 0.1)	0.2 (± 0.1)	0.0	0	1.2 (± 1.7)	2.7 (± 3.6)	0.8 (± 0.9)	1.7 (± 1.8)	0.0	0.0	8 (± 9.3)	17.5 (± 19.8)	29.6 (± 49)	65.2 (± 105.1)	0.0	0.0	0.3	0.7
Apr	1.5 (± 3)	3 (± 5.5)	35.7 (± 65.4)	81.8 (± 152.1)	0.2 (± 0.2)	0.4 (± 0.4)	2.2 (± 3.5)	4.3 (± 6.4)	0.1 (± 0.1)	0.2 (± 0.1)	19.1 (± 39.5)	37.9 (± 73.8)	5.2 (± 8.4)	10.7 (± 15.3)	0.0	0.0	1.1 (± 1.7)	2.2 (± 3.2)
May	0.3 (± 0.4)	0.8 (± 0.9)	12.9 (± 17.5)	31.4 (± 36.2)	0 (± 0)	0.1 (± 0.1)	0.3 (± 0.2)	0.7 (± 0.6)	0.0	0.0	1 (± 1.1)	2.6 (± 2.5)	0.3 (± 0.2)	0.8 (± 0.6)	0.0	0.0	0.1 (± 0.1)	0.2 (± 0.2)
Jun	53 (± 91.5)	91.3 (± 144.8)	2.5 (± 3.8)	9 (± 14.8)	0.6 (± 0.6)	1.5 (± 1)	1 (± 1.5)	1.8 (± 2.3)	0.0	0.0	6.5 (± 11.6)	11.1 (± 18.5)	0.5 (± 0.5)	1.2 (± 1.6)	0.0	0.0	0.5 (± 0.6)	0.8 (± 1)
Jul	1.6 (± 1.2)	4.6 (± 2.8)	0.6 (± 0.9)	1.7 (± 2.6)	2 (± 2.5)	4.6 (± 4.1)	0.2 (± 0.2)	0.5 (± 0.4)	0.0	0.1	1.4 (± 1.6)	3.2 (± 3.6)	2 (± 2.4)	6.5 (± 7.6)	0.0	0.0	3.3 (± 5.7)	10.3 (± 17.6)
Aug	6.1 (± 11.2)	11.7 (± 18)	0.0	0	4.3 (± 5.2)	8.8 (± 7.6)	0.2 (± 0.3)	0.4 (± 0.5)	0.1 (± 0.1)	0.3 (± 0.1)	2.6 (± 3.2)	4.4 (± 5.1)	5.6 (± 7.6)	18.3 (± 25.5)	0.0	0.0	1.2 (± 1.6)	1.9 (± 2.6)
Sep	0.9 (± 1.2)	1.7 (± 2.2)	0.0	0.1	15.8 (± 15.4)	37.9 (± 35.6)	0.0	0.1 (± 0)	0.1 (± 0.2)	0.2 (± 0.3)	3.8 (± 5.7)	7.2 (± 10.4)	6.7 (± 4.6)	16.8 (± 12.2)	0.0	0.0	0.1	0.2
Oct	47.2 (± 68.3)	95.4 (± 133.1)	0.0	0	6 (± 6.7)	11.9 (± 12.9)	0.0	0.1	0.0	0.0	4.4 (± 5.5)	8.7 (± 10.8)	16.5 (± 19.2)	33 (± 37.2)	0.0	0.0	0.0	0.0
Dec	0.0	0.1 (± 0.1)	1.9 (± 2.3)	5.1 (± 5.6)	6.5 (± 5.6)	18.1 (± 15.2)	0.1 (± 0)	0.3 (± 0.1)	0.0	0.0	0.0	0.1 (± 0.1)	0.9 (± 0.3)	2.4 (± 0.8)	0.0	0.1	0.0	0.1
Feb	0.0	0.0	0.1 (± 0.1)	0.2 (± 0.1)	5.7 (± 7.2)	15.1 (± 21.6)	0.8 (± 1)	1.6 (± 1.9)	0.0	0.1 (± 0.1)	0.0	0.0	3.3 (± 3.8)	6.7 (± 7.3)	0.0	0.0	0.0	0.0
night																		
Mar	0.3 (± 0.3)	0.6 (± 0.6)	0.0	0.0	171.7 (± 315.2)	406.1 (± 738.5)	2.1 (± 2.5)	5.4 (± 5.6)	0.1 (± 0.1)	0.2 (± 0.3)	1.2 (± 1.2)	2.8 (± 2.8)	20.3 (± 33)	48.5 (± 77.1)	1.9 (± 2.9)	4.5 (± 6.7)	0.4 (± 0.5)	0.9 (± 1.2)
Apr	1.7 (± 2)	3.9 (± 3.6)	5.7 (± 10.1)	12.2 (± 19.3)	11.7 (± 9.4)	30.1 (± 14.9)	2.5 (± 3.9)	5.5 (± 7.3)	0.1 (± 0.1)	0.2 (± 0.2)	2.4 (± 4)	5 (± 7.6)	5.2 (± 6.9)	11.9 (± 12.5)	0.2 (± 0.1)	0.7 (± 0.5)	0.6 (± 1)	1.4 (± 1.9)
May	0.2 (± 0.2)	0.6 (± 0.5)	1.6 (± 1.6)	4.2 (± 4.3)	1 (± 0.6)	2.8 (± 1.5)	1.1 (± 1.7)	2.8 (± 4.5)	0.0	0.1 (± 0.1)	0.3 (± 0.4)	0.7 (± 1)	0.1 (± 0)	0.2 (± 0.1)	0.1 (± 0.1)	0.2 (± 0.2)	0.1 (± 0)	0.2 (± 0.1)
Jun	24.5 (± 33)	43.9 (± 49.9)	539.5 (± 919)	2021.2 (± 3462.3)	11.6 (± 22.4)	18.7 (± 35.4)	1.1 (± 1.9)	1.8 (± 3)	0.2	0.3	5.9 (± 10.6)	9.9 (± 16.5)	0.2 (± 0.3)	0.3 (± 0.4)	0.0	0.0	1.9	3.0
Jul	11.1 (± 20.8)	19.8 (± 34.9)	25.7 (± 42.6)	44.7 (± 71.7)	232.9 (± 396.5)	399.9 (± 672.6)	2.1 (± 2.7)	3.6 (± 4.5)	0.6 (± 0.9)	1 (± 1.5)	2.7 (± 4)	5 (± 6.5)	431.6 (± 862.1)	735.6 (± 1468.1)	0.0	0.0	16.3 (± 23)	27.7 (± 39.1)
Aug	9.6 (± 15.3)	20.1 (± 25.6)	0.2 (± 0.1)	0.5 (± 0)	150.5 (± 143.1)	340.4 (± 254.1)	0.6 (± 0.9)	1 (± 1.3)	0.8 (± 0.8)	1.4 (± 1.1)	52.4	85.3	66.5 (± 111)	120.4 (± 173.6)	0.0	0.0	7.8 (± 15.3)	12.9 (± 24.7)
Sep	4.2 (± 9)	8.1 (± 15.8)	0.0	0.0	1188.7 (± 1312)	3184.8 (± 3379.6)	0.0	0.1	1.2 (± 1.4)	2.4 (± 2)	55.1 (± 94)	98.5 (± 167.5)	77.6 (± 82.1)	223.5 (± 262.3)	0.0	0.0	1.1	1.9
Oct	27.4 (± 26.1)	57.8 (± 49)	0.0	0.0	2570.5 (± 3104.1)	5527.3 (± 5932.6)	0.3 (± 0.4)	0.6 (± 0.7)	1.5 (± 1.9)	3 (± 3.5)	3.3 (± 2.7)	8.2 (± 7.9)	349.1 (± 558.5)	735.6 (± 1069.3)	0.0	0.0	0.6 (± 0.8)	1.2 (± 1.4)
Dec	0.0	0.1 (± 0)	0.0	0.1 (± 0)	70.1 (± 76.4)	214.1 (± 232.5)	0.4 (± 0.1)	1.1 (± 0.4)	0.1 (± 0)	0.2 (± 0.1)	0.1 (± 0.1)	0.2 (± 0.2)	2 (± 0.4)	5.8 (± 1.1)	0.0	0.1 (± 0.1)	0.0	0.0
Feb	0.0	0.0	0.0	0.1 (± 0)	42.6 (± 57.7)	127.7 (± 171.5)	0.4 (± 0.4)	1.1 (± 0.9)	0.1 (± 0.1)	0.2 (± 0.3)	0.0	0.0	1.4 (± 1.5)	3.7 (± 3.8)	0.1 (± 0)	0.2 (± 0.1)	0.0	0.0

Tab. A.4: Biological trait variables of the species caught in the salt-marsh creeks in St. Peter-Ording and in the adjacent subtidal area in April, May, July, August, September and October 2015. Traits were collected from multiple sources (Franco et al., 2008; Neal and Pizzolla, 2008; Breine et al., 2010; Rice et al., 2013; Florin et al., 2014; Luna, 2019). Trait modalities of the different sources were combined using fuzzy coding as described by Chevenet et al. (1994). For example the literature sources ascribed *B. belone* either to “marine migrants” or to “marine stragglers” within the estuarine use functional group, therefore *B. belone* was ascribed in the species-trait-matrix to both by 50% each.

trait	**category**	***Agonus cataphractus***	***Ammodytes tobianus***	***Ammodytidae***	***Belone belone***	***Carcinus maenas***	***Chelon labrosus***	***Ciliata mustela***	***Clupea harengus***	***Crangon crangon***	***Gadus morhua***	***Gasterosteus aculeatus***
Estuarine use functional group	Freshwater species	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33
	Anadromous species	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33
	Catadromous species	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Marine migrants	0.00	0.00	0.00	0.50	0.50	1.00	1.00	1.00	0.00	1.00	0.00
	Marine stragglers	1.00	0.50	0.50	0.50	0.00	0.00	0.00	0.00	0.67	0.00	0.00
	Estuarine species	0.00	0.50	0.50	0.00	0.50	0.00	0.00	0.00	0.33	0.00	0.33
Feeding mode functional group	Benthivores	1.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.33
	Planktivores	0.00	1.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.33
	Omnivorous	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
	Hyperbenthivores / Piscivores	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
	Detritivores	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00
	Hyperbenthivores / Zooplanktivores	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.33
	Piscivores	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00
	Algaevore	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00
Reproductive mode functional group	oviparous with adhesive eggs	1.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	oviparous with benthic eggs	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	oviparous with pelagic eggs	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00	0.00	1.00	0.00
	oviparous guarders	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	oviparous shelterers	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	viviparous	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	oviparous egg-bearing	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
Stratum adults	demersal	1.00	1.00	0.00	0.00	0.00	1.00	1.00	0.00	0.50	1.00	0.00
	pelagic	0.00	0.00	1.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	1.00
	benthic	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.50	0.00	0.00
Taxon	fish	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00
	crustacea	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
Adult longevity	<=3 years	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00
	>3-10 years	0.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00
	>10-20 years	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	>20 years	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00
Maximum length	<=10 cm	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
	>10-20 cm	0.00	1.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	>20-50 cm	1.00	0.00	0.50	0.00	0.00	0.00	1.00	1.00	0.00	0.00	0.00
	>50-90 cm	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
	>90 cm	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00

Tab. A.4 (continued): Biological trait variables of the species caught in the salt-marsh creeks in St. Peter-Ording and in the adjacent subtidal area in April, May, July, August, September and October 2015. Traits were collected from multiple sources (Franco et al., 2008; Neal and Pizzolla, 2008; Breine et al., 2010; Rice et al., 2013; Florin et al., 2014; Luna, 2019). Trait modalities of the different sources were combined using fuzzy coding as described by Chevenet et al. (1994). For example the literature sources ascribed *B. belone* either to “marine migrants” or to “marine stragglers” within the estuarine use functional group, therefore *B. belone* was ascribed in the species-trait-matrix to both by 50% each.

trait	**category**	***Hemigrapsus sanguineus***	***Hyperoplus lanceolatus***	***Limanda limanda***	***Liocarcinus holsatus***	***Liparis liparis***	***Merlangius merlangus***	***Myoxocephalus scorpius***	***Osmerus eperlanus***	***Palaemon sp.***	***Platichthys flesus***	***Pleuronectes platessa***
Estuarine use functional group	Freshwater species	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Anadromous species	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	Catadromous species	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Marine migrants	0.00	0.00	1.00	0.00	0.50	0.50	0.50	0.00	0.00	1.00	1.00
	Marine stragglers	0.00	1.00	0.00	0.00	0.00	0.50	0.00	0.00	0.67	0.00	0.00
	Estuarine species	0.00	0.00	0.00	0.00	0.50	0.00	0.50	0.00	0.33	0.00	0.00
Feeding mode functional group	Benthivores	0.00	0.00	1.00	0.50	1.00	0.33	0.33	0.33	0.00	0.67	1.00
	Planktivores	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Omnivorous	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00
	Hyperbenthivores / Piscivores	0.00	0.67	0.00	0.50	0.00	0.33	0.67	0.33	0.00	0.33	0.00
	Detritivores	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00
	Hyperbenthivores / Zooplanktivores	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Piscivores	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.33	0.00	0.00	0.00
	Algaevore	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00
Reproductive mode functional group	oviparous with adhesive eggs	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
	oviparous with benthic eggs	0.00	1.00	0.00	0.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00
	oviparous with pelagic eggs	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00
	oviparous guarders	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
	oviparous shelterers	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	viviparous	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	oviparous egg-bearing	1.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
Stratum adults	demersal	1.00	1.00	1.00	1.00	0.50	1.00	0.50	0.00	0.50	0.50	0.50
	pelagic	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	benthic	0.00	0.00	0.00	0.00	0.50	0.00	0.50	0.00	0.50	0.50	0.50
Taxon	fish	0.00	1.00	1.00	0.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00
	crustacea	1.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
Adult longevity	<=3 years	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
	>3-10 years	0.00	0.00	0.00	1.00	0.00	0.00	1.00	1.00	1.00	0.00	0.00
	>10-20 years	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00
	>20 years	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Maximum length	<=10 cm	1.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	>10-20 cm	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00
	>20-50 cm	0.00	1.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	>50-90 cm	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00
	>90 cm	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	1.00

Tab. A.4 (continued): Biological trait variables of the species caught in the salt-marsh creeks in St. Peter-Ording and in the adjacent subtidal area in April, May, July, August, September and October 2015. Traits were collected from multiple sources (Franco et al., 2008; Neal and Pizzolla, 2008; Breine et al., 2010; Rice et al., 2013; Florin et al., 2014; Luna, 2019). Trait modalities of the different sources were combined using fuzzy coding as described by Chevenet et al. (1994). For example the literature sources ascribed *B. belone* either to "marine migrants" or to "marine stragglers" within the estuarine use functional group, therefore *B. belone* was ascribed in the species-trait-matrix to both by 50% each.

trait	**category**	***Pomatoschistus microps***	***Pomatoschistus minutus***	***Pomatoschistus spec.***	***Pungitius pungitius***	***Scophthalmus maximus***	***Solea solea***	***Sprattus sprattus***	***Syngnathus rostellatus***	***Trachurus trachurus***	***Zoarces viviparus***
Estuarine use functional group	Freshwater species	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
	Anadromous species	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Catadromous species	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Marine migrants	0.00	0.33	0.00	0.00	0.50	1.00	1.00	0.00	0.00	0.00
	Marine stragglers	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	1.00	0.33
	Estuarine species	1.00	0.67	1.00	0.00	0.00	0.00	0.00	1.00	0.00	0.67
Feeding mode functional group	Benthivores	1.00	1.00	1.00	1.00	0.00	1.00	0.00	0.00	0.00	1.00
	Planktivores	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.67	0.00	0.00
	Omnivorous	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Hyperbenthivores / Piscivores	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00
	Detritivores	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Hyperbenthivores / Zooplanktivores	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00
	Piscivores	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	1.00	0.00
	Algaevore	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Reproductive mode functional group	oviparous with adhesive eggs	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	oviparous with benthic eggs	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
	oviparous with pelagic eggs	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00	1.00	0.00
	oviparous guarders	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
	oviparous shelterers	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	viviparous	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	oviparous egg-bearing	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Stratum adults	demersal	0.00	0.00	0.00	1.00	0.00	0.50	0.00	0.00	1.00	0.00
	pelagic	0.00	0.00	0.00	0.00	1.00	0.00	1.00	0.50	0.00	0.50
	benthic	1.00	1.00	1.00	0.00	0.00	0.50	0.00	0.50	0.00	0.50
Taxon	fish	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	crustacea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Adult longevity	<=3 years	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	>3-10 years	0.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	1.00
	>10-20 years	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
	>20 years	0.00	0.00	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00
Maximum length	<=10 cm	1.00	0.00	0.50	1.00	0.00	0.00	0.00	0.00	0.00	0.00
	>10-20 cm	0.00	1.00	0.50	0.00	0.00	0.00	1.00	1.00	0.00	0.00
	>20-50 cm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	>50-90 cm	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	1.00	1.00
	>90 cm	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00

Tab. A.5: Comparison of abundances of the nine most common nekton species in the grazed and ungrazed salt marshes at St. Peter-Ording in 2015-2016

calculated from mean CPUE (N / 1000 m^3)	grazed			ungrazed			Paired Wilcoxon signed rank test	
							H1: CPUE in grazed is higher than in ungrazed	
species	mean	sd	median	mean	sd	median	V-value	p-value
Carcinus maenas	224.93	573.39	33.37	29.32	49.02	5.48	187	0.0000***
Clupea harengus	50.70	131.45	0.00	470.47	2741.97	0.18	68	0.1732
Crangon crangon	3796.45	13729.22	75.94	1086.94	3811.89	18.15	135	0.0567
Gasterosteus aculeatus	11.36	19.52	3.60	1.43	1.76	0.76	184	0.0000***
Osmerus eperlanus	2.23	6.02	0.00	0.30	0.60	0.02	97	0.0191
Palaemon spec.	90.99	217.21	19.62	2.22	6.81	0.30	153	0.0002***
Pomatoschistus microps	881.09	2826.16	62.91	108.40	332.00	14.44	153	0.0090***
Pomatoschistus minutus	1.78	8.55	0.00	0.35	1.26	0.00	17	0.8689
Syngnathus rostellatus	18.76	51.14	0.38	0.37	0.78	0.00	129	0.0009***
all species above together	5078.29	16227.02	393.40	1699.79	4858.25	128.64	150	0.0129*

Tab. A.6: Comparison of abundances of the nine most common nekton species in the creeks G1 and G2 in the grazed salt marsh at St. Peter-Ording in 2015-2016

calculated from mean CPUE (N / 1000 m^3)	G1			G2			Paired Wilcoxon signed rank test	
							H1: CPUE in G1 is lower than in G2	
species	mean	sd	median	mean	sd	median	V-value	p-value
Carcinus maenas	82.50	163.87	11.54	405.33	823.43	56.95	7	0.0006**
Clupea harengus	3.49	9.36	0.00	110.49	183.75	0.00	3	0.0122**
Crangon crangon	1021.06	3547.37	39.83	7311.95	20110.36	246.86	1	0.0001***
Gasterosteus aculeatus	5.08	7.36	2.25	19.31	26.60	6.20	3	0.0027**
Osmerus eperlanus	0.10	0.25	0.00	4.93	8.44	1.38	1	0.0025**
Palaemon spec.	14.43	15.91	10.71	187.97	304.72	79.70	10	0.0013**
Pomatoschistus microps	59.89	68.50	22.54	1921.27	4092.24	163.81	10	0.0013**
Pomatoschistus minutus	0.40	1.75	0.00	3.54	12.74	0.00	0	0.0907
Syngnathus rostellatus	6.81	28.43	0.00	33.88	68.47	7.17	11	0.0087**
all species above together	1473.81	4165.91	193.59	9998.67	23590.29	1225.69	2	0.0001***

Tab. A.7: Comparison of abundances of the nine most common nekton species in the creeks U1 and U2 in the ungrazed salt marsh at St. Peter-Ording in 2015-2016

calculated from mean CPUE (N / 1000 m^3)	U1			U2			Paired Wilcoxon signed rank test	
							H1: CPUE in U1 is lower than in U2	
species	mean	sd	median	mean	sd	median	V-value	p-value
Carcinus maenas	29.15	44.31	6.46	29.51	55.20	3.09	91	0.7563
Clupea harengus	10.58	33.99	0.17	984.46	3989.15	0.27	16	0.0712
Crangon crangon	226.44	376.10	22.23	2048.67	5455.67	14.08	29	0.0116*
Gasterosteus aculeatus	1.75	2.02	0.98	1.08	1.39	0.57	91	0.7563
Osmerus eperlanus	0.18	0.36	0.00	0.42	0.78	0.06	23	0.1120
Palaemon spec.	1.85	4.19	0.39	2.63	9.03	0.29	49	0.6101
Pomatoschistus microps	34.07	41.70	13.37	191.47	474.62	17.27	68	0.3559
Pomatoschistus minutus	0.43	1.56	0.00	0.25	0.85	0.00	14	0.3120
Syngnathus rostellatus	0.17	0.31	0.00	0.60	1.06	0.08	1	0.0040**
all species above together	288.29	403.40	94.72	3259.09	6823.09	142.51	21	0.0033

Tab. A.8: Comparison of abundances of the nine most common nekton species during day and night in the salt-marsh creeks at St. Peter-Ording in 2015-2016

calculated from mean CPUE (N / 1000 m^3)	day			night			Paired Wilcoxon signed rank test	
							H1: CPUE during day is lower than during night	
species	mean	sd	median	mean	sd	median	V-value	p-value
Carcinus maenas	173.77	564.62	9.48	122.55	263.62	16.57	157	0.0232*
Clupea harengus	21.21	73.40	0.00	527.51	2862.38	0.07	100	0.4333
Crangon crangon	37.15	63.92	11.92	5051.99	14163.00	499.99	4	0.0000***
Gasterosteus aculeatus	5.01	12.01	0.95	8.37	17.39	2.48	100	0.0098**
Osmerus eperlanus	0.24	0.52	0.00	2.38	6.08	0.06	23	0.0007***
Palaemon spec.	41.57	123.29	2.20	57.46	194.16	1.05	216	0.6207
Pomatoschistus microps	81.44	191.79	17.27	943.02	2869.61	33.37	157	0.0133*
Pomatoschistus minutus	0.00	0.02	0.00	2.22	8.69	0.00	1	0.0011**
Syngnathus rostellatus	5.46	21.95	0.00	14.33	48.46	0.27	60	0.0280*
all species above together	365.85	723.22	116.19	6729.82	16753.68	800.22	52	0.0000***

Tab. A.9: Comparison of species assemblages in the salt marshes and in the adjacent subtidal including only day hauls in April, May, July, August, September and October 2015

	saltmarsh night (22 hauls in total)		saltmarsh day (24 hauls in total)		subtidal day (18 hauls in total)	
Crustacean species	Number of hauls with presence	frequency of occurrence [%]	Number of hauls with presence	frequency of occurrence [%]	Number of hauls with presence	frequency of occurrence [%]
Carcinus maenas	22	100.0	24	100.0	4	22.2
Crangon crangon	22	100.0	24	100.0	18	100.0
Hemigrapsus sanguineus	4	18.2	5	20.8	0	0.0
Liocarcinus holsatus	0	0.0	0	0.0	5	27.8
Palaemon sp.	18	81.8	20	83.3	5	27.8
Fish species						
Agonus cataphractus	0	0.0	0	0.0	7	38.9
Ammodytes tobianus	0	0.0	0	0.0	8	44.4
Ammodytidae	0	0.0	1	4.2	0	0.0
Belone belone	0	0.0	2	8.3	0	0.0
Chelon labrosus	2	9.1	1	4.2	0	0.0
Ciliata mustela	0	0.0	0	0.0	7	38.9
Clupea harengus	12	54.5	11	45.8	18	100.0
Gadus morhua	0	0.0	0	0.0	1	5.6
Gasterosteus aculeatus	15	68.2	17	70.8	5	27.8
Hyperoplus lanceolatus	0	0.0	0	0.0	1	5.6
Limanda limanda	0	0.0	0	0.0	6	33.3
Liparis liparis	0	0.0	0	0.0	1	5.6
Merlangius merlangus	0	0.0	0	0.0	5	27.8
Myoxocephalus scorpius	3	13.6	0	0.0	0	0.0
Osmerus eperlanus	14	63.6	9	37.5	18	100.0
Platichthys flesus	4	18.2	1	4.2	14	77.8
Pleuronectes platessa	6	27.3	7	29.2	14	77.8
Pomatoschistus microps	22	100.0	23	95.8	5	27.8
Pomatoschistus minutus	7	31.8	1	4.2	12	66.7
Pomatoschistus spec.	0	0.0	0	0.0	5	27.8
Pungitius pungitius	4	18.2	1	4.2	0	0.0
Scophthalmus maximus	0	0.0	0	0.0	1	5.6
Solea solea	1	4.5	0	0.0	4	22.2
Sprattus sprattus	3	13.6	2	8.3	16	88.9
Syngnathus rostellatus	16	72.7	14	58.3	13	72.2
Trachurus trachurus	0	0.0	0	0.0	2	11.1
Zoarces viviparus	1	4.5	0	0.0	3	16.7

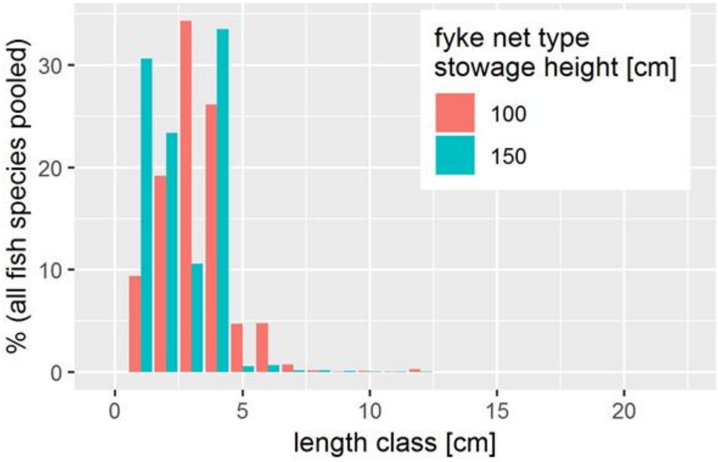


Fig. A.1: Fish length distributions of the two fyke net types.

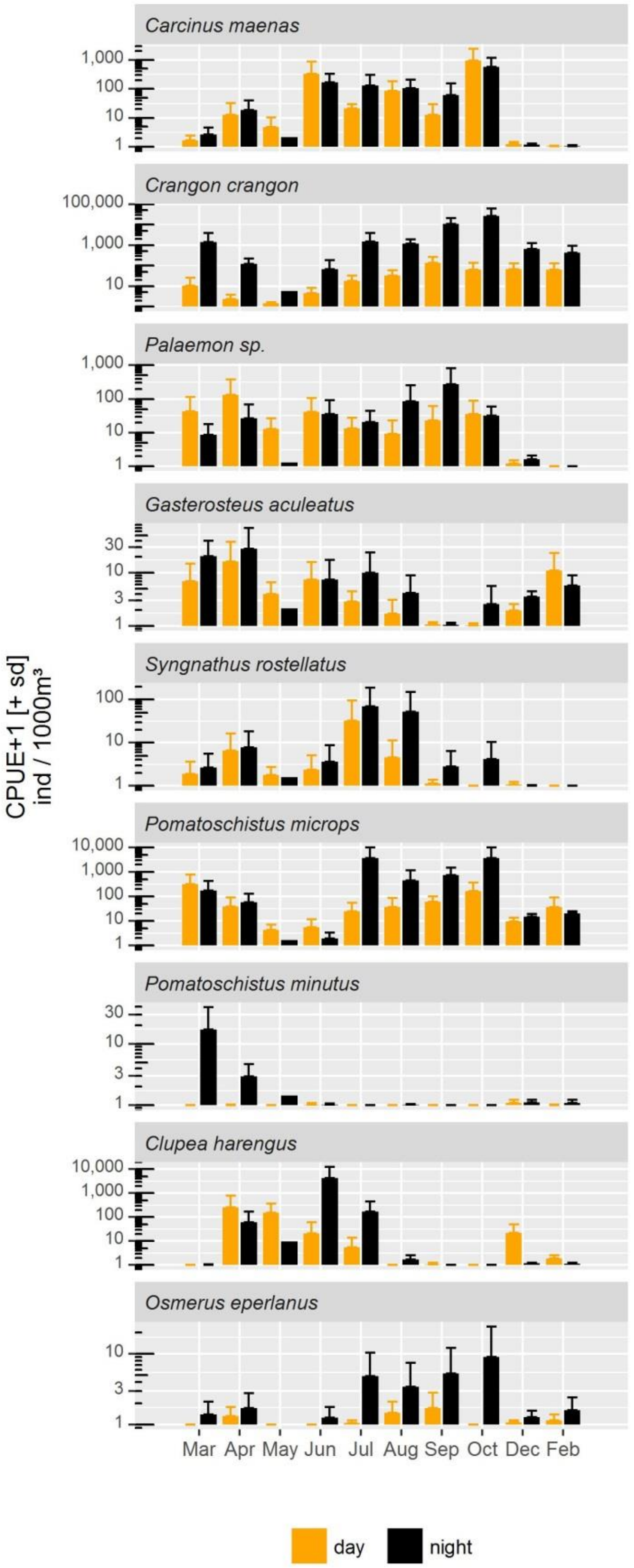


Fig. A.2: Seasonal mean catch per unit effort (CPUE+1) in numbers per 1000 m³ plus standard deviation on a logarithmic scale. Abundance patterns of *C. maenas* can only be interpreted relatively, not absolutely, as this species is attracted by fyke nets.

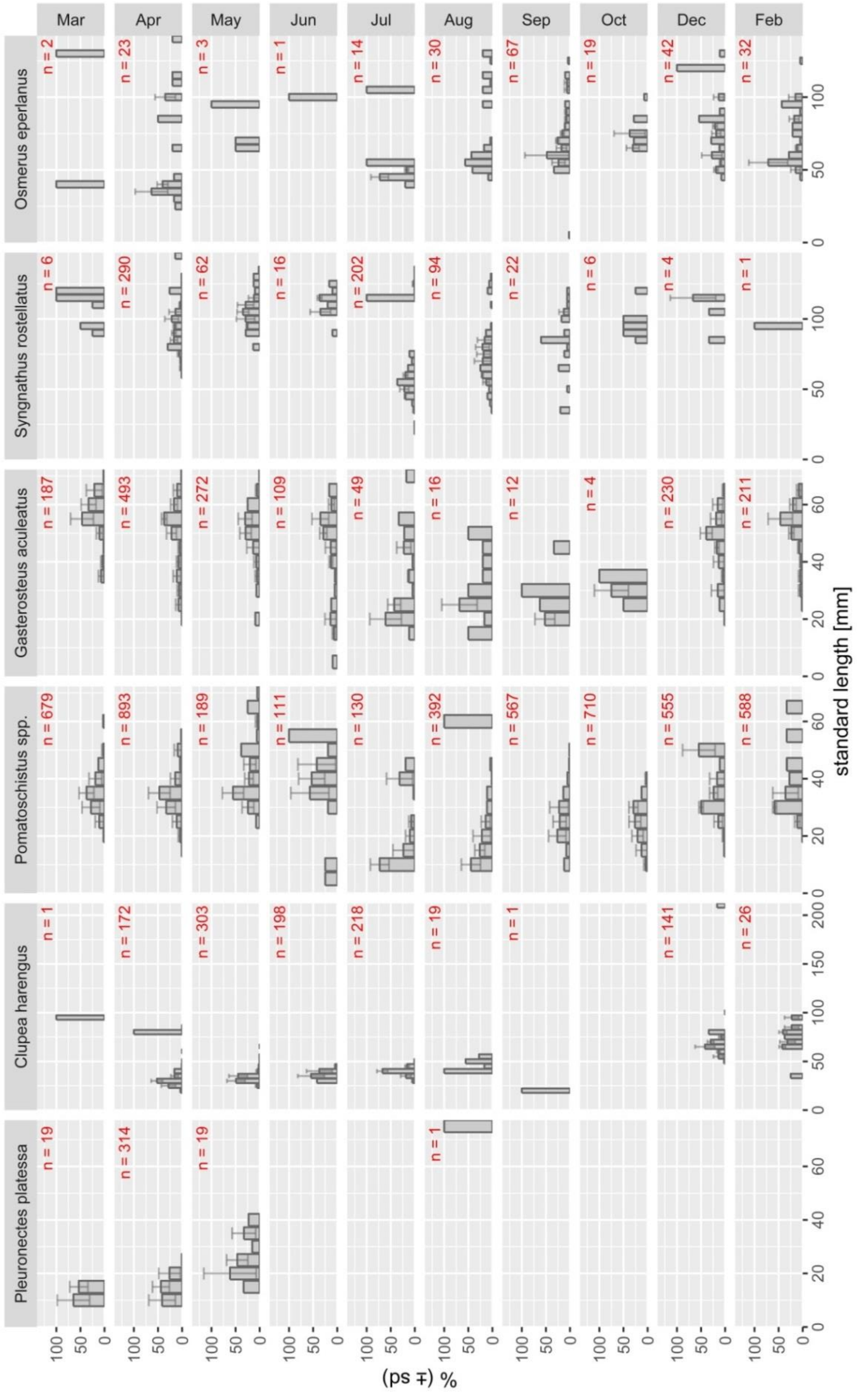


Fig. A.3: Seasonal length frequency distribution of the some abundant fish species the salt-marsh creeks in St. Peter-Ording during the sampling campaign 2015-2016. Percentages are based on CPUE, n = number of measured individuals

Supplement B

Tab. B.1: Seasonal sample sizes and volumes of zooplankton samples. For a map of the sampling locations see also Chapter 2

Sampling location	Geographic coordinates	Number of samples and filtration volume per sampling month											
		Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb
Creek G1	54° 17.300' N 008° 42.222' E	1 x 51 L	1 x 150 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	-	5 x 30 L	-	5 x 30 L
Creek G2	54° 17.242' N 008° 42.228' E	1 x 51 L	1 x 150 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	-	5 x 30 L	-	5 x 30 L
Creek U1	54° 16.667' N 008° 41.560' E	1 x 51 L	1 x 120 L	4 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	-	5 x 30 L	-	5 x 30 L
Creek U2	54° 16.650' N 008° 41.344' E	1 x 51 L	1 x 150 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	-	5 x 30 L	-	5 x 30 L
subtidal *Vollerwiek by feet*	54° 16.863' N 008° 42.610' E	-	1 x 150 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	5 x 30 L	-	5 x 30 L	-	5 x 30 L
subtidal *Vollerwiek by ship*	54°17.051' N 008°43.513' E	-	-	-	-	5 x 0 L	-	-	-	-	-	-	-
subtidal *Westerplate Nord*	54°15.046' N 008°39.511' E	-	-	-	-	5 x 30 L	-	-	-	-	-	-	-

Tab. B.2: The parameters k and b from Eq. 4.3 calculated from the length-weight-relationship using robust regression

species	**sex**	**k**	**b**
herring	-	1.76965E-05	2.812725
three-spined stickleback	F	1.07374E-05	3.019776
	M	1.03885E-05	3.062189
common goby	F	1.41729E-05	2.988147
	M	6.44774E-06	3.223357
sand goby	F	9.38104E-06	3.024550
	M	2.97998E-06	3.327468

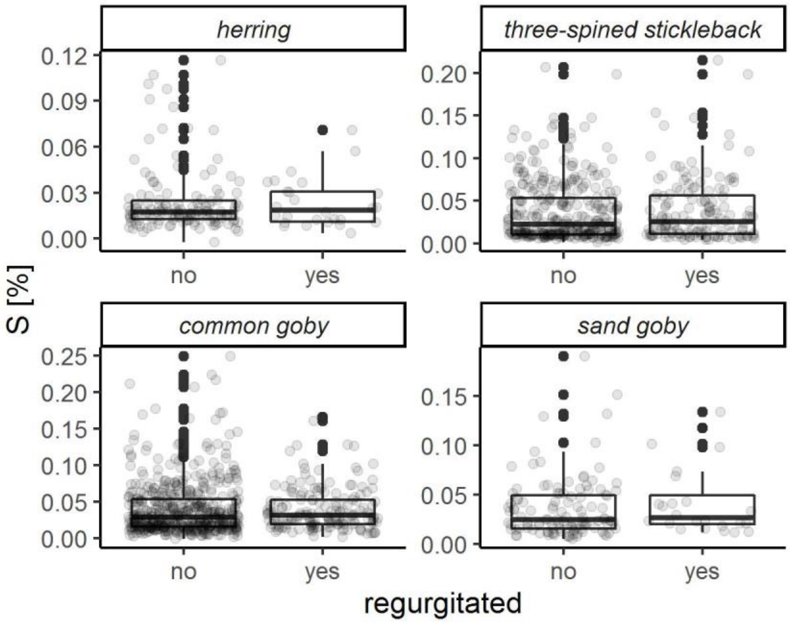


Fig. B.1: Relative stomach content weight in regurgitated and non-regurgitated stomachs per predator

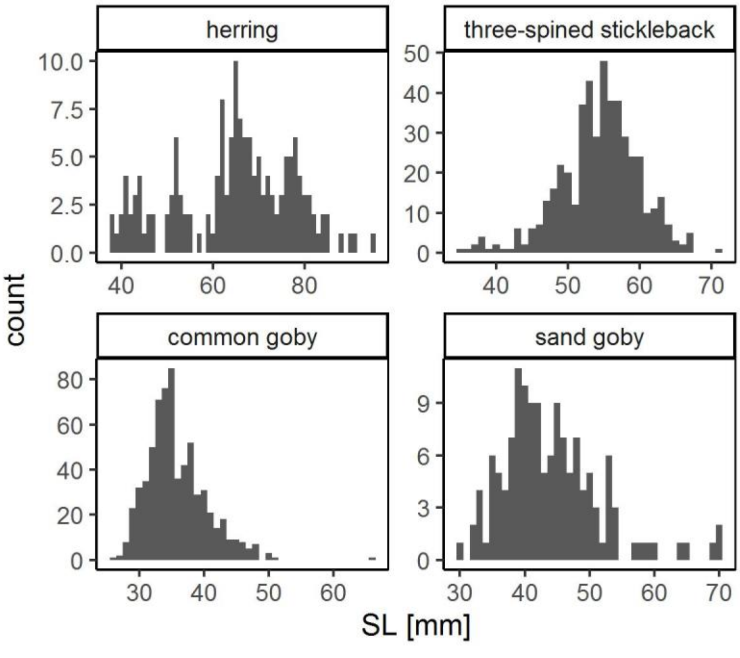


Fig. B.2: Length distribution of analysed fish measured in standard length

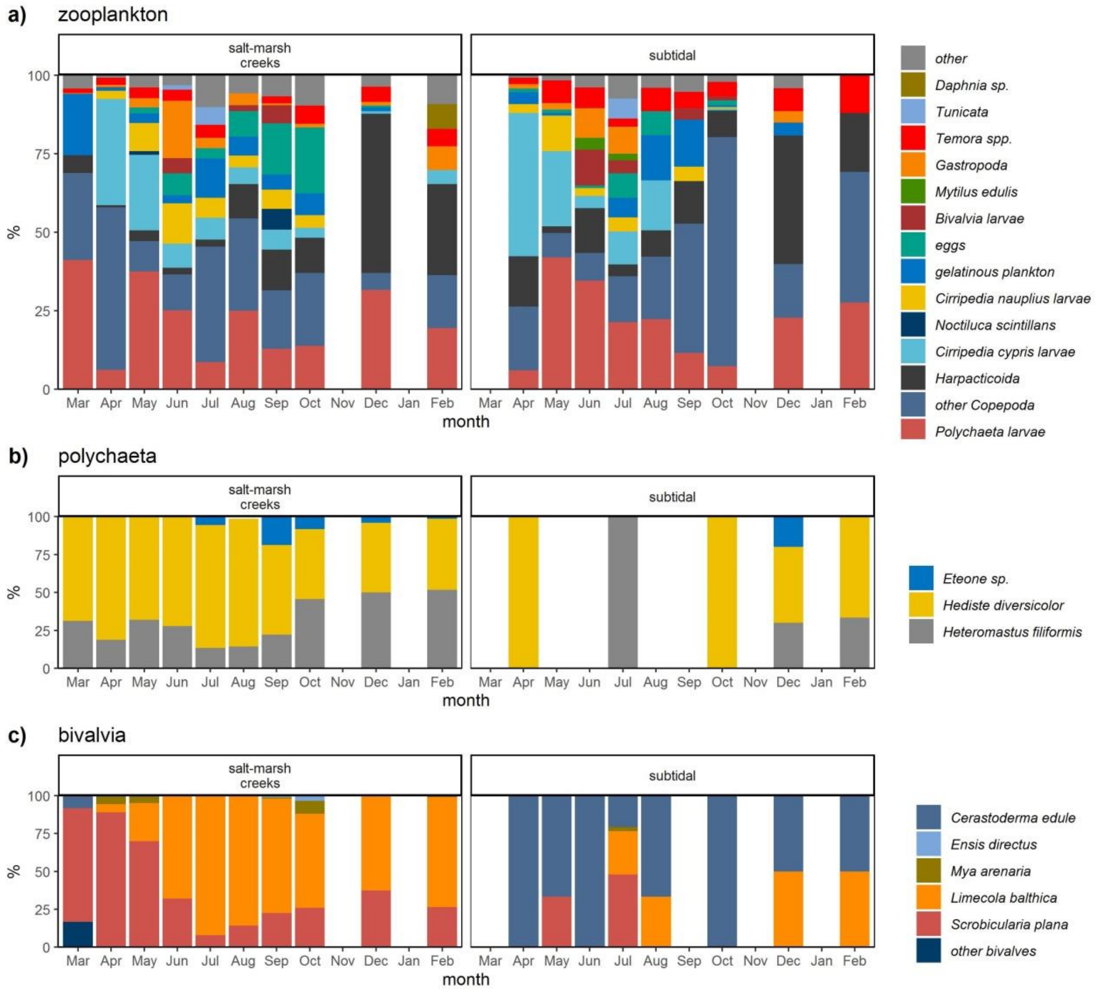


Fig. B.3: Seasonal composition (based on counts) of a) zooplankton, b) polychaetes and c) bivalves in the salt-marsh creeks as well as in the adjacent subtidal (or tidal flat at *Vollerwieker Priel* and *Westerplate Nord*). Sampling started in March 2015 and finished in February 2016. The zooplankton category “other” consists of Acari, Amphipoda, Appendicularia, Brachiolaria larvae, Brachyura larvae, other Annelida, Chaetognatha, Cladocera, Collembola, *Corophium volutator*, Cumacea, Decapoda, fish larvae, Insecta, Isopoda, Mysida, Nematoda/ Nemertini, Ostracoda, *Peringia ulvae*, Plathelmynthes larvae, and Trematoda.

Tab. B.3: Composition of species categories from the zooplankton samples (all samples pooled).

aggregated species category	species type	%
copepoda	*Acartia sp.*	46.6
	calanoida*	0.1
	Calanus sp.	< 0.1
	Candacia sp.	< 0.1
	Centropages sp.	3.0
	nauplius larvae	1.9
	copepodit	0.7
	Eurytemora sp.	0.7
	harpacticoida	36.5
	Oithona sp.	0.1
	oncaeidae	0.5
	Pleuromamma sp.	< 0.1
	Pseudocalanus sp.	3.2
	sapphirinidae	< 0.1
	Temora sp.	6.6
other	*Anurida maritima*	0.7
	Brachiolaria Larvae	0.0
	chaetognatha	0.5
	cladocera	0.0
	Corophium volutator	0.2
	Daphnia sp.	1.0
	eggs	12.0
	fish egg	47.9
	fish larvae	1.0
	idotera	0.7
	isopoda	0.9
	mysidacea	0.7
	natantia	0.5
	Noctiluca scintillans	7.8
	ostracoda	0.1
	plathelminthes larvae	0.3
	sipuncula	0.3
	trematoda	0.3
	unknown	25.0

aggregated species category	species type	%
amphipoda	amphipoda	100.0
decapoda	zoea larvae	61.7
	megalopa larvae	38.3
cumacea	cumacea	100.0
cirripedia	cypris larvae	70.4
	nauplius larvae	29.6
gastropoda	gastropoda*	49.2
	gastropoda larve	0.7
	Littorina littorea (egg capsule)	48.0
	Peringia ulvae	2.1
polychaeta	*Lanice conchilega* larvae	4.3
	polychaeta	2.7
	polychaeta larvae	93.0
Capitella capitata	*Capitella capitata*	100.0
bivalvia	larvae	84.9
	Mytilus edulis	15.1
tunicata	tunicata	100.0
appendicularia	appendicularia	100.0
nematoda/ nemertini	nematoda/ nemertini	100.0
gelantinous plankton	anthozoa polyp	1.0
	cnidaria	8.4
	cnidaria polyp	4.5
	ctenophora	3.6
	ctenophora larvae	0.6
	ctenophora/ cnidaria*	0.2
	hydrozoa	74.5
	hydrozoa polyp	0.6
	hydrozoa actinula larvae	1.7
	scyphozoa ephyra larvae	5.0
terrestrial arthropods	acari	20.1
	aphidina	2.2
	coleoptera	4.5
	insecta	73.2

* unknown/ damaged

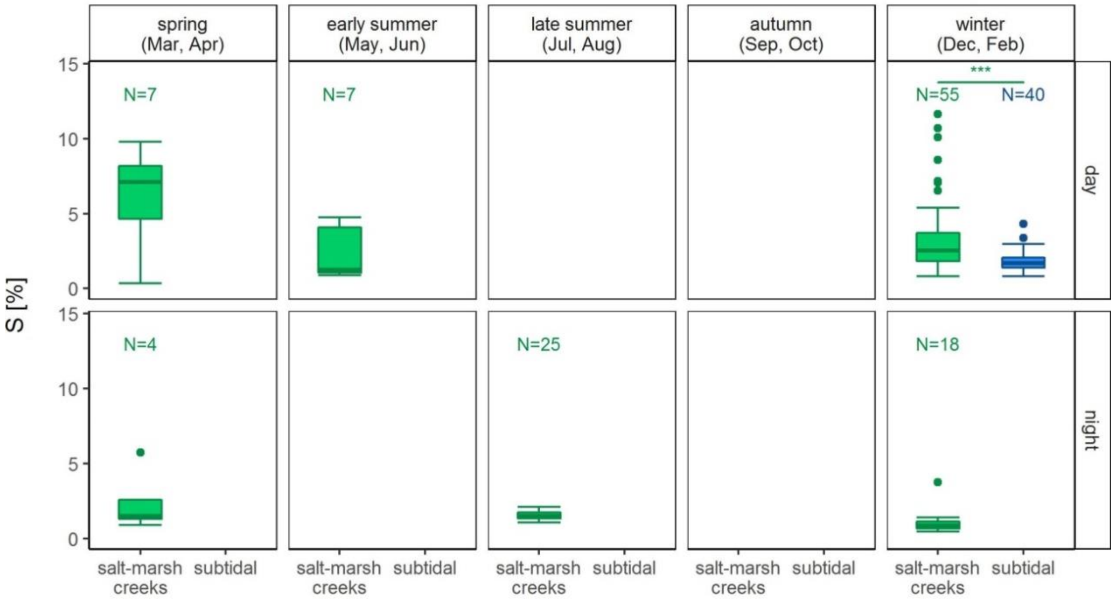
Tab. B.4: Number of hauls and fishes per predator combination for diet overlap analyses

	Number of hauls	Number of fishes	
		species a	species b
a) intra-specific diet overlap			
herring	8	96	
three-spined stickleback	41	410	
common goby	57	484	
sand goby	12	101	
b) inter-specific diet overlap			
three-spined stickleback - common goby	33	292	278
three-spined stickleback - sand goby	9	115	77
three-spined stickleback - herring	7	80	86
common goby - herring	7	65	58
common goby - sand goby	9	82	74

Tab. B.5: Prey categories and their English synonyms for diet overlap analysis

prey category	**english synonyms**
Insecta	insects
Orchestia gammarellus	beach hopper
Arachnida	spiders
Acari	mites
Collembola	springtails
other Arthropoda	other arthropods
Nemertea	ribbon worms
other Annelida	other ringed worms
Polychaeta	bristle worms
Bivalvia	clams
Corophium volutator	mud shrimp
Gastropoda	snails
Peringia ulvae	mud snail
Brachyura	crabs
Pagurus bernhardus	common hermit crab
Palaemon spp.	common prawn
Crangon crangon	brown shrimp
Mysida	mysid shrimps
other Crustacea	other crustaceans
eggs	eggs
Ostracoda	mussel shrimps
Harpacticoida	harpacticoid copepods
Temora spp.	-
other Copepoda	other copepods
Cirripedia	barnacles
Chaetognatha	arrow worms
Hyperia galba	big-eye amphipod
Bathyporeia spp.	-
Actinopteri	fish

a) herring



b) three-spined stickleback

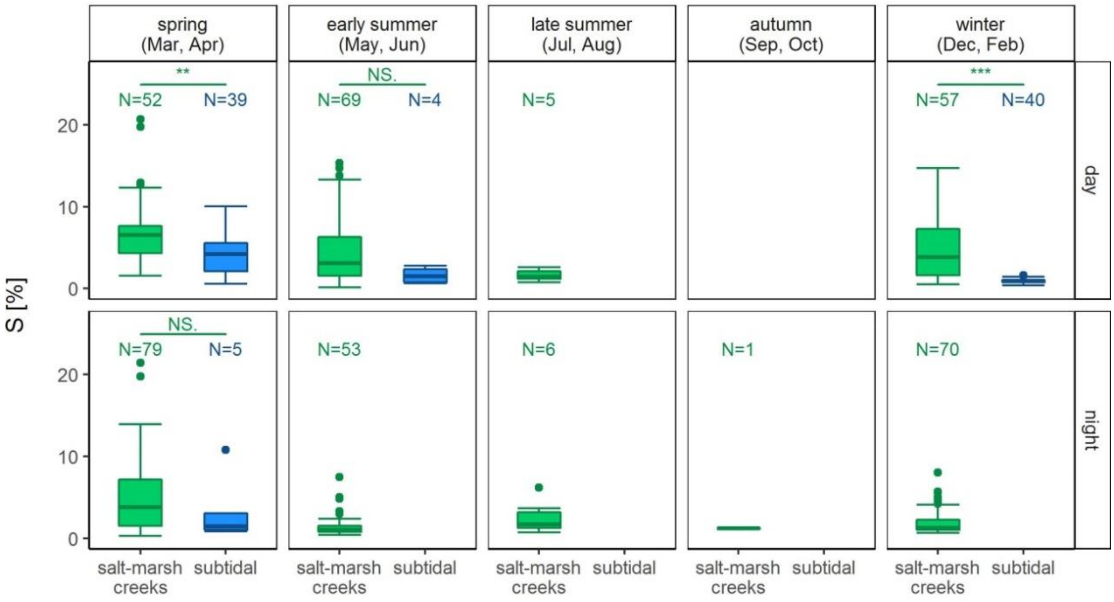
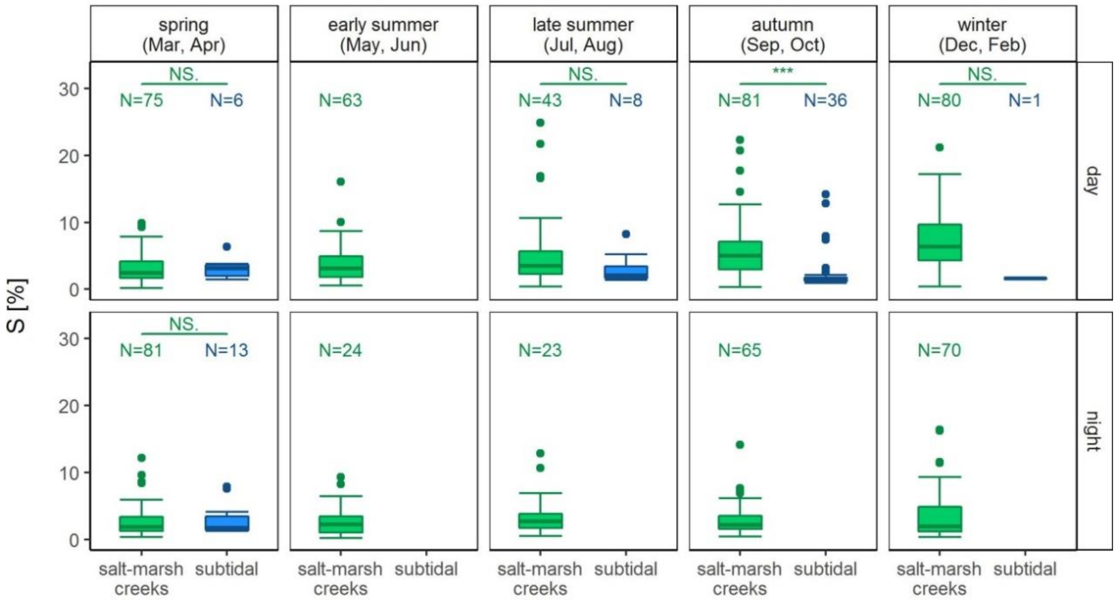


Fig. B.4: Relative stomach content weight *S* of a) herring, b) three-spined stickleback, c) common goby and d) sand goby based on wet weights in the salt-marsh creeks and in the subtidal per season and daytime. Sample sizes are given above each boxplot. Differences between the salt marsh and the subtidal were tested using the Mann-Whitney-Wilcoxon Test. Non-significant differences are mapped with “NS”, p-values of significant differences are classified in three categories: "***" ≤ 0.001, "**" ≤ 0.01, "*" ≤ 0.05

c) common goby



d) sand goby

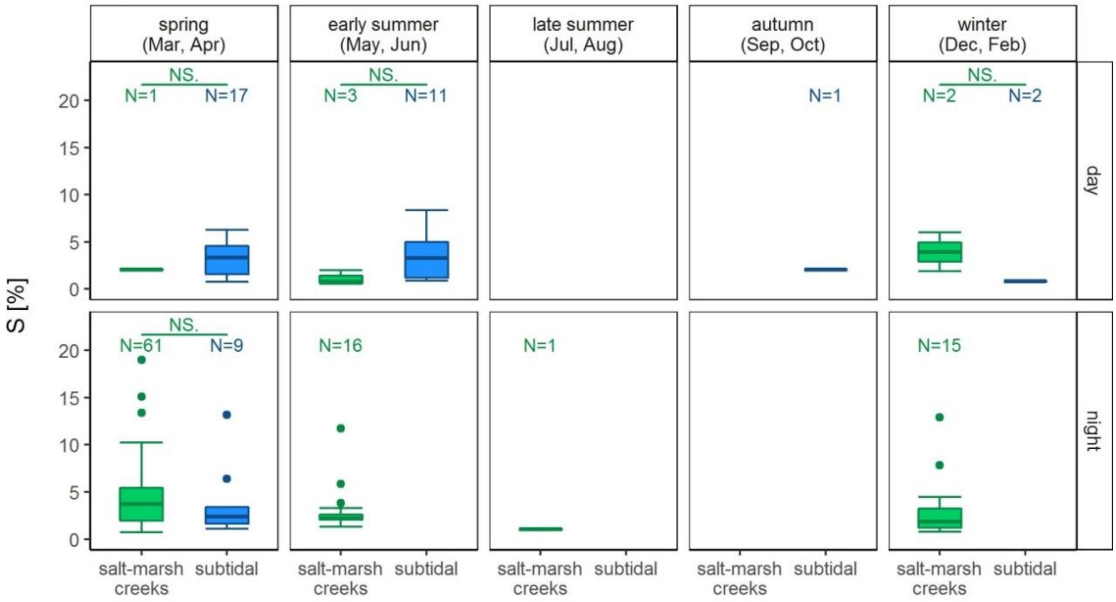
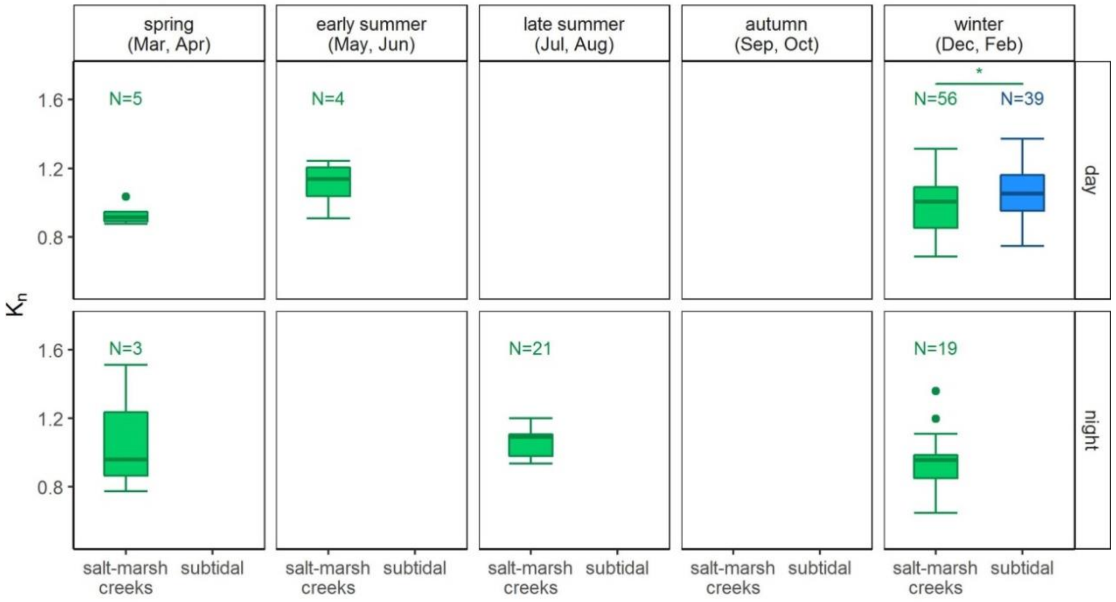


Fig. B.4 (continued): Relative stomach content weight *S* of a) herring, b) three-spined stickleback, c) common goby and d) sand goby based on wet weights in the salt-marsh creeks and in the subtidal per season and daytime. Sample sizes are given above each boxplot. Differences between the salt marsh and the subtidal were tested using the Mann-Whitney-Wilcoxon Test. Non-significant differences are mapped with “NS”, p-values of significant differences are classified in three categories: "***" ≤ 0.001, "**" ≤ 0.01, "*" ≤ 0.05

a) herring



b) three-spined stickleback

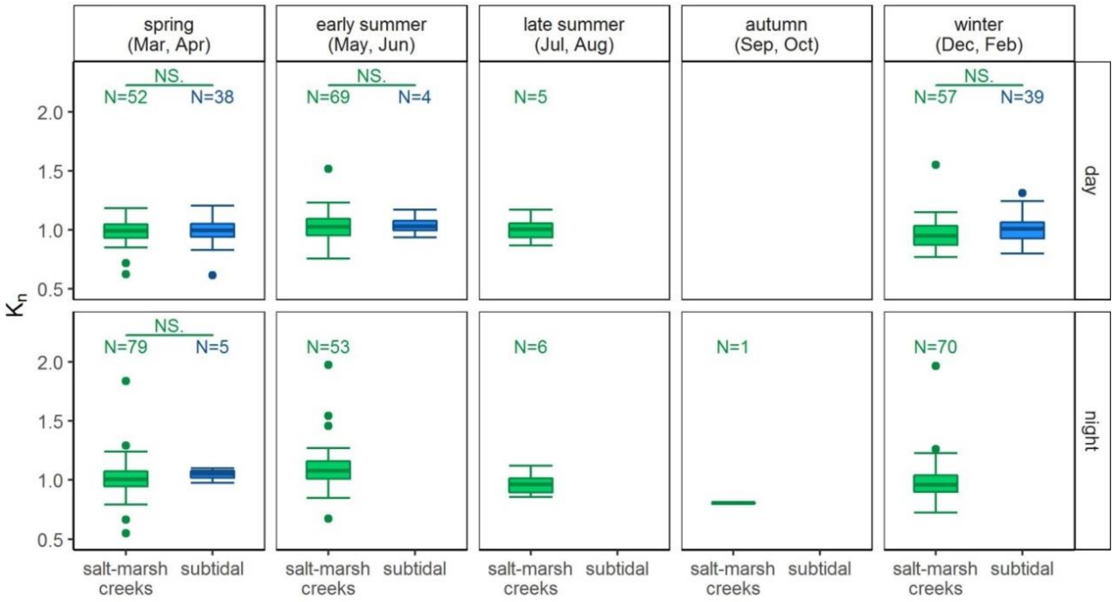
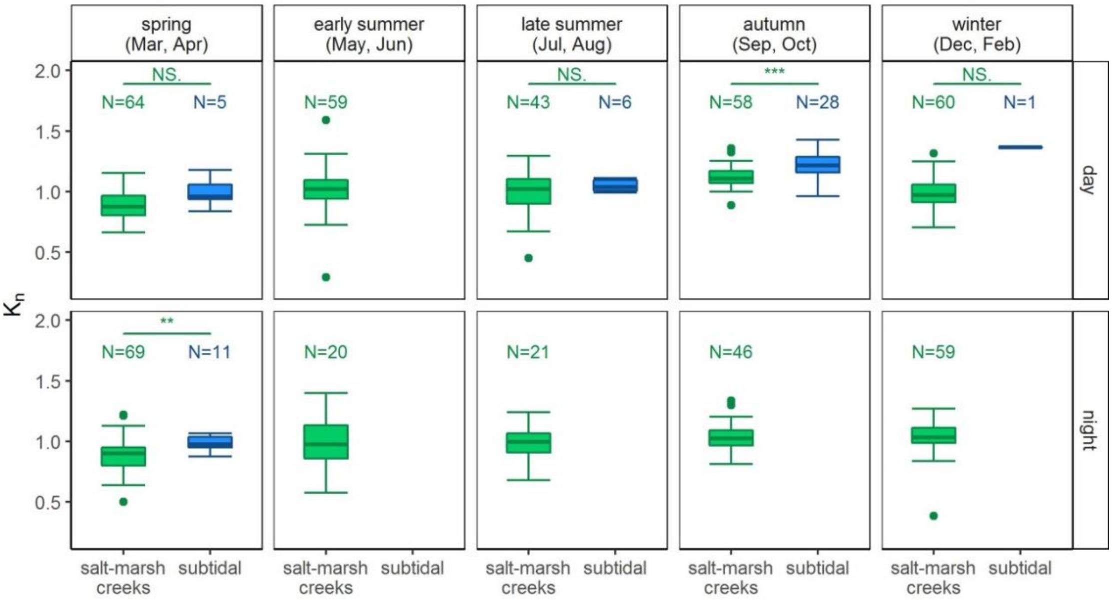


Fig. B.5: Relative condition factor K_n of a) herring, b) three-spined stickleback, c) common goby and d) sand goby based on wet weights in the salt-marsh creeks and in the subtidal per season and daytime. Sample sizes are given above each boxplot. Differences between the salt marsh and the subtidal were tested using the Mann-Whitney-Wilcoxon Test. Non-significant differences are mapped with “NS”, p-values of significant differences are classified in three categories: "***" ≤ 0.001, "**" ≤ 0.01, "*" ≤ 0.05

c) common goby



d) sand goby

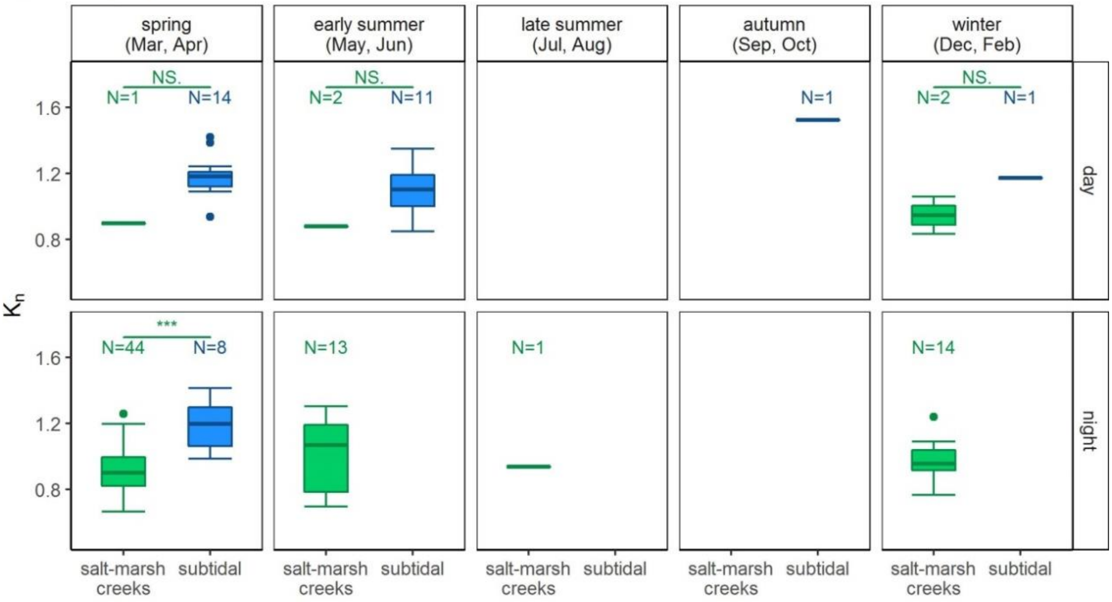
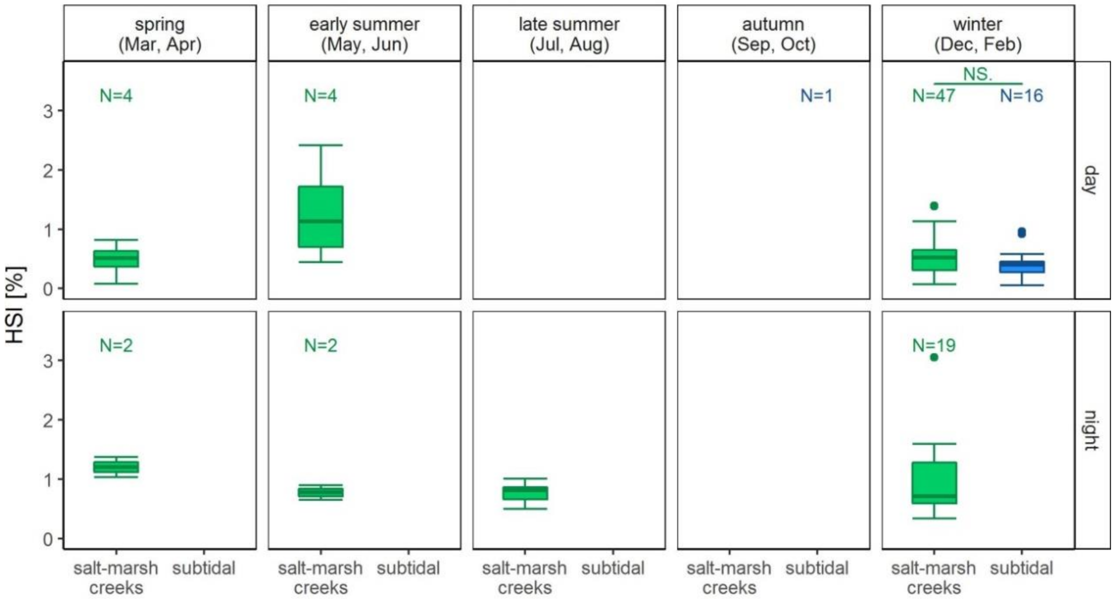


Fig. B.5 (continued): Relative condition factor K_n of a) herring, b) three-spined stickleback, c) common goby and d) sand goby based on wet weights in the salt-marsh creeks and in the subtidal per season and daytime. Sample sizes are given above each boxplot. Differences between the salt marsh and the subtidal were tested using the Mann-Whitney-Wilcoxon Test. Non-significant differences are mapped with "NS", p-values of significant differences are classified in three categories: "***" ≤ 0.001, "**" ≤ 0.01, "*" ≤ 0.05

a) herring



b) three-spined stickleback

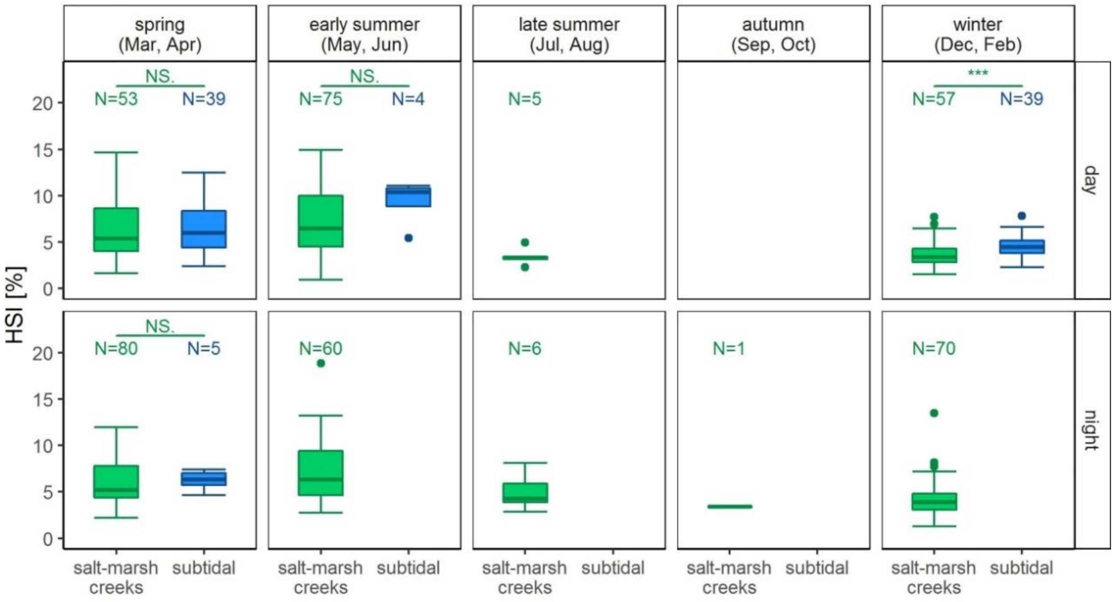
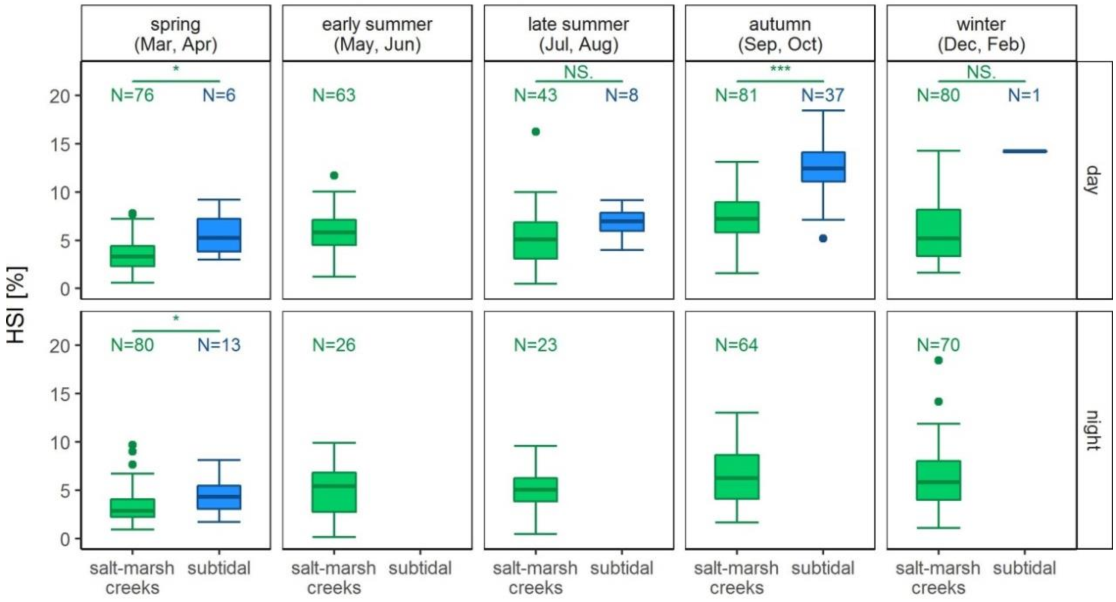


Fig. B.6: Hepatosomatic index *HSI* of a) herring, b) three-spined stickleback, c) common goby and d) sand goby based on wet weights in the salt-marsh creeks and in the subtidal per season and daytime. Sample sizes are given above each boxplot. Differences between the salt marsh and the subtidal were tested using the Mann-Whitney-Wilcoxon Test. Non-significant differences are mapped with “NS”, p-values of significant differences are classified in three categories: "***" ≤ 0.001, "**" ≤ 0.01, "*" ≤ 0.05

c) common goby



d) sand goby

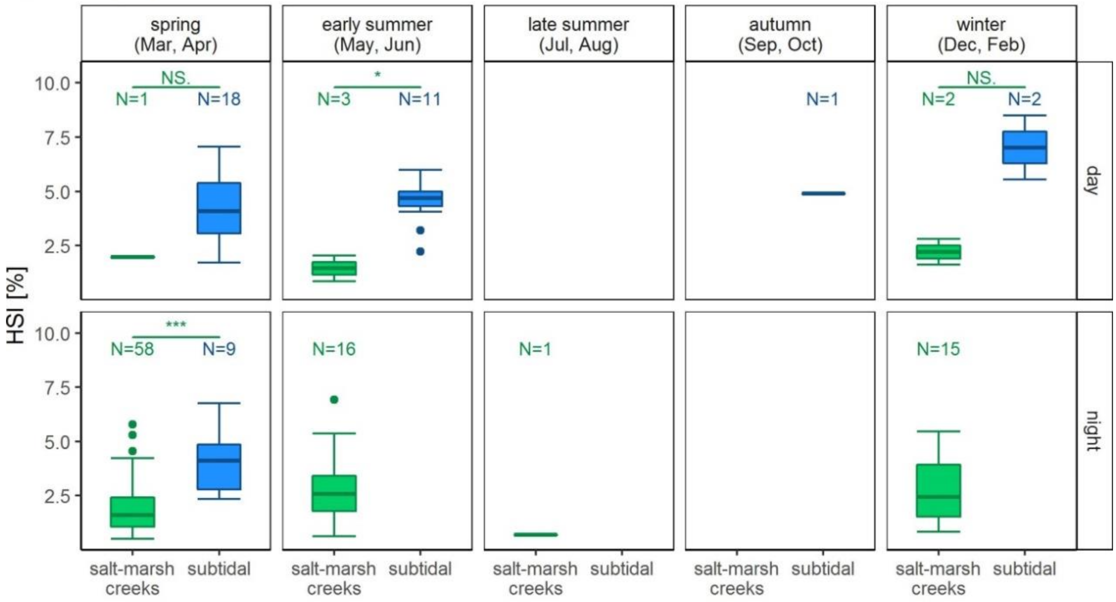


Fig. B.6 (continued): Hepatosomatic index *HSI* of a) herring, b) three-spined stickleback, c) common goby and d) sand goby based on wet weights in the salt-marsh creeks and in the subtidal per season and daytime. Sample sizes are given above each boxplot. Differences between the salt marsh and the subtidal were tested using the Mann-Whitney-Wilcoxon Test. Non-significant differences are mapped with “NS”, p-values of significant differences are classified in three categories: "***" ≤ 0.001, "**" ≤ 0.01, "*" ≤ 0.05

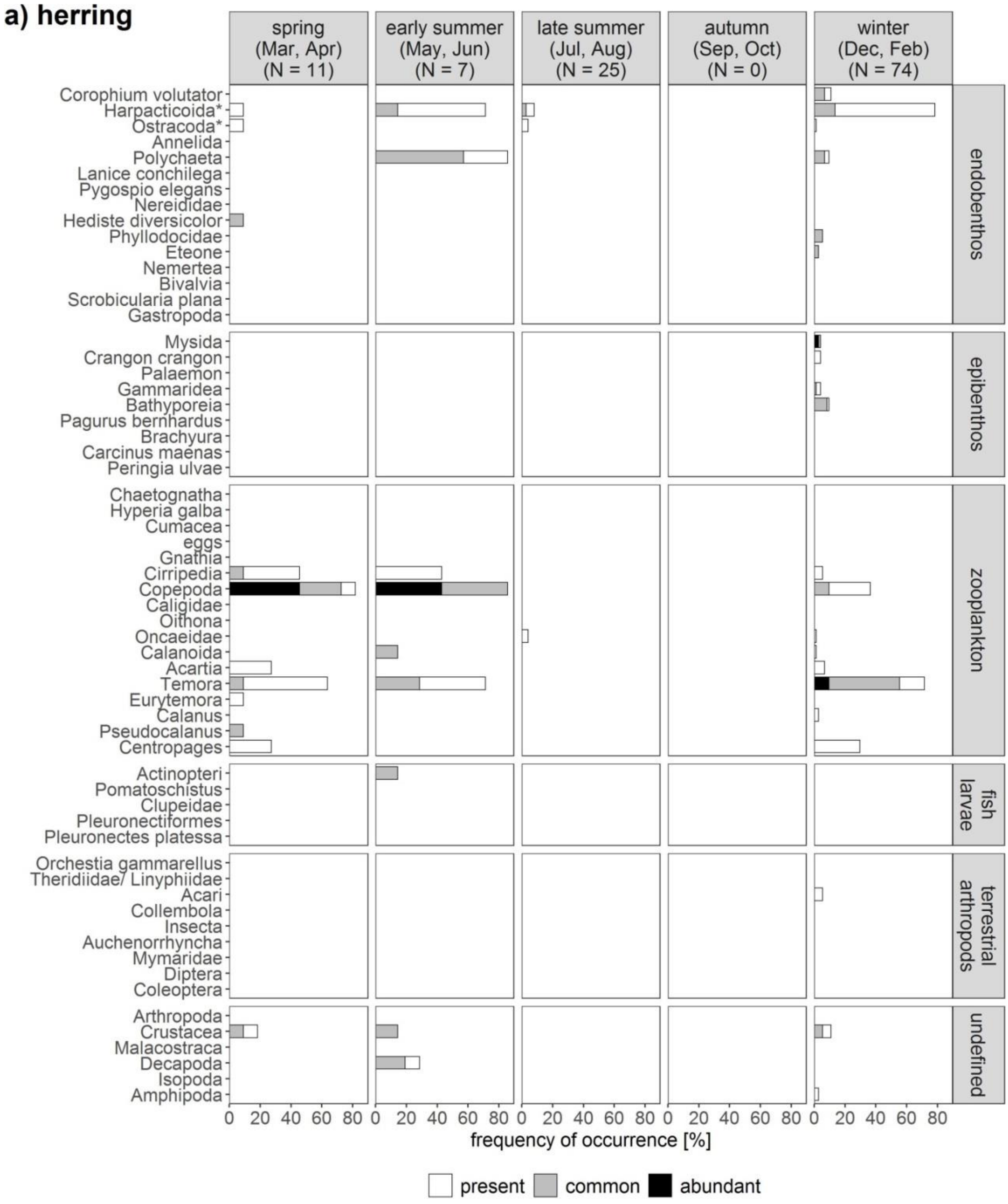


Fig. B.7: Seasonal prey composition in the salt-marsh creeks for a) the herring. N: number of analysed fish, including those with only mucus or undefined material in their stomach. Prey abundance classes (white = present, grey = common, black = abundant) indicate the percentage a certain prey type contributed to the total stomach content. Present: < 10 % of the stomach content; common: ≥ 10 – 50 % of the stomach content; abundant: ≥ 50 % of the stomach content.

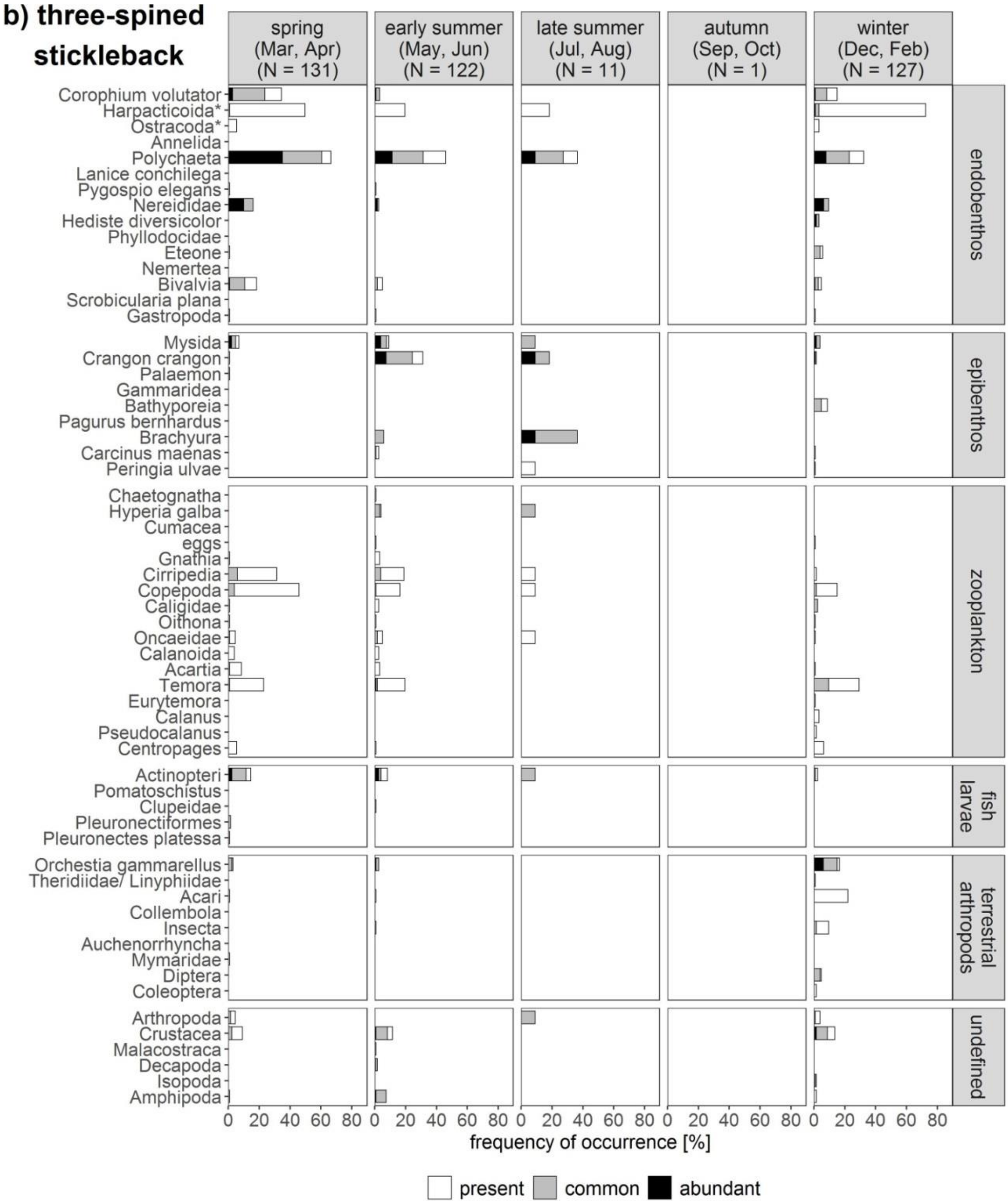


Fig. B.7 (continued): Seasonal prey composition in the salt-marsh creeks for b) the thee-spined stickleback. N: number of analysed fish, including those with only mucus or undefined material in their stomach. Prey abundance classes (white = present, grey = common, black = abundant) indicate the percentage a certain prey type contributed to the total stomach content. Present: < 10 % of the stomach content; common: ≥ 10 – 50 % of the stomach content; abundant: ≥ 50 % of the stomach content.

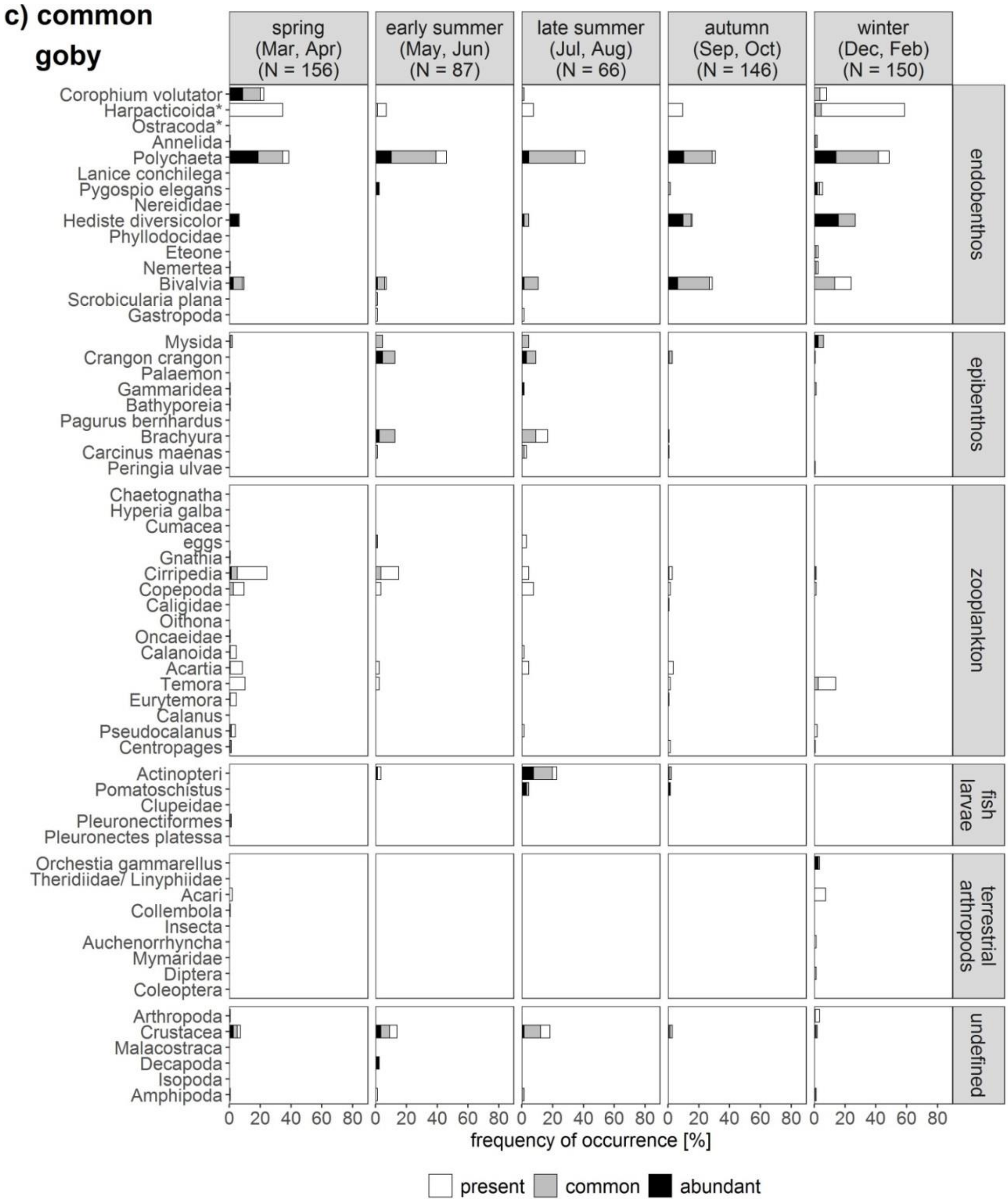


Fig. B.7 (continued): Seasonal prey composition in the salt-marsh creeks for c) the common goby. N: number of analysed fish, including those with only mucus or undefined material in their stomach. Prey abundance classes (white = present, grey = common, black = abundant) indicate the percentage a certain prey type contributed to the total stomach content. Present: < 10 % of the stomach content; common: ≥ 10 – 50 % of the stomach content; abundant: ≥ 50 % of the stomach content.

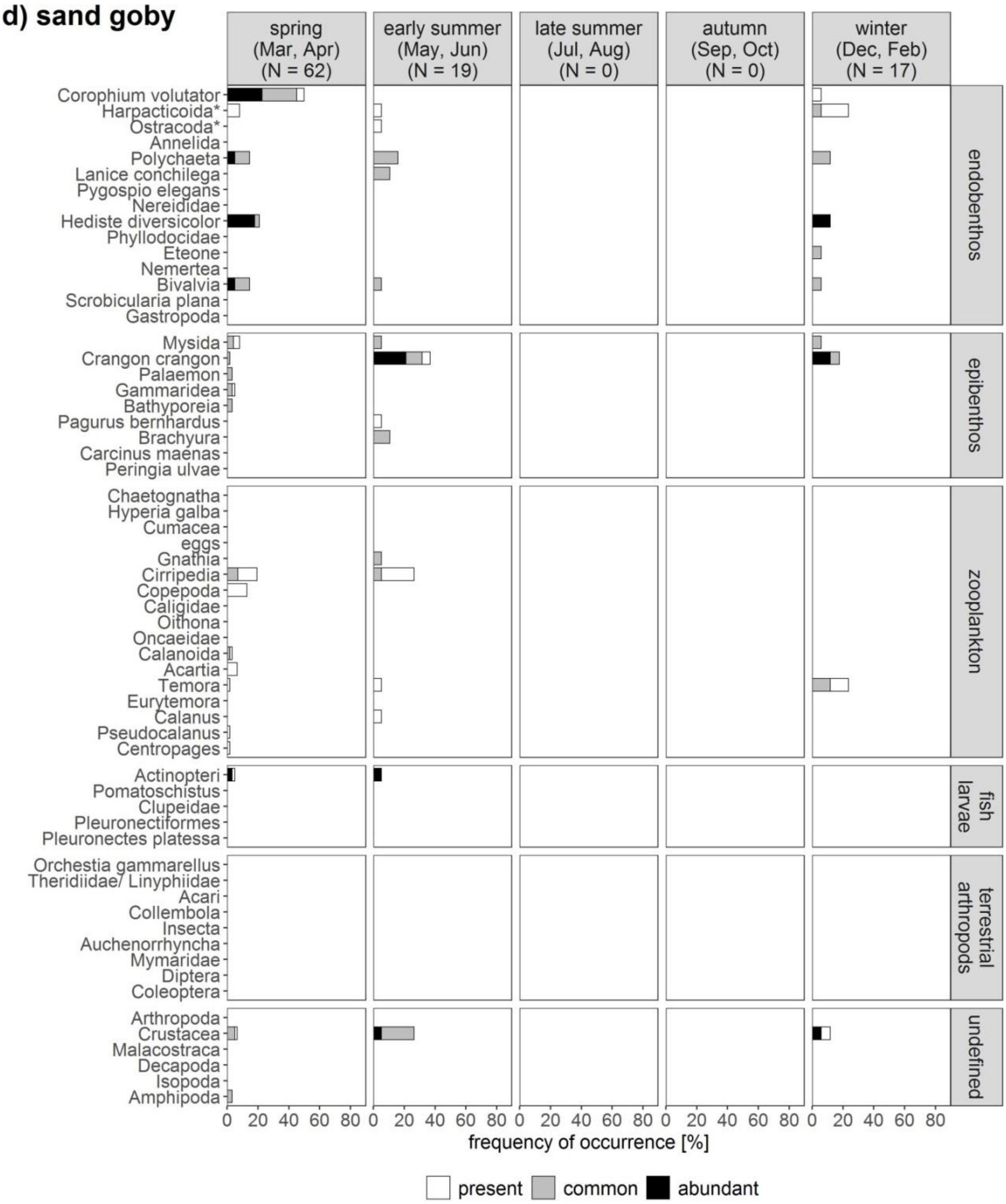


Fig. B.7 (continued): Seasonal prey composition in the salt-marsh creeks for d) the sand goby. N: number of analysed fish, including those with only mucus or undefined material in their stomach. Prey abundance classes (white = present, grey = common, black = abundant) indicate the percentage a certain prey type contributed to the total stomach content. Present: < 10 % of the stomach content; common: ≥ 10 – 50 % of the stomach content; abundant: ≥ 50 % of the stomach content.

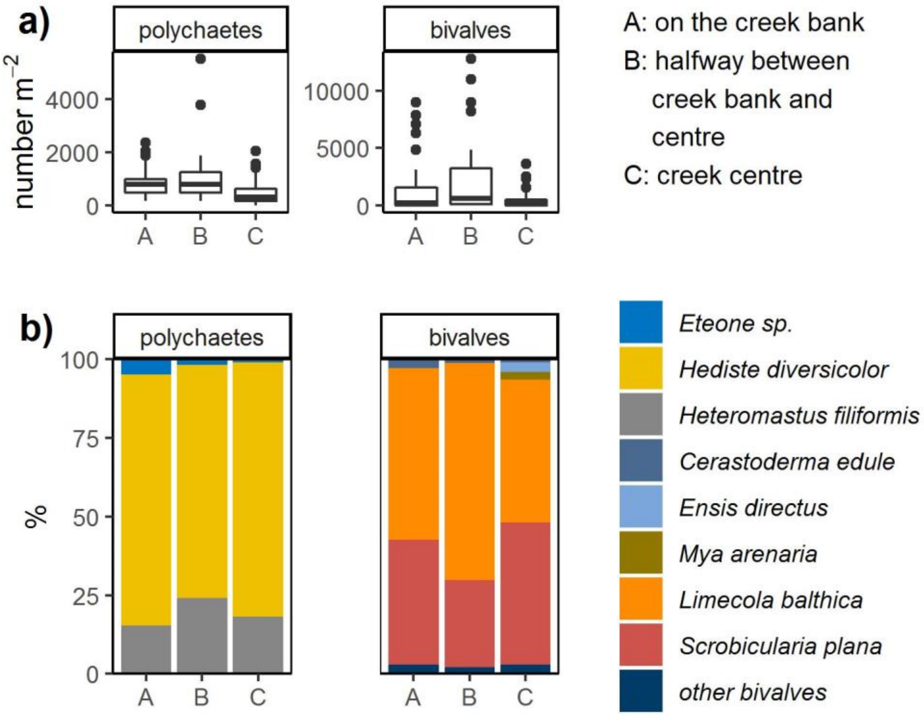


Fig. B.8: Small-scale a) density and b) composition (based on counts) of polychaetes and bivalves with the salt-marsh creek cross-section from the creek bank (A) to the centre of the creek (B).

Supplement C

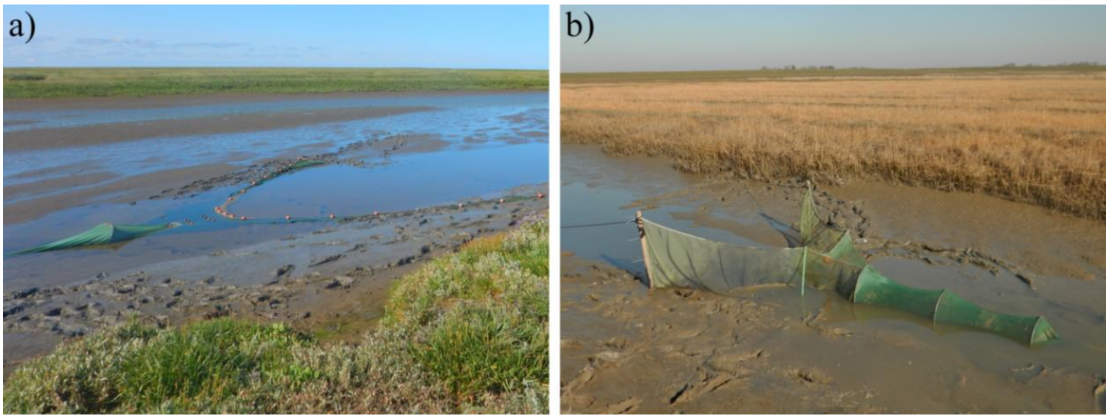


Fig. C.1: a) Fyke net with 1.5 m stowage height in the creek U2, b) fyke net with 1.0 m stowage height in the creek U1

Tab. C.1: Seasonal characteristic values of the analysed fish species in salt-marsh creeks. N: number of analysed specimens

year	month	Standard length (mm)	relative stomach content weight (%)	N		% occurence of terrestrial prey		% terrestrial prey biomass	
		mean (range)	mean (range)	G	U	G	U	G	U
			Gasterosteus aculeatus						
2015	Mar	57 (37-67)	4.93 (0-14.14)	26	29	7.69	20.69	0.21	2.51
	Apr	56 (42-67)	4.78 (0.7-18.69)	35	38	2.86	7.89	0.04	0.85
	May	53 (38-63)	3.05 (0.08-11.43)	22	29	13.64	6.90	5.71	1.52
	Jun	53 (38-67)	2.13 (0.35-7.56)	25	35	4.00	0.00	0.37	0.00
	Jul	50 (48-57)	1.62 (0.59-3.32)	6	1	0.00	0.00	0.00	0.00
	Aug	42 (38-47)	2.24 (1.08-4.76)	1	3	0.00	0.00	0.00	0.00
	Sep	43	1.36	0	1	-	0.00	-	0.00
	Oct	-	-	0	0	-	-	-	-
	Dec	52 (37-66)	1.93 (0.56-7.87)	25	36	40.00	55.56	4.50	34.43
2016	Feb	54 (42-64)	4.51 (0.65-15)	20	37	35.00	56.76	5.01	27.00
			Pomatoschistus microps						
2015	Mar	36 (28-46)	3.8 (0.34-12.6)	38	26	7.89	3.85	0.17	0.57
	Apr	36 (29-45)	2.97 (0.78-9.53)	33	34	0.00	2.94	0.00	0.14
	May	37 (29-51)	2.66 (0.18-7.54)	18	29	0.00	0.00	0.00	0.00
	Jun	37 (30-48)	3.73 (0.47-12.29)	7	21	0.00	0.00	0.00	0.00
	Jul	40 (33-46)	4.86 (1.1-18.36)	1	24	0.00	0.00	0.00	0.00
	Aug	38 (30-48)	4.92 (1.37-21.08)	3	21	0.00	0.00	0.00	0.00
	Sep	35 (29-50)	6.19 (1.28-20.43)	23	18	0.00	0.00	0.00	0.00
	Oct	33 (27-42)	3.81 (1.03-13.25)	31	31	0.00	0.00	0.00	0.00
	Dec	35 (28-45)	5.75 (0.46-18.53)	37	37	16.22	27.03	0.81	11.37
2016	Feb	33 (27-39)	5.68 (0.37-13.09)	26	31	3.85	16.13	0.00	5.87
			Pomatoschistus minutus						
2015	Mar	41 (32-50)	4.14 (0.83-10.15)	19	17	0.00	0.00	0.00	0.00
	Apr	39 (33-54)	5.93 (1.63-20.69)	4	18	0.00	0.00	0.00	0.00
	May	49 (39-70)	3.19 (1.74-9.38)	2	9	0.00	0.00	0.00	0.00
	Jun	50 (40-58)	1.47 (0.77-2.19)	0	3	-	0.00	-	0.00
	Jul	-	-	0	0	-	-	-	-
	Aug	53	1.1	0	1	-	0.00	-	0.00
	Sep	-	-	0	0	-	-	-	-
	Oct	-	-	0	0	-	-	-	-
	Dec	44 (32-53)	3.34 (1-13.42)	3	8	0.00	0.00	0.00	0.00
2016	Feb	55 (46-64)	4.29 (2.58-6.69)	0	3	-	0.00	-	0.00
			Clupea harengus						
2015	Mar	91	1.57	0	1	-	0.00	-	0.00
	Apr	55 (44-84)	4.22 (1.13-8.02)	5	1	0.00	0.00	0.00	0.00
	May	45 (38-54)	0.58 (0.00-4.80)	17	10	5.88	40.00	< 0.00	< 0.00
	Jun	40 (37-43)	0.62 (0.00-4.67)	0	10	-	0.00	-	0.00
	Jul	40 (35-46)	0.05 (0.00-1.48)	5	22	0.00	4.55	0.00	< 0.00
	Aug	39	1.87	1	0	0.00	-	0.00	-
	Sep	-	-	0	0	-	-	-	-
	Oct	-	-	0	0	-	-	-	-
	Dec	65 (53-81)	3.45 (1.02-11.04)	20	24	0.00	12.50	0.00	< 0.00
2016	Feb	72 (62-90)	2.56 (0.78-12.49)	2	16	0.00	6.25	0.00	< 0.00

Author contributions

Chapter 2

Julia Friese designed the study, organized and carried out the field work, performed all data analyses, and wrote the initial manuscript. Axel Temming was involved in the study design, supported data analyses, and reviewed the manuscript. Andreas Dänhardt designed the study, organized and carried out field work, supported data analyses, and edited the manuscript.

Chapter 3

Julia Friese designed the study, organized and carried out the field work, performed all data analyses, and wrote the initial manuscript. Axel Temming was involved in the study design, supported data analyses, and reviewed the manuscript. Andreas Dänhardt designed the study, carried out field work, supported data analyses, and edited the manuscript.

Chapter 4

Julia Friese designed the study, organized and carried out the field and laboratory work, performed all data analyses, and wrote the initial manuscript. Axel Temming was involved in the study design, supported data analyses, and reviewed the manuscript. Andreas Dänhardt designed the study, carried out field work, supported data analyses, and edited the manuscript.

Chapter 5

Julia Friese designed the study, organized and carried out the field and laboratory work, performed all data analyses, and wrote the initial manuscript. Axel Temming was involved in the study design, supported data analyses, and reviewed the manuscript. Andreas Dänhardt designed the study, carried out field work, supported data analyses, and edited the manuscript.

Hereby, I confirm the accuracy of the statements above,

Hamburg, 29.09.2020

Julia Friese

Prof. Dr. Axel Temming
(on behalf of the supervisors)

Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, 29.09.2020

Julia Friese

Certification of Written English Quality

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24.09.2020

To Whom It May Concern,

I have briefly reviewed the thesis "*An Empirical Evaluation Of The Quality Of Salt Marshes For Nekton in The Wadden Sea Habitat Mosaic*" by PhD candidate Julia Friese. English is my second native language, and I can attest that the writing (grammar/syntax/punctuation) is fully satisfactory. Some minor "Germanisms" notwithstanding, the English writing within this thesis is of sufficient quality to move forward with the submission and review process.

Yours faithfully

Elisa Schaum

In the Wadden Sea, a shallow coastline and a large tidal amplitude result in an overlap of land and sea, creating a unique pulsing ecosystem. The landward edge of this intertidal area is framed by salt marshes, that evolve, where low flow velocities allow for sediment accretion and settlement of halophytic plants. Salt marshes are valued worldwide as high-quality habitats for fish and crustaceans, because they provide shelter from predators and profitable feeding conditions. In the Wadden Sea, however, land reclamation, coastal protection measures, and agriculture have changed shape and function of salt marshes over centuries. Naturally meandering salt-marsh creeks connecting i. a. intertidal pools were largely replaced with short and straight creeks to ensure optimal dike drainage. Whether these mostly artificially created salt marshes can still support marine fauna and which species enter the confined salt-marsh creeks, hazarding beaching and unfavourable temperatures, was mostly unknown and is now addressed by this thesis. For the Wadden Sea area, it is the first comprehensive study showing which nekton species are characteristic for marine Wadden Sea salt marshes, evaluating habitat quality based on abiotic conditions, predation pressure, food availability and the body condition of fish, and examining the human impact on this habitat type, particularly sheep grazing.